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MADAGASCAR CONSERVATION & DEVELOPMENT

INVESTING FOR A SUSTAINABLE NATURAL ENVIRONMENT FOR FUTURE GENERATIONS OF HUMANS, ANIMALS AND PLANTS OF MADAGASCAR

IN THIS ISSUE

Research for PA management

Wildlife hunting and health

Opuntia seeds for development

TABLE OF CONTENTS

EDITORIAL

ARTICLES

SHORT NOTE

ESSAY

MCD SPECIAL SECTION: WHALES

EDITORIAL

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Fair and equitable conservation: do we really want it, and if so, do we know how to achieve it?

The Convention on Biological Diversity (which will celebrate its 25th anniversary of ratification when this issue is published) requires conservation to be “fair and equitable” (CBD 2000). This proposition seems almost universally accepted, yet we see a gap between rhetoric and reality. In our experience, the notion of equity is still contested in Malagasy conservation, with certain questions recurring frequently. Here we present our own answers to those questions.

WHAT SHOULD ‘FAIR AND EQUITABLE’ MEAN?

We believe that for conservation to be fair and equitable, local people (who in Madagascar are almost exclusively among the world’s very poorest) should bear no net negative impacts from conservation. It follows that they must be compensated for any residual costs of protected areas and other interventions, including opportunity costs. Ideally, this should be achieved by capturing global benefits and transferring them to local people. Conservation should not exacerbate poverty.

DOES EQUITY IMPLY COMPENSATION?

Fifteen years after Balmford & Whitten (2003) argued that the global benefits of conservation generally come at local costs, Bedelian and Woodhouse (2018) identified the assertion that conservation is necessarily a win-win (because local people depend on ecosystem services) as their top “myth” in protected area management. In our experience, this myth remains prevalent in conservation discourse in Madagascar, despite numerous studies estimating net local costs of conservation (e.g., Shyamsundar and Kramer 1996, 1997, Kremen et al. 2000, Poudyal et al. 2018, see also Scales 2014, Neudert et al. 2017, though note that Rasolofoson et al. (2017) found no impacts, positive or negative, of community forest management). This evidence cannot be dismissed by pointing to hydrological or climatic benefits (which are frequently overstated: Bruijnzeel 2004, also Zwartendijk et al. 2017) or asserting that benefits from swidden agriculture are short-lived (they are not: Rakotonarivo et al. 2017, Poudyal et al. 2018). Nor can we assume that conservation is preventing a tragedy of the commons that would have impoverished local people, since it is difficult to disentangle traditional management from more than a century of state conservation action (and state-endorsed deforestation). Traditional tenure arrangements have evolved in response to state intervention (Muttenzer 2006), and any tragedy of the commons could have resulted from state conservation crowding out traditional norms (Rabesahala Horning 2003). In sum, while many knowledge gaps remain in Malagasy conservation, we need to shift to a default expectation that local people will bear costs of conservation that are significant in local terms, over long timescales, unless proven otherwise.

IS COMPENSATION LEGITIMATE?

Even when the prevalence of local costs is accepted, some question the legitimacy of compensation, noting that opportunity costs often result from the cessation of activities (e.g., swidden agriculture of primary forests) that are already illegal. Although internally consistent, it is inconsistent with the proposition that local people should not bear costs of conservation. The laws that prohibit deforestation are conservation laws, which have been reinforced and re-legitimised through the actions of the international conservation community (Kull 2004, Corson 2016, 2017). In particular, protected areas cannot claim additionality of avoided deforestation (e.g., for carbon credits or biodiversity offsets) while disclaiming the negative social impacts that result (Bidaud et al. 2018).

IS COMPENSATION AFFORDABLE?

Some who accept the legitimacy of compensation doubt its affordability. We think the evidence is strong that conserving Madagascar’s rich ecosystems has global and national benefits that vastly outweigh (in monetary terms) its local costs (e.g., Kremen et al. 2000, Hockley 2008, Poudyal et al. 2018). If we did not believe this was the case, we could not support conservation in Madagascar (could anyone justify a policy that was both inequitable and inefficient?). Capturing these global benefits is challenging, but this should not provide an excuse for not compensating local people: conservation should not facilitate ‘free-riding’ by the already wealthy. Conditionality is an increasingly popular concept in conservation discourse: that any payments for ecosystem services must be conditional on their provision. We simply argue for symmetry: provision of ecosystem services by the poorest should surely be conditional on their compensation.

DO WE KNOW HOW TO ACHIEVE FAIR AND EQUITABLE CONSERVATION?

If we agree that compensation for local costs is necessary, legitimate and affordable, do we know how to achieve it? As a result of discussing this question with government officials, conservation organisations and people who live around protected areas we have identified a number of challenges. Each of these is the focus of considerable efforts in Madagascar and elsewhere, but all remain substantially unresolved in our opinion.

ESTIMATING COSTS. As noted above, we have sufficient information from several Malagasy protected areas to conclude that local costs are likely to be significant and widespread. Nevertheless, these estimates are conceptually challenging, and contingent on many (often implicit) factors (Hockley 2008). The best available methods appear to perform quite well (e.g., Rakotonarivo et al. 2017), but given the timescales involved they are

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difficult to verify and robust tests remain the exception (Rakotonarivo et al. 2016). The distribution of costs over time and within households (across genders) remains an area deserving of more attention, as does qualitative evidence. Finally, all available methods can under- or overestimate costs when used to inform compensation for illegal or sensitive activities, if respondents understate sensitive behaviours (for fear of sanctions) or overstate (to inflate compensation).

COMPENSATION MECHANISMS. Estimates of opportunity costs are necessary but not sufficient to ensure adequate compensation. We need to know how much needs to be spent, for how long, and on what, to compensate for given costs, while allowing for transaction costs (Poudyal et al. 2016, 2018, Brimont et al. 2017, MacKinnon et al. 2017). Yet cost-effective mechanisms to reliably raise rural residents' wellbeing remain elusive. We suspect that most compensatory interventions are designed to fit within available budgets, not achieve compensation targets. At best, this is not discouraged by donors, and conservation NGOs may feel pressured to understate the true costs of achieving effective and equitable conservation. Donors who wish to support (and claim credit for) conservation in Madagascar need to demand evidence-based compensation plans, and recognise that donor commitments measured in years rather than decades are not commitments.

TARGETING COMPENSATION. The question of who should be targeted for compensation is thorny. Approaches that seek to avoid compensating individuals who have not borne costs are likely to have high implementation costs and be vulnerable to elite capture (Poudyal et al. 2016). Broader-scale compensation that seeks instead to minimise uncompensated individuals (while potentially over-compensating some) may be more efficient and equitable. Even then, if costs (and therefore compensations) will occur over multiple generations, how should newly formed households be treated (along with immigration and emigration)?

EVALUATION AND OVERSIGHT. How do we know if what we are doing is working? Randomised Controlled Trials cannot be used to assess real compensatory interventions (where no eligible households should be excluded from compensation). Yet without them, it is difficult to be sure that compensation is succeeding. It might be useful to adopt pragmatic rules that approximate compensation, e.g., that incomes must rise, and must rise at least as fast as surrounding populations (though income growth in comparator communities may be negative). However, we should still invest in evaluations of compensation interventions that are as rigorous and independent as possible (e.g., Andrianandrasana 2016, Poudyal et al. 2018). Relatedly, how should fair and equitable compensation be monitored? At present, oversight tends to be top-down, and empirically weak. Mechanisms by which local communities can raise grievances are frequently absent or at best ad hoc, often mediated by conservation organisations, who therefore play judge and jury. The rights of local communities are poorly defined and understood. Current legal and administrative standards may not ensure adequate compensation (or seek to), and state enforcement capacity remains inadequate. Civil society in Madagascar is as yet inadequately developed to defend the interests of often remote rural communities.

IS IT TIME FOR A RADICAL RETHINK?

Two of us have argued elsewhere (Rakotonarivo and Hockley 2017) that one approach, which could alleviate some of the above problems, is to radically rethink tenure and consent in Madagascar's threatened habitats. Secure private (but not necessarily individual) tenure would be highly valued by communities (Rakotonarivo et al. 2018). Combined with voluntary conservation easements it would have several attractive characteristics. Free Prior Informed Consent is impossible without freedom of action (are communities free to refuse conservation?), and individuals, choosing freely, are probably the best judge of the worth of compensatory interventions. Committing to symmetrical conditionality might provide useful checks and balances on conservation and build local communities with a real stake in protecting natural capital against outsiders. However, such a radical approach is not without its own challenges. To name just a few: how to decide who owns forests? How would communities consent to, or reject, conservation collectively? Critically, the legal framework for this approach is absent in Madagascar (Jones et al. 2018) though this does not stop conservation organisations from acting, and pledging to act, as if it existed. Without secure local tenure of ecosystems, consent and compensation become much harder to ensure. It is therefore even more important to establish robust, independent oversight of the social impacts of conservation. Donors should demand (and fund) this oversight, and refuse to fund conservation activities that do not budget realistically for compensation. Without these changes, we are not optimistic about achieving fair and equitable conservation in Madagascar.

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ARTICLE

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Taboo adherence and presence of Perrier's sifaka (*Propithecus perrieri*) in Andrafiamena forest

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ABSTRACT

Habitat loss and poaching are among the most serious threats to the fragile and unique biodiversity of Madagascar. In the past, traditional taboos (*fady*), commonly associated with folk stories, have had a buffering effect on several lemur species. Here, we examine the status of hunting taboos with reference to the conservation of the critically endangered Perrier's sifaka (*Propithecus perrieri*). We also provide an update on *P. perrieri*'s presence in the protected area of Andrafiamena in the face of ongoing habitat fragmentation and poaching. The Andrafiamena forest represents one of the key refuges for this species, which has a very limited and fragmented range in northern Madagascar. We report the results of a 2016 presence/absence survey in Andrafiamena and from interviews on Perrier's sifaka taboo adherence, conducted in 2012 across the whole species range. Our results confirm the presence of Perrier's sifakas in Andrafiamena and that in 2012, across the species' range, the hunting taboo was observed by most (>95%) interviewees who answered (N = 23). Forest clearing and a decrease of taboo adherence may intensify the pressure on the already small and fragile population of *P. perrieri*. A deeper knowledge of the human-wildlife interconnections, as well as regular monitoring of this rare species' distribution, may be crucial for the success of its conservation.

RÉSUMÉ

La perte de l'habitat et le braconnage sont parmi les menaces les plus graves pour la fragile biodiversité de Madagascar. Les tabous traditionnels (*fady*), communément associés à des contes et mythes, ont eu historiquement un effet de préservation sur la plupart des espèces de lémuriens. Le propithèque de Perrier (*Propithecus perrieri*) est une espèce de lémurien en danger critique d'extinction. Il a l'une des distributions les plus restreintes parmi les propithèques. Quelques témoignages anecdotiques relevés dans la littérature suggèrent qu'un tabou protégerait cette espèce de la chasse. La forêt protégée d'Andrafiamena représente à ce jour l'un des principaux refuges pour cette espèce mais la population de ce propithèque n'y a pas été évaluée régulièrement depuis 2013. Cette étude apporte une mise à jour de la présence de *P. perrieri* dans la forêt d'Andrafiamena et évalue l'importance des tabous pour la conservation de cette espèce, sous la forme de résultats émanants d'une brève étude sur le terrain menée à Andrafiamena en 2016. Les données d'entretiens succincts sur l'adhésion aux tabous liés à la chasse de *P. perrieri* menés en 2012 sur l'aire de distribution de l'espèce incluant l'aire protégée d'Andrafiamena-Andavakoera, la Réserve Spéciale d'Analamerana et le Parc National de l'Ankarana sont également présentées. Les résultats confirment la présence de *P. perrieri* dans trois des sept sites visités de la forêt d'Andrafiamena considérée comme étant l'une des zones les plus importantes pour sa conservation. Les résultats montrent également que, sur l'ensemble de l'aire de distribution du propithèque de Perrier, le tabou de chasse est observé par la plupart (> 95%) des répondants (N = 23), une valeur élevée en comparaison avec d'autres zones de Madagascar abritant des populations du genre *Propithecus*. Un conte traditionnel associé au tabou de *P. perrieri* est présenté et rappelle d'autres récits du folklore malgache. Le répertoire des récits concernants les différentes espèces de propithèques semble avoir des éléments stéréotypés et la permanence du récit peut augmenter la probabilité de respect du tabou. Le déboisement et la diminution de l'adhérence aux tabous peuvent intensifier la pression sur la population de *P. perrieri* qui est déjà modeste et fragile. Une connaissance plus approfondie des interconnexions homme-faune ainsi qu'une surveillance régulière de cette espèce menacée peuvent être cruciales pour le succès de sa conservation.

INTRODUCTION

Slash-and-burn agriculture, hard-wood logging, poaching and mining activities represent serious threats to Madagascar's unique biodiversity (Styger et al. 2007, Dunham et al. 2008, Golden 2009, Schuurman and Lowry II 2009, Allnutt et al. 2013, Borgerson 2015).

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Although our knowledge of lemur biology and distribution has increased in past decades (e.g., Mittermeier et al. 2015), the persistence of human-driven threats makes it necessary to regularly re-evaluate human-wildlife interactions on a local scale and to monitor populations of species threatened with extinction (Plumptre and Cox 2006).

In Madagascar, poaching is driven by both socio-economic and cultural trends (Jenkins et al. 2011, Golden et al. 2014, Golden and Comaroff 2015a,b, Borgerson et al. 2016, Rizzolo et al. 2016) such as the erosion of traditional taboos (*fady*) passed down from the ancestors. Traditionally, taboos have played a crucial role in community interactions and attitudes towards wildlife (Jones et al. 2008). With the exception of a common but not globally spread harmful fady towards the aye-aye (*Daubentonia madagascariensis*, Shaw 1896, Ruud 1960, Simons and Meyers 2001), all lemur taboos reported in the literature provide positive conservation outcomes (Jones et al. 2008). The origins of these taboos are in most cases memorialized by a rich repertoire of orally transmitted traditional stories. Origin stories may link mankind or specific tribes to lemur origin, kinship, and altruistic actions towards humans, like in the case of indriids (Ferrand 1893, Decary 1950, Ruud 1960, Thalmann et al. 1993, Harpet 2011a,b). Additional data on taboo spread and cultural forms are necessary for a better understanding of people living closest to biodiversity-rich areas on which conservation depends.

Perrier's sifaka (*Propithecus perrieri*, Lavauden 1931) is a diurnal lemur. It is listed on Appendix I of CITES and has been considered Critically Endangered by the IUCN Red List since 1996 (IUCN 2014) and one of the 25 most endangered primate species (Salmona et al. 2017a). Perrier's sifaka population size ranges from ca. 1,000 to ca. 2,600 individuals (Banks et al. 2007, Banks 2013, Salmona et al. 2017a) and shows low levels of genetic diversity (Salmona et al. 2015, 2017b, Bailey et al. 2016), with an estimated effective population size (N_e,) of about 230 individuals, according to field surveys by Banks et al. (2007) and 50–100 individuals estimated from genetic data (Salmona et al. 2015, 2017b). *Propithecus perrieri* occurs in dry deciduous forests on limestone karst and semi-evergreen transitional forests on sandstone soils in the extreme north of Madagascar, around 50 km to the south of Antsiranana (Salmona et al. 2017a). It has one of the most restricted distribution ranges among sifakas. Its range includes the Analamerana Special Reserve, the Andrafiamena-Andavakoera Protected Area, and possibly the eastern part of the Ankarana National Park, with the Andrafiamena mountains forming its southern limit (Banks et al. 2015).

In Andrafiamena, the presence of Perrier's sifaka was first documented in 1988 as rare (Meyers and Ratsirarson 1989). It was re-assessed in 2005 (Ranaivoarisoa et al. 2006) and in 2012, when a total of 17 groups was found (Salmona et al. 2013). In 2007, Matthew Banks habituated five groups in the forest of Anjahankely. In 2008, 18 individuals were equipped with radio collars (Banks 2013). The groups were followed until 2011 (M. Banks, pers. comm.). The absence of regular surveys since 2013 appears to have favoured the rise of threats such as habitat loss, land conversion, fire, and poaching (Banks et al. 2015).

In the last decade, researchers failed to find Perrier's sifakas in the Ankarana National Park (Banks et al. 2007, Rasoloharijaona et al. 2005, Salmona et al. 2013, Gilles and Reuter 2014) and in Andavakoera (Zaonarivelo et al. 2007, Salmona et al. 2013). Andrafiamena and the western forest of Analamerana can be considered crucial refuges for the species. Considering the restricted species range and the persistence of threats, an update on the presence in Andrafiamena was regarded as essential. In this paper, we therefore report the results of a quick survey of the Andrafiamena forest conducted in 2016 aimed at assessing the presence/absence of sifakas, and we integrate them with bibliographic as well as unpublished data from previous surveys. In addition, as Perrier's sifaka has been reported to be protected by a hunting taboo (Lavauden 1931, Meyers and Ratsirarson 1989, Mayor and Lehman 1999, Harpet 2011b, Banks 2013), we report results of the first interviews attempting to examine taboo adherence in the Perrier's sifaka region.

METHODS

SURVEY AREA. All site visits were conducted in the Andrafiamena Protected Area (Figure 1), located at E049º 19', S12º 55', within the Région de Diana, District d'Antsiranana II, Commune Rurale d'Anivorano-Nord, Fokontany d'Andrafiabe. Andrafiamena-Andavakoera is an 85,000 ha Protected Area (IUCN category V) created only in October 2008 (Buřivalová 2011), and is managed by the Association Fanamby since 2006. Undisturbed and disturbed dry deciduous and transitional forests are interspersed with grasslands (Buřivalová 2011, Banks 2013). The fragments of dry forests are frequently surrounded and/or connected by riparian corridors or fragments of smaller size, extended riparian forests are present as well (Moat and Smith 2007, Salmona et al. 2015). The 2016 informal conversations were conducted in the village of Anjahankely (E049° 18' 49", S12° 54' 31"), located within Andrafiamena (Figure 1). The village consists of approximately 25 wooden houses belonging to the Antankarana (or Antakarana) ethnic group (92 inhabitants in 2011, Buřivalová 2011).

SURVEY METHODS. Seven sites were visited to detect the presence of Perrier's sifakas. Surveys were carried out daily by AA, RR, and two local guides (from the guide association of Anjahankely), from 31 May to 7 June 2016 from 0630h to 1700h. The visited forest fragments were selected based on the guides' suggestions. We visited Anjahankely, Beangivy, Dilanandrevo, Andohan'i Barabanjabe, Andohan'Ampantsona, Ambatombazaha and Andohan'Ambilobe (Figure 1). The forest of Anjahankely was visited several times (6 out of 8 days), as the habitat status ap-

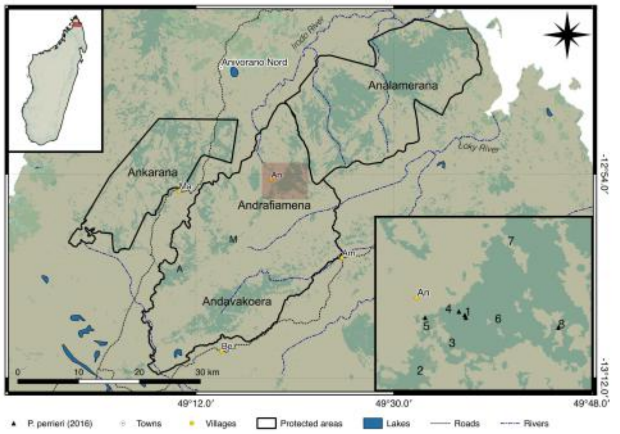

Figure 1. Sites visited during the 2016 survey. Perrier's sifaka was directly observed only in Anjahankely, Andohan'Ambilobe, and Ambatombazaha forests. (M = Mahanoro, AM = Ambohibe; 1–8 = sites visited in Andrafiamena Forest as follow 1 = Anjahankely, 2 = Beangivy, 3 = Dilanandrevo, 4 = Andohan'i Barabanjabe, 5 = Andohan'Ambilobe, 6 = Andohan'Ampantsona, 7 = Ambatombazaha Nord, 8 = Ambatombazaha Sud)

peared better than in other sites and we aimed to find and determine the size of groups followed by Banks until 2011 (Banks 2013). All the other sites were visited only once (1/2–1 day). We carried out presence/absence site visits, and no quantitative survey or distance sampling technique was used. We walked along existing trails. Recorded data included sifaka group size, geographic location, and a quick assessment of the forest type (dry deciduous, transitional semi-humid, humid, and humid riverside forest).

Playbacks were performed to acoustically detect sifakas and their presence was always confirmed visually. We used the integrated speakers of a Marantz recorder PMD660, and played the 'Zzuss-Tsk' and the 'lost' calls of diademed sifaka (*Propithecus diadema*), recorded by AA in Maromizaha forest, eastern Madagascar in 2014. These call types are generally used by eastern sifakas and *P. perrieri*, with, among others, cohesive functions (Macedonia and Stanger 1994, Garbutt 2007, Patel and Owren 2012). Although our targets were sifakas, we additionally recorded the presence of other lemur species, which were detected visually or acoustically, without the use of playbacks.

SURVEY GEOGRAPHIC DATA. The GPS data was recorded from the global positioning of a Canon EOS 6D camera. Geolocalised sites and sifaka sightings were projected on the Forest Cover layer (Conservation International, Harper et al. 2007) using QGIS 2.18. We additionally represented the Protected Areas (Rebioma SAPM 2010, http://www.rebioma.net), roads (http://www.mapcruzin.com), lakes and rivers (http://www.diva-gis.org/datadown) layers.

ETHICAL STATEMENT. All interviews and conversations were conducted in Malagasy by native and/or non-native speakers. We obtained verbal consent to conduct the interviews and to record the discussions from all the participants. Participants could stop the interview at any time. Participation was not paid nor incentivized in any other way. Interviews, conversations as well as the other research described in this manuscript adhered to the current laws of Madagascar, Portugal, France, and Germany and complied with the International Primatological Society Guidelines for the Use of Nonhuman Primates in Research (https://www.asp.org/welfare/socialhousingpolicystatement.cfm) and the MCD guidelines for ethical research conduct in Madagascar (Wilmé et al. 2016). The authorization to conduct this research was granted by the Ministry of Ecology, Environment and Forests of Madagascar.

INTERVIEWS. We analysed the results of 34 structured interviews conducted between May and September 2012 in the region encompassing Andrafiamena-Andavakoera Protected Area (17 interviews), Analamerana Special Reserve (14 interviews), and Ankarana National Park (3 interviews). Participants included ER, FJ, JS. Interview subjects included 31 men (18–65 years old) and 3 women (36–76 years old). Most of them were farmers apart from five reserve officers, one sapphire panner, and one unemployed individual. The five-minute interviews used a prepared questionnaire of 50 questions and investigated *fady(s)* and hunting habits with particular focus on lemurs. First, subjects were shown lemur pictures in order to assess their ability to identify locally present species. The subjects able to recognize locally present lemur species were then asked: (1) whether they adhere to lemur-related *fady* in general and (2) whether they have observed wildlife specific taxa (each locally present lemur genus, birds, tenrecs, bats, fossa, and Malagasy civet), adhere to *fady* and/or hunt each of these same wildlife specific taxa (16 taxa with 3 questions each). In this study, we only report the analysis of the results concerning sifaka and other lemurs *fady* adherence and hunting.

INFORMAL CONVERSATIONS. In June 2016, informal conversations were conducted by AA in the Anjahankely village. Questions and answers were translated by native speaker RR. No pre-arranged questionnaire was used. All participants were men living in the village. Nine local guides were asked in which sites in Andrafiamena they had recently observed sifakas. An elderly ex-guide, at that time nurseryman, was asked: (1) whether traditionally sifakas were hunted or considered *fady* and, in this latter case, (2) whether he knew a traditional tale associated with the sifaka *fady*.

RESULTS

PRESENCE OF LEMURS IN ANDRAFIAMENA. Overall, five lemur species were visually recorded during our visits (Table 1), including one diurnal (*Propithecus perrieri*), one nocturnal (*Lepilemur* cf *ankaranensis* in Anjahankely), and three cathemeral species (*Hapalemur occidentalis* in Andohan'i Barabanjabe, *Eulemur coronatus*, *E. sanfordi*). *E. coronatus*, locally called *ankomba mavo* (literally 'grey lemur'), was found in Anjahankely and Andohan'Ambilobe, while *E. sanfordi*, whose vernacular name is *ankomba mavo beharavoaka* (literally 'grey lemur with large mustache'), was observed only in Anjahankely. The presence of other individuals of *Eulemur* spp. was recorded in Ambatombazaha, Andohan'Ambilobe, and Dilanandrevo forests.

PRESENCE OF SIFAKAS IN ANDRAFIAMENA. In Anjahankely village, sifakas are called *ankomba joby* (literally 'black lemur'). We directly observed sifakas only in Anjahankely, Andohan'Ambilobe, and Ambatombazaha forests (Table 2). In Andohan'Ambilobe, a guide reported the presence of sifakas observed a few weeks before the survey, on the riverside, not far from where he witnessed the presence of two groups during the survey. Local guides also observed sifakas in Beangivy. One group of five individuals was also reported by local guides in Dilanandrevo two weeks before the survey, but we failed to find it during our survey. One group of four individuals was observed independently by some guides in Andohan'i Barabanjabe during the week, but we failed to find it on the following day. We found no evidence of sifaka presence in Andohan'Ampantsona. A guide reported that some sifakas had been observed in Antsandrotona in the past, but we had no time to visit the site. In addition, an ex-guide told us that in the past, four groups were present on the way between Anjahankely and Ambatombazaha. A bibliographic review of surveys across *Propithecus perrieri* range since 2003 is shown in Table 2 and includes unpublished data on the sites surveyed in

Table 1. Observed species in Andrafiamena in 2016. (GR = According to local guide's report)

Site	Observed species
Ambatombazaha	*Propithecus perrieri*, *Eulemur* sp.
Andohan'Ambilobe	*E. coronatus*, *Eulemur* sp., *P. perrieri*
Andohan'i Barabanjabe	*P. perrieri* (GR), *Hapalemur occidentalis*
Anjahankely	*P. perrieri*, *E. coronatus*, *E. sanfordi*, *Lepilemur* cf *ankaranensis*
Bengivy	*P. perrieri* (GR)
Dilanandrevo	*P. perrieri* (GR), *Eulemur* sp.

2012–2013 (see Salmona et al. 2013). The mean group size for the five directly observed groups was (4.6 ± 3.8); when also considering reports by locals (9 groups), the mean was (4.3 ± 2.7). Group size ranged from one to nine individuals.

Two of the five groups habituated in Anjahankely forest by Banks in 2007–2011 were found in 2016. The presence of radio and GPS collars on some individuals facilitated the identification. Sifakas produced terrestrial disturbance alarm calls (mostly Zzuss-Tsk calls) in a contagious fashion and then started an ordered group movement when the presence of the team was detected. One of these groups showed higher tolerance to human presence and did not exhibit fleeing behavior. All observed groups and isolated individuals produced terrestrial alarm calls before fleeing. Zzuss-Tsk call playbacks efficiently allowed us to determine the presence of sifakas.

LANDSCAPE AND HABITAT OBSERVATIONS. Perrier's sifakas were observed in transitional semi-humid forests (Anjahankely), dry deciduous forest patches (Ambatombazaha), and humid riverside forests (Andohan'Ambilobe). These observations ranged from 276 to 727 m of altitude. Andrafiamena is a patchy area, with huge grazing zones surrounding forest fragments, and some rice fields. Several areas between Ampantsona village and Ambatombazaha, in Ambatombazaha itself, and not far from Beangivy had been burned not much long before our survey. Almost in every site we recorded traces of past or recent selective logging, with the vegetation sometimes degraded down to short shrubs. In Andohan'Ambilobe, we observed one lonely individual in a riverside forest, surrounded by the bleak landscape of a recently slashed area, reduced to low grassland.

TABOO ADHERENCE AND HUNTING IN PERRIER'S SIFAKA AREA. The 2012 interviews showed that most of the interviewees (~90%) were aware of the presence of *Propithecus perrieri* in those neighboring forests where the species is supposed to still occur (presence = 29, absence = 2) and that the large majority of those who answered (>95%) declared to adhere the taboo prohibiting the hunting of *P. perrieri* (*fady* = 22, hunting = 1, no response = 11). Results for *P. perrieri* are comparable with those relative to other lemur taxa, such as *Eulemur* species (90%, *fady* = 18, hunting = 2, no response = 14), *Lepilemur* species (95%, *fady* = 19, hunting = 1, no response = 14), *Microcebus* species (94%, *fady* = 16, hunting = 1, no response = 17), and *Daubentonia madagascariensis* (100%, *fady* = 15, hunting = 0, no response = 19). In contrast, 30% of the respondents declared hunting lemurs (whithout species distinction, yes = 10, no = 23, no response = 1), and most interviewees (76%) admitted hunting at least one of the following wildlife groups (birds, lemurs, tenrecs, bats, fossa and Malagasy civet, yes = 26, no = 8, no response = 0).

SIFAKA TABOO ORIGIN STORY. During a 2016 conversation, an elder ex-guide from Anjahankely stated that the ancestors used to hunt *Eulemur* species but not *Propithecus perrieri*, as sifakas were considered *fady*. He also said that, according to a local tale, an unruly child who did not obey to his parents was once hit by them with a ladle as punishment. Consequently, he transformed into a sifaka and this is the reason why sifakas were considered family members by the ancestors and it was forbidden to kill them and consume their meat.

DISCUSSION

PRESENCE OF SIFAKAS AND OTHER LEMURS IN ANDRAFIAMENA. We confirmed the presence of *Eulemur coronatus*, *E. sanfordi*, *Lepilemur* cf. *ankaranensis*, and *Hapalemur occidentalis* in Andrafiamena, where these species had already been documented (Ranaivoarisoa et al. 2006, Mittermeier et al. 2015). Andriafamena also continues to host sifaka populations. The results of the 2016 survey allowed us to confirm the presence of Perrier's sifakas in three of seven visited sites, although their presence was reported by local guides for six sites. The survival of two groups studied in 2007–2011 in Anjahankely forest (Banks 2013) is cause for hope and the forest appears one of the safest blocks for sifakas. Despite the presence of sifakas in Andohan'Ampantsona forest was reported in literature (Mittermeier et al. 2015), we could not detect it, confirming the results of the surveys carried out in 2012–2013.

In Andrafiamena, mean recorded sifaka group size is slightly larger than the one reported from Camp Antobiratsy in Analamerana (Mayor and Lehman 1999), which counted (3.7 ± 0.6) individuals (3 study groups). Interestingly, we observed sifakas at

Table 2. Bibliographic review of *Propithecus perrieri* surveys since 2003. (P = Presence, N.O. = Not Observed, G.R. = Presence according to guides' reports; (1) Rasolaharijaona et al. 2005, (2) Ranaivoarisoa et al. 2006, (3) Zaonarivelo et al. 2007, (4) Banks et al. 2007, (5) Banks 2013, (6) Salmona et al. 2013 and unpub. data, (7) This study)

Protected Area	Sites	2003 (1)	2005 (2)	2006 (3)	2003–2004 (4)	2003–2012 (5)	2012–2013 (6)	2016 (7)
Andrafiamena-Andavakoera	Ambatombazaha					P	N.O.	P
	Ambery				P			
	Ampantrogno-Ampantsogno						P	
	Andohan'Ambilobe							P
	Andohan'Ampantsona						N.O.	N.O.
	Andohan'i Barabanjabe							G.R.
	Anjahankely		P			P	P	P
	Antsahabe					N.O.	P	
	Antsahandrontogno						P	
	Beangivy					P	N.O.	G.R.
	Dilanandrevo						P	G.R.
	Madorimasina					P	P	
	Ambohibe					P		
	Ampondrabe-Antserasera					P	N.O.	
	Mahanoro					P	P	
	Andavakoera			N.O.		N.O.	N.O	
Analamerana	Analamerana	P	P		P	P		
	Antsohy	P	P		P		P	
Ankarana	Ankarana	N.O.			N.O.	N.O.	N.O	

an altitude of 727 m, which is much higher than the maximum altitude of 500 m that is usually reported (Mittermeier et al. 2015). We found that playbacks could be a potentially useful means for detectings.

TABOO ADHERENCE IN PERRIER'S SIFAKA AREA. Our interviews are of limited reach but clearly suggest that in 2012 the Perrier's sifaka-related *fady* was strongly adhered to in the species region, while overall consumption of other wildlife species was common. We found a very high adherence to sifaka-related *fady* (>95%) compared to the Alaotra-Mangoro Region (eastern Madagascar). In that region, *Propithecus diadema* was considered *fady* by less than 10% interviewees and 58% of the interviewees from rural communes declared that had eaten sifaka meat at least once in their lifetime, in strong contrast with the results from urban communes (Jenkins et al. 2011). Our result is even more striking when compared to data from *Propithecus candidus* range: in Marojejy National Park (northeastern Madagascar) only 2% householders reported a *fady* protecting this species (Loudon et al. 2017), despite the existence of a large number of animal taboos (including lemur *Eulemur albifrons*). A similar trend was reported in Makira National Park (northeastern Madagascar), where only 5% of male householders adhered to a taboo prohibiting *P. candidus* meat consumption (Golden and Comaroff 2015a).

Previous studies reported that most but not all sifaka species are protected by a traditional *fady*. Whereas the taboo exists and had some protection outcomes for *Propithecus coronatus* (Harpet 2011b, Salmona et al. 2014a), *P. coquereli* (Kun-Rodrigues et al. 2014, Salmona et al. 2014b), *P. deckenii* (Durbin et al. 2003), *P. edwardsi* (Harpet 2011b), *P. tattersalli* (Meyers 1993, Vargas et al. 2002), and *P. verreauxi* (Hawkins 1999, Loudon et al. 2006, Lawler 2008, Harpet 2011b), it is nearly absent in *P. candidus* and *P. diadema* (Patel et al. 2005, Jenkins et al. 2011, Golden and Comaroff 2015a, Loudon et al. 2017). Like all other lemur species, sifakas are also protected by Malagasy legislation (Rakotoarivelo et al. 2011), and their killing causes legal sanctions to the hunter (Jenkins et al. 2011). Despite the existence of traditional taboos and national laws, restrictions are not applied ubiquitously by a given ethnic group and most species are still hunted in some or even all areas of their range, including *P. coquereli* (Garcia and Goodman 2003, Razafimanahaka et al. 2012, Salmona et al. 2014b), *P. coronatus* (King et al. 2012, Rakotonirina et al. 2014, Salmona et al. 2014a), *P. deckenii* (Rakotonirina et al. 2014), *P. diadema* (Jenkins et al. 2011), *P. edwardsi* (Irwin et al. 2000, Lehman and Ratsimbazafy 2000, Lehman and Wright 2000, Irwin et al. 2005, Lehman et al. 2006), *P. tattersalli* (Meyers 1996, Mittermeier et al. 2015), *P. verreauxi* (Goodman and Raselimanana 2003, Randrianandrianina et al. 2010) or they were hunted in areas where they have now disappeared as in the case of *P. verreauxi* (Gardner and Davies 2004). This trend is common to another diurnal indriid, the indri (*Indri indri*), traditionally protected by a *fady* in Betsimisaraka regions (Harpet 2011b) and nevertheless threatened by hunting in several areas of eastern Madagascar (Thalmann et al. 1993, Powzyk and Thalmann 2003, Golden 2009, Jenkins et al. 2011).

SIFAKA TABOO ORIGIN STORY. The existence and persistence of an origin story (*tantara*) associated with a given taboo is not insignificant for a species' conservation, as the knowledge of an oral story can make an individual up to seven times more likely to adhere to the taboo (Golden and Comaroff 2015a). The origin stories through which food taboos are explained can have different forms, such as educational (humans learned skills from animals), security (humans were saved by animals), and direct indigenous descent (Golden and Comaroff 2015b). For instance, the folklore traditionally depicted the sifaka as the savior of a founding ancestor who learned lemur healing powers (*Propithecus coronatus*), a metamorphosed man (*P. verreauxi*, *P. edwardsi*) or a descendant from a common/founding ancestor (*P. verreauxi*, *P. coronatus*) (Loudon et al. 2006, Harpet 2011b). These last two themes exist also for *P. perrieri*.

The story recorded in Anjahankely shows a strong similarity with other stories from the Sakalava region of Boina (northwestern Madagascar) and the Mayotte Island (Harpet 2005). In these stories, the theme is also the disobedience of a child, which causes an excess of anger of the mother (or both parents) and the transformation into lemur as the resulting punishment. As in the Anjahankely story, this punishment is triggered by a spoon blow, a common element with other two types of origin stories. In the second type, a man (called Rajako/Radjako/Rajaka or Itovo) is hit by his nasty wife with a spoon and transformed into *maque* lemur (probably *Lemur catta*, Szumski 1968), indri (Decary 1950) or *rajako* (probably *Propithecus perrieri*, Abinal and De la Vaissière 1885) according to the version. A conjugal quarrel triggers the transgression of a sorcerer's rule by the woman and the metamorphosis of her husband. This type was recorded in the Antandroy and Betsimisaraka regions. A third type, with two envious women married to the same husband transforming each other into lemurs (*L. catta* and *P. verreauxi*) through a spoon, was documented in Beza Mahafaly, southern Madagascar (Loudon et al. 2006). All these stories appear to provide norms of behavior and to explain the kinship between humans and lemurs.

For the Antankarana people living close to the Analamerana forest, Rajako was regarded as the name of a legendary hero of whom sifakas would be the descendants (Lavauden 1931) and is one of the local names used for Perrier's sifaka (Mittermeier et al. 2015). Another Antankarana belief is that sifakas harbor the spirits of deceased ancestors that have been buried in the sacred forests where these lemurs often reside (Banks 2013). The richness of folklore regarding human's kinship with indriids, especially *Indri indri* (Abinal and De la Vaissière 1885, Ferrand 1893, Catat 1895, Decary 1950, Ruud 1960, Dahle and Sims 1992, Harpet 2011a,b) may be explained with their "vertical clinging and leaping" upright posture (Napier and Walker 1967), possibly reminding of humans. For instance, lack of preference for some lemur meats by locals lacking taboos was connected to lemur resemblance to humans (Jones et al. 2008). This could possibly explain why diademed sifakas are not considered top-ranking meat by people from the Alaotra-Mangoro region (eastern Madagascar) although *fady* adherence is low there (Jenkins et al. 2011). Nevertheless, a regional variability in food preference seems apparent, as in an area close to Betampona, Antsinanana region (eastern Madagascar), diademed sifakas were conversely reported as a favored food (Welch and Katz 1992).

LEMUR HUNTING IN PERRIER'S SIFAKA AREA. According to the interviews, lemur hunting in Perrier's sifaka region appears less common (30% of the interviewees) than in Makira, where 49% of households declared hunting of lemurs (Golden et al. 2014), although wildlife is widely hunted in both areas. Our result is more alarming when compared to the Ankarana National Park, which is located nearby Andrafiamena, on its west side. In the buffer zone surrounding the park, only 11.4% of villagers reported to have hunted lemurs at least once in lifetime despite only 20.7% stating that they have taboos against lemur consumption/hunting (Gilles and Reuter 2014).

Hunting of Perrier's sifakas for food has been documented since the 1990s in some parts of their range like Analamerana (Harcourt and Thornback 1990, Meyers 1996), where it was possibly pushed by the breaking down of the *fady* (Mayor and Lehman 1996). At that time, a lemur taboo was spread in Ankarana (Fowler 1989), where this species probably later disappeared. Some recent reports suggest the persistence of the hunting practice of this species (Banks et al. 2015, Mittermeier et al. 2015).

Besides the limited sample size of the interviews, hunting was probably underestimated in the present study for several reasons. First, people generally hesitate to admit to hunting species that are protected by national or informal institutions as they may fear self-incrimination or that they may be negatively judged by their community. Second, people who are forbidden to kill sifakas may purchase them for food and we did not consider in our questionnaire the case in which interviewees received a carcasse from someone else, without hunting the animal by themselves. Moreover, stating to personally observe a taboo does not necessarily mean that interviewees adhere to it over the whole life, or that the taboo is shared with the whole ethno-linguistic group or with the local community (Boucher 2011, Golden and Comaroff 2015a). An observation-based local monitoring of transported, offered for sale, and consumed wildlife in the villages (a method that was adopted by Jenkins et al. 2011) may be an useful tool for veryfing our results and provide a reliable measure of the fady adherence degree in the future. Nevertheless, unlike other areas in Madagascar (Golden and Comaroff 2015b), we have reason to think that food taboos in this region are likely to serve as a direct form of conservation.

Lemur hunting can be undertaken using slingshots, blowguns, firearms, spears, dogs, traps, and snares (Irwin et al. 2000, Golden 2009). Sifakas are generally reported to be hunted using slingshots and dogs (Goodman and Raselimanana 2003, Randrianandrianina et al. 2010). In the Diana region, snares and the remains of slingshots have been found in forests and along fragment edges within *Propithecus perrieri* range (Banks 2013). However, during our quick survey, we did not detect the presence of snares nor remains of slingshots or bullet shells. Despite past detections, hunting in the Diana region did not show a strong effect on lemur populations (Banks 2013), but one should be mindful that even occasional bushmeat consumption may significantly pressure an already fragile population (Jenkins et al. 2011).

Hunting is not the only human-driven menace responsible for sifaka killing. Introduced mammalian carnivorans such as wildcats (*Felis silvestris*) and dogs (*Canis lupus familiaris*) constitute a concrete threat to sifakas in some areas (Brockman et al. 2008). In addition to being used by poachers, dogs are known to attack Perrier's sifakas descending to the ground to cross open areas (Banks 2013), a common behavior in this lemur species (Mayor and Lehman 1999). Dog attacks were reported from an area very close to Anjahankely village and throughout the wider region (Banks 2013). In 2016, we interviewed a villager who reported a recent case of a dog killing a Perrier's sifaka in Anjahankely. This additional predation pressure may be fatal as carnivore attacks can make lemur species disappear from small forest fragments in a very short time (Irwin 2006). Therefore, both taboo persistence and different forms of anthropogenic threats (including forest clearing, hunting, and dogs attacks) are factors to be considered and monitored in future.

CONCLUSIONS

Our quick survey confirmed the presence of the rare Perrier's sifaka in Andrafiamena, three years after the last visit by researchers. Within the area, Anjahankely forest appears one of the safest areas for sifakas. On the contrary, we had difficulties in finding sifakas in forests away from Anjahankely, where the presence of single individuals in small forest fragments is not reassuring. Although limited in sample size, and possibly biased by non-response, our interviews showed that in 2012 the sifaka-related *fady* was declared to be observed by most interviewees. While the strong taboo adherence is expected to act as hunting deterrent, it does not prevent logging and *tavy*. Forest clearing and fragmentation as well as occasional attacks by dogs and a progressive erosion of the traditional taboos may put the fragile Perrier's sifaka population increasingly at risk. Regular, more extensive and systematic surveys across the species' range are needed to monitor the population trend, especially in a crucial refuge like Andrafiamena. For instance, some sites like Ambery, close to the border with Analamerana, have not been surveyed since the discovery of sifakas in 2003-2004, and an update on that population is needed. Furthermore, as taboo systems are in continuous evolution and adherence to them can change over a generation or an individual lifetime, monitoring their persistence and confirming their effectiveness with observational data on hunting is of major importance for conservation aims.

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Mind the gap: the use of research in protected area management in Madagascar

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ABSTRACT

It is increasingly well recognised that a lot of conservation-related research is not being used to improve conservation practice. However, much of the research in this area has been conducted with conservation managers in high income countries, where the barriers to accessing and using research may be different. We conducted questionnaires (n=85) and face to face interviews (n=54) with managers of protected areas in Madagascar to explore their use of research results. Despite considering research results—including peer reviewed articles, theses, in-house research and research by other organisations—a very useful information source, many managers do not use research results regularly to inform their on-the-ground actions. Instead they tend to rely on experience, or advice from others. The reasons for the low use of research results are many and varied but include barriers to accessing research, especially peer-reviewed publications and reports published by other organisations. Managers also raised concern about the practical relevance of some of the research being conducted in their protected areas. We identify a series of resources which can be useful to managers to improve the access they have to research results and highlight a series of steps which researchers can follow to increase the likelihood of their research being used. We also suggest there is a role for the Malagasy authorities in improving the ways in which research reports—received as part of the conditions of research permits—are shared and archived. Researchers are increasingly aware of the moral imperative that research conducted should be available to inform practice, and protected area managers want access to the best possible information to inform their decisions. With such good intentions, overcoming the gap between research and practice should not be difficult with good communication and essential to improving conservation management in Madagascar.

RÉSUMÉ

L'existence d'un fossé entre la recherche et la pratique est un phénomène de plus en plus reconnu en conservation. Cependant, relativement peu d'études sur ce sujet ont été conduites dans les pays en développement riches en biodiversité. La présente étude explore ainsi l'utilisation des résultats de recherche dans la gestion des aires protégées, principale stratégie de conservation à Madagascar. Des enquêtes par questionnaires (n=85) et des entretiens face-à-face (n=54) ont été menés avec des gestionnaires d'aires protégées. Bien que les gestionnaires considèrent les résultats de recherche, à savoir les publications à comité de lecture, les thèses universitaires ainsi que les recherches internes et externes, comme étant très utiles comme source d'information, peu d'entre eux les utilisent pour motiver des décisions de gestion, à l'exception des recherches menées à l'interne. Les gestionnaires tendent à s'appuyer sur leur expérience ou sur les avis d'autres gestionnaires ou chercheurs. Les facteurs contribuant à la faible utilisation des résultats de recherche sont nombreux et variés mais comprennent en particulier la difficulté d'accès aux publications à comité de lecture et aux recherches externes. Les gestionnaires ont aussi soulevé le fait que certains résultats de recherche effectuée dans leur aire protégée sont peu pertinents à la gestion de celle-ci. Nous avons identifié une série de ressources qui pourraient s'avérer utiles aux gestionnaires pour pallier en partie au problème d'acquisition de résultats de recherche. Nous avons également mis en exergue un ensemble d'étapes que les chercheurs pourraient adopter afin d'augmenter les chances d'utilisation de leur recherche. Par ailleurs, nous soulignons le rôle important que les autorités malgaches ont à jouer dans l'amélioration du mécanisme de partage et d'archivage des rapports de recherche qui leur sont remis conformément aux conditions d'obtention du permis de recherche. Les chercheurs reconnaissent de plus en plus l'impératif moral de mettre leur recherche à disposition des gestionnaires de ressources. Ces derniers, quant à eux, aspirent à accéder aux meilleures sources d'information possibles pour motiver leurs décisions. Avec de telles bonnes intentions, réduire le fossé entre la recherche et la pratique est possible avec une bonne communication et est essentiel pour surmonter les défis de la conservation à Madagascar.

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INTRODUCTION

Conservation science has been widely described as a crisis discipline requiring urgent action (Soulé 1985, Robinson 2006). The purpose of conservation research is to provide knowledge to improve management or policies to address the ongoing biodiversity crisis; making translation of knowledge into action one of conservation's most pressing goals (Segan et al. 2011, Hambler and Canney 2013, Fuller et al. 2014). However, despite the rapid growth over the last two decades in the volume of applied conservation research being conducted (Fazey et al. 2005, Robinson 2006, Roux et al. 2015), it has been regularly noted that much of this research does not go on to influence conservation practice (Knight et al. 2008, Keene and Pullin 2011, Milner-Gulland et al. 2012, Habel et al. 2013). The gap between research being conducted and being used has been explored for a range of research areas including addressing bioinvasion (Bayliss et al. 2013, Kuebbing et al. 2013, Matzek et al. 2014, 2015), bird conservation (Seavy and Howell 2009, Walsh et al. 2015), governance of marine resources (Cvitanovic et al. 2014, 2015), peatland restoration (Anderson 2014), and protected area management (Cook et al. 2010, 2012). There has been quite extensive research into the extent to which research informs the management of protected areas (Pullin et al. 2004, Cook et al. 2010, 2012, Giehl et al. 2017); however, the bulk has been carried out in high income countries where the challenges facing managers may be quite different. Two exceptions are Young and Van Aarde (2011) who explored the use of research in elephant conservation in South Africa, and Gossa et al. (2015) who explored the use of peer-reviewed literature by researchers and practitioners in less developed countries more widely.

A number of authors have highlighted a tension between the research that conservation practitioners need to inform management, and what conservation scientists produce (Bayliss et al. 2012, Cook et al. 2013, Balme et al. 2014). This is at least partly due to the reward structure in research institutions such as universities which promote publications in high impact journals over applied impact (Gibbons et al. 2008, Arlettaz et al. 2010). The high impact journals may require studies of a different scale and concerning types of research questions quite different to those of most value to practitioners (Griffiths 2004, Milner-Gulland et al. 2010, Laurance et al. 2012). There is, however, a big change underway in research with increasing value being put on research which is used. For example, funding bodies such as the UK government research councils require evidence of a planned 'pathway to impact' and the UK government's Research Excellence Framework gives explicit credit for the 'impact' of research (Watermeyer 2014). Increasingly, conservation scientists are looking to base their research on the real research needs of practitioners. There have been a number of attempts to gather and collate research needs of practitioners (Sutherland et al. 2009, 2012, Caudron et al. 2012), and to improve information delivery and communication between researchers and practitioners (Roux et al. 2006, Neßhöver and Timaeus 2013, Young et al. 2014, Chapman et al. 2015).

Protected areas are rapidly expanding as a conservation approach (Jenkins and Joppa 2009, Watson et al. 2014). Their goals and objectives are increasingly complex; as well as providing habitat for threatened species and conserving iconic landscapes, they are also expected to contribute to social objectives (Watson et al. 2014). However, despite these good intentions, managing protected areas so that biodiversity objectives are met without harming local communities is challenging (Brockington and Wilkie 2015). The International Union for Conservation of Nature (IUCN) has developed the following protected area categories (Dudley 2008): Category Ia: Strict Nature Reserve, Category Ib: Wilderness Area, Category II: National Park, Category III: Natural Monument or Feature, Category IV: Habitat/Species Management Area, Category V: Protected Landscape/Seascape, Category VI: Protected Area with sustainable use of natural resources. Category V is currently more and more widespread but also stirs much debates (Shafer 2015). Increasingly, conservation research is moving beyond studies of threatened species and habitats and is tackling issues such as equity, local livelihoods, and land tenure (Mace 2014, Marvier 2014, Pooley et al. 2014).

Madagascar is a country of global importance to conservation due to its incredible biodiversity and the numerous and pressing threats imperilling this biodiversity (Dinerstein et al. 2017). In 2003 the president of Madagascar decreed that the country would triple the extent of its protected area network (Gardner et al. 2013), i.e., up to 10% of the national territory. This led to a major scientifically-driven process for identifying priorities for the establishment of new protected areas (Kremen et al. 2008). The expansion has been largely achieved, and by 2015, 59 of new protected areas had been gazetted. These new protected areas, and Madagascar's existing network of protected areas, some of which date back to the colonial era, face many challenges in terms of conserving biodiversity without undermining local welfare (Raik et al. 2008, Brimont et al. 2015, Poudyal et al. 2016). In the new protected areas, however, poverty alleviation is more explicitly listed as a goal (Gardner et al. 2013, Shafer 2015). There is an enormous amount of research conducted in Madagascar every year by academic institutions—both those based in Madagascar and from overseas—and some non-governmental organisations (NGOs). However, there is very little information available on how this research is used to contribute to the management of protected areas, and what the barriers are for more use.

In this paper, we attempt to understand the sources of information used by managers of protected areas in Madagascar, particularly the research results, using questionnaires and semi-structured interviews with conservation managers from all over the country. These are the people making decisions every day which affect both the biodiversity for which they have management responsibility and the lives of local communities who may depend on the natural resources within the protected areas. We explore (i) how useful managers feel different sources of information are to guide their management actions, (ii) the extent to which different information sources are used to inform their management actions, (iii) how they access research and (iv) what barriers they perceive to using research more in their management. We then discuss practical ways to overcome these barriers.

METHODS

DEFINITIONS. We developed information types based on the categorisation by Cook et al. (2012). We consider three sources of information: (i) research, including peer-reviewed literature, academic theses, in-house reports and external reports; (ii) experiential, including personal experience, advice from managers, advice from specialists; or (iii) intermediate, including management plans, manuals and guidelines.

In this paper, research results refer to any output of a scientific investigation or synthesis carried out by researchers and following the research process. Any discipline in the natural or social sciences pertaining to conservation is considered, such as ecology, biology, sociology, governance, politics, climate change, systems research, and management sciences. Such breadth is necessary given the complexity of nature conservation today. Our definition of research results is not limited to peer-reviewed publications (cf. Gossa et al. 2015) but also includes the research grey literature (technical reports, theses, newsletters written by practitioners) (Aina 2000). We include this wider definition of research results because the grey literature is important, is less subject to publication bias and may include more practice-oriented results than the peer reviewed literature (Haddaway and Bayliss 2015). However, the risk of using the grey literature for decision making or to inform management is that the quality of the evidence may be weaker.

There are basically two concepts of research utilisation: that of outcome and that of process (Rich 1997). In this study we conceived research utilisation as a process which involves research results being acquired, read, understood or not, and some action is taken by the user (Rich 1997). The barriers to research use are therefore the barriers encountered at each step of the process.

SAMPLING APPROACH. Our target population was conservation professionals working in protected areas who have responsibility for decision-making concerning conservation actions. These site-based professionals, hereafter referred to as managers, may hold a general (e.g., park director) or a more specific (e.g., conservation officer) managerial position. These people design and update the management plan of the protected area they are responsible for. As of 2015, we considered 100 protected areas in Madagascar with a clear promoter, distributed into six categories (Table S1). Strict Nature Reserve, National Parks and Special Reserves (category I, II and IV, respectively, in the IUCN categorisation) are managed by Madagascar National Parks (MNP), a parastatal agency. Natural Monuments, Protected Landscapes, and Natural Resources Reserves (category III, V and VI, respectively) are managed by national or international non-governmental organisations or private companies.

For organisations managing more than one protected area, we initially approached the central office (for example Madagascar National Parks and some of the larger NGOs such as Conservation International and Durrell Wildlife Conservation Trust), introduced our research and obtained permission to contact site-managers and their contact details. For smaller organisations or where central office did not respond to our approach, we used our personal and professional network to contact some protected area managers directly.

We contacted site-based managers by email and/or phone initially and invited them to complete our questionnaire and/or take part in a more in-depth face-to-face interview. In the course of the research we visited protected areas throughout the country except the south east and north east. We found that personal visits were very important for generating interest in the research.

QUESTIONNAIRE. The majority of the results presented below comes from our questionnaire survey (Supplementary Material 2). The questionnaire development was informed by previous similar studies (e.g., Pullin et al. 2004, Cook et al. 2010, Gossa et al. 2015) and adjusted after piloting when necessary. We predominantly used rating scales. The questionnaire collected demographic data, and asked participants to rate how often and how useful different information sources were to guide management decisions, how they access research results, and how often they have experienced a series of known, literature-based barriers when using research evidence.

We conducted a pilot survey with five conservation managers working for NGOs in Madagascar based in the capital city (testing both the English and French versions). Based on their feedback, some questions were reformulated and the vocabulary simplified. The final version was in French as it is easier for our target population to understand our topic and the terms we used in the questionnaire if these were in French. We sent the questionnaire via email as an attachment to all primary site-based contacts (typically the Park Director) of each of the 100 protected area we considered in this study; they were encouraged to share with colleagues with whom they share management responsibility for the park. In total 85 questionnaires from 53 protected areas were returned. Questionnaires were completed between June and November 2016. It is difficult to give a precise return rate given that the population size of potential participants (those with management responsibility for a protected area) is unknown. However we estimate the potential participants to be between 200 and 300, assuming 2 to 3 potential participants per protected area. With these estimates, the return rate lies between 28 and 42%.

We used diverging stacked bar charts to display the patterns for categorical variables with semantic differential levels such as frequency of use, perceived usefulness, ease of access, and barriers to research use using the package HH (Heiberger and Robbins 2014). We used the R statistical software (R Core Team 2017) to produce the charts.

INTERVIEWS. We also conducted semi-structured interviews in person that focused around the question "In your experience, what are the barriers you have encountered when it comes to using research results in your work?". These allowed us to capture the barriers not covered in the questionnaire and to add depth to our understanding of the barriers to research use. The barriers to research use are therefore the barriers encountered at each step of the process. The semi-structured interviews were done using a blend of Malagasy and French, which is very common in technical conversations.

These semi-structured interviews (n=54 from 29 protected areas) were conducted in person with managers of protected areas at their place of work (Figure S3). The participants in the interviews were selected based on a combination of the logistics of accessing particular protected areas, and managers' willingness to be interviewed. Amongst the participants we interviewed, 87% also filled out the questionnaire. We used thematic analysis (Braun and Clarke 2006) to explore the barriers pertaining to knowledge production, access, understanding, and implementation using research utilization as a process of our analysis framework.

RESEARCH ETHICS. This research was approved under the Bangor University research ethics framework. We obtained informed consent from everyone who took part in the research by explaining the purpose of the research and how the research results would be used. We emphasised that they were not obliged to answer our questions and that we would not be passing their responses on to anyone else (including senior people in their organisations). We emphasised that we would not report the results in a way which made it possible to identify the responses of individuals.

RESULTS

DATA DESCRIPTION. A total of 85 managers returned the questionnaires (42 from managers working in parks and reserves managed by MNP and 43 from those working in protected areas managed or co-managed by NGOs) representing 53 protected areas. In terms of educational attainment, 80% of the managers who returned the questionnaire have postgraduate degrees (74% Masters and 6% Ph.D.). Participants' work experience in conservation or environmental management, excluding formal education, ranges from 1 to 31 years with a mean of 12 years.

We interviewed 54 participants (26 worked for MNP and 28 for NGOs) from 29 protected areas. Three-quarters (75%) of the managers we interviewed have a Masters degree. Their work experience in conservation or environmental management ranges from 1 to 25 years with a mean of 11 years. There were 47 participants who both returned the questionnaires and were interviewed.

DO MANAGERS PERCEIVE RESEARCH RESULTS AS USEFUL TO INFORM THEIR ACTIONS? Managers perceived all information (including our four categories of research) to be useful to their decision-making (Figure 1). In-house and external research results are perceived as the most useful compared to academic outputs, although not by much.

WHAT INFORMATION SOURCES ARE MANAGERS USING? Exeriential sources of information (especially personal experience or advice from managers) is the main source of information used by research managers (Figure 2). Management plans and manuals and guidelines are also widely used. Research results vary in how widely they are used: commissioned studies and in-house research are used but external research, theses and especially peer-reviewed publications are seldom used (Figure 2). The difference between the perceived usefulness of peer-reviewed research (Figure 1) and the extent to which it is used (Figure 2) is especially noteworthy.

HOW EASILY CAN RESEARCH RESULTS BE ACCESSED BY MANAGERS? There are clear differences in the accessibility of different types of research results. Managers find it relatively straightforward to access in-house research from their own organisation, although it is still surprising to see some found it difficult. However, accessing other forms of research results (theses, external research results or peer-reviewed publications) is difficult for the majority of respondents (Figure 3).

HOW DO MANAGERS OBTAIN RESEARCH RESULTS? When actively searching for research results, managers primarily ask their colleagues who are researchers or specialists, browse the web, and use internal documentation (their personal collection or organisation library) (Figure 4). The importance of professional networks is particularly notable. Online fora and research databases are less used, although it is unclear whether this is due to a lack of awareness of their existence and purpose by managers or due to other factors.

There are of course occasions when research results are received by managers who were not actively searching for them.

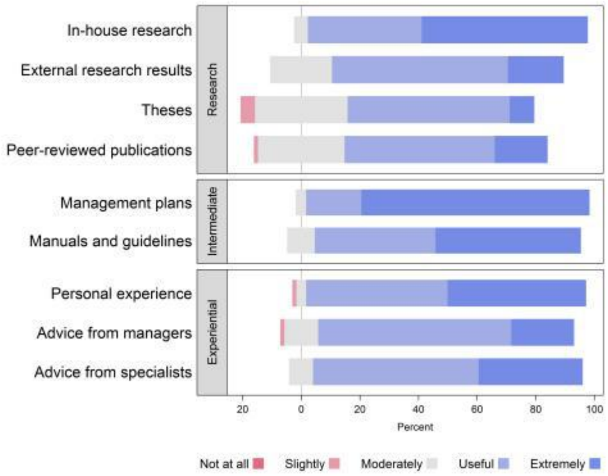

Figure 1. How useful protected area managers in Madagascar perceive various information sources are to inform their actions (n=85).

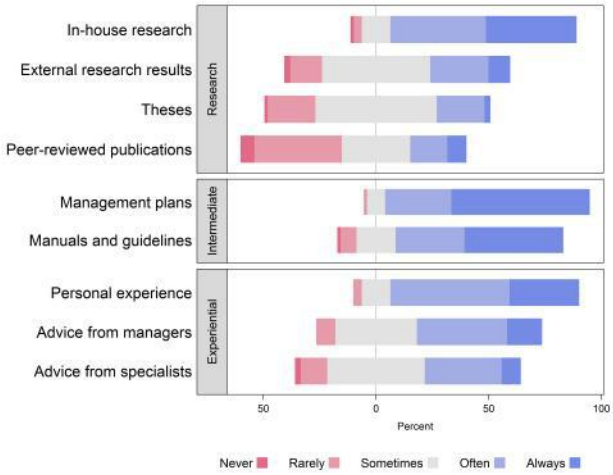

Figure 2. How often protected area managers in Madagascar use various information sources to inform their actions (n=85).

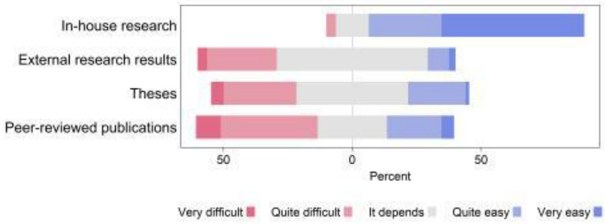

Figure 3. Ease of access to different types of research results by protected area managers in Madagascar (n=85).

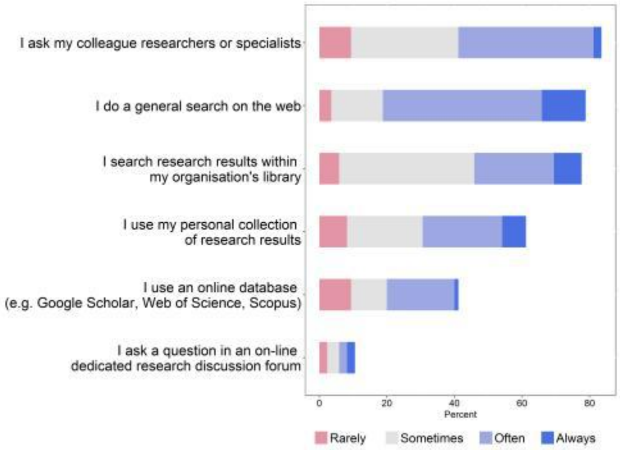

Figure 4. How protected area managers in Madagascar search for the research results they need (n=85).

Research results are received by managers through colleagues who send them research results, or mention it during workshops (Figure 5). Social media, journal alerts or formal professional networks (e.g., Madagascar Environmental Justice Network) are less used. This again highlights the importance of managers' informal professional networks for obtaining research results.

WHAT ARE THE BARRIERS TO THE USE OF RESEARCH RESULTS? Several managers suggested that one of the reasons they do not use research results is that they felt there was limited research of relevance to them and their needs. There was a tendency among managers making this point to talk about the lack of research at their specific site (implying that they are particularly interested in research carried out at their site, rather than research at other sites on relevant themes). The lack of research was particularly highly reported by managers of newly established PA but the same issue was also reported by some long-established PAs (especially where poor roads or insecurity means few researchers visiting).

"In our case, the research results themselves are lacking" (Director of a Protected Area with sustainable use of natural resources (category VI), Eastern Madagascar)

"The problem with our PA is that there are very few researchers who come here because the roads are so challenging. The last time there were researchers here was in 2008." (Director of a Habitat/Species Management Area (category IV), Eastern Madagascar)

Sometimes it is not a case of there not being any research, but that managers do not perceive that the research which has been conducted is relevant to their needs. There is a sense that the research which researchers like to do (and perhaps which feeds into large scale analysis) has limited management relevance at a specific site.

"But there are results that we don't know really what to do with these. Take research on ants for example. It's true that it is interesting to know about the species that exist and their ecology and so on, but for us managers what really matters is how we can measure our management effectiveness of the PA. Lemurs monitoring for example speaks to us directly as the population dynamics reflects our management effectiveness. In short, [we need] research that is important to us and that is related to our target species or indicator species." (Director of a Habitat/Species Management Area (category IV), Northern Madagascar)

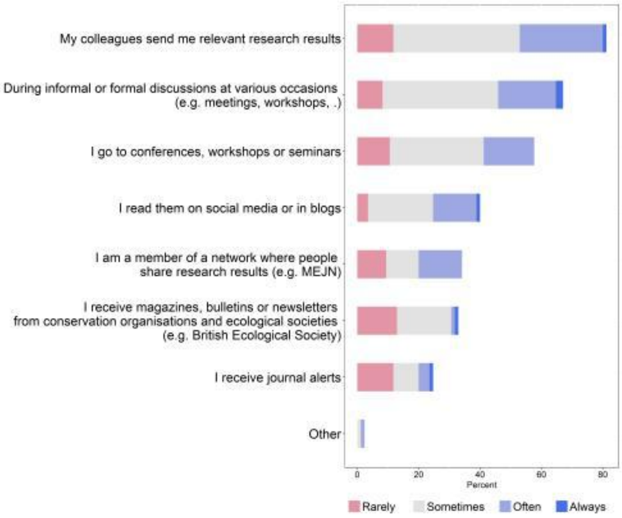

Figure 5. How protected area managers in Madagascar hear about research results (n=85).

In many cases, even if relevant research had been conducted, managers were not able to access research. A very common complaint among the managers interviewed was that researchers do not give the results back. Given the challenges of accessing peer-reviewed publications, reports returned by researchers to managers are invaluable.

"If there are, say 50 research investigations done in our PA, I'd say only two or three reach us back. That is one big problem. You see the process starts with the institution that delivers or grants research permits. If that institution is not enforcing the restitution of research results, then researchers simply disregard us". (Director of a Habitat/Species Management Area (category IV), Northern Madagascar)

The importance of researchers returning reports (ideally in French), and any published papers, to managers was also highlighted by our questionnaire data (Figure 6). The most important barrier reported is that organisations lack subscriptions to journals. It is interesting to note that managers also report problems in accessing external research results (e.g., reports carried out by a different organisation on a theme of interest to the managers).

The language of higher education in Madagascar is French and all managers are fluent in French while only a sub-set can read English (the language of many international journals). Just over a quarter of respondents considered the English language to be an issue. The language used in reports presenting research results (both in terms of writing in languages which are understood locally and avoiding technical jargon) are also important for the managers to get buy in for implementation of research results locally.

"One of our biggest difficulties is to translate the research findings into terms that local partners can apprehend." (Director of a Protected Landscape (category V), Southern Madagascar)

Finally, there are barriers occurring at the implementation stage, and these include the lack of local capacity, budget constraint, and lack of organisational support.

"Another barrier is also financial resources, because often … in our case for example, we function as a project, so if the recommendations from a relevant piece of research are not planned within the project there is hardly anything we can do about it." (Director of a Protected Area with sustainable use of natural resources (category VI), Eastern Madagascar)

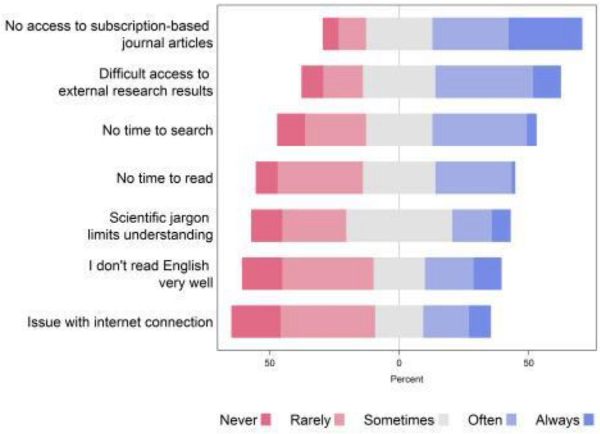

Figure 6. Barriers to research use experienced by protected area managers in Madagascar (n=85).

DISCUSSION

MANAGERS CONSIDER RESEARCH RESULTS BUT FACE MANY CHALLENGES. Managers of protected areas in Madagascar value all sources of information open to them for informing their practice. These include research-based information (found in peer-reviewed research and in-house research most greatly valued), experiential information (from personal experience, advice from specialists and advice from senior colleagues), and intermediate information such as management plans, manuals and guidelines. However, despite the value placed on research results by managers, it is interesting to note that most categories of research results (the exception being in-house research) are not widely used. For example, a large majority of managers who responded to our survey never or rarely uses peer-reviewed publications. The fact that research results are relatively less used compared to experiential and intermediate sources of information in guiding management actions has been found by a number of other studies exploring the use of conservation evidence (e.g., Pullin et al. 2004, Sutherland et al. 2004, Cook et al. 2013).

There are two plausible reasons why research results are not more widely used by protected area managers in Madagascar. First, not every aspect in managing a PA requires research-based information. Indeed, protected area management contains a great deal of routine activities and urgent problem solving that does not require research-based information. The second reason why research based information is seldom used is due to barriers to research use. In our experience, these two explanations are not mutually exclusive but rather co-occur in the context of protected area management.

By exploring the barriers to research use based on both qualitative and quantitative data we have built up a picture of why managers do not use research results more often in their practice. Firstly, there is the issue that much of the research conducted by researchers does not appear relevant to the management needs of the protected area managers. However physically gaining access to research results is clearly a significant issue for many managers. It is clear that managers are making use of their networks to access research results (with the most common means of searching for research results and receiving research results being asking colleagues, researchers or specialists). This approach and searching their institution's library and use of their own personal collection is particularly important as many research results are published behind a paywall that protected area managers cannot access (lack of access to subscription journals was reported as the top barrier to accessing research results). It is worrying that research conducted by other organisations in Madagascar was perceived as so difficult to access; qualitative interviews suggest there is a perception that organisations do not like to share their work even when it could help other organisations. There are of course other reasons why research results are difficult to access—time (to access and read results), challenges with language, and access to the internet are all commonly reported issues. Finally, even where relevant research has been conducted, and the managers can access it and understand it, sometimes budget or capacity constraints mean the results do not influence practice.

WHAT COULD BE DONE TO IMPROVE THE USE OF RESEARCH RESULTS IN MADAGASCAR? There is evidence that the conservation practice and policy community are evidence complacent (Sutherland and Wordley 2017). Our discussions with managers across Madagascar suggest that many managers are indeed motivated to use research results but maybe unsure how to progress. We argue that managers are more likely to use research results if these are findable, relevant, accessible, and understood (although resource constraints will also play an important role in influencing the extent to which research results are put into practice). Considering the findings of this study, we propose the following practical recommendations to improve the use of research results in PA management in Madagascar.

MAKING RESEARCH MORE RELEVANT TO MANAGERS' NEEDS. Our results show that in-house research is the most common type of research used by protected area managers in Madagascar. In-house research is designed to respond to management needs as is commissioned by the organisation itself or one of its partners. Most research conducted in Madagascar is initiated by researchers themselves and it is perhaps not surprising that managers feel much of it lacks relevance. This lack of management relevance of much conservation research is a well-documented issue (Milner-Gulland et al. 2010, Laurance et al. 2012, Matzek et al. 2014, Chapman et al. 2015).

While there will always be researchers wishing to conduct research which does not have obvious and direct applied relevance (and it is important to note that such research may still be useful in longer term or for larger-scale decision making), there are increasing numbers of researchers very keen to ensure their research is useful. Therefore, researchers require mechanisms for learning about the research needs of managers and may then be able to adapt their research questions to provide useful information to managers. There is currently no clear mechanism for researchers to know managers' needs in Madagascar. The simplest way maybe for managers to post their research needs on their organisation's website, so that it can be used to inform the agenda of the research community. There have been a number of exercises where researchers and practitioners teamed up to produce lists of top research questions (Sutherland et al. 2006, Pretty et al. 2010, Rudd et al. 2011). Such schemes have been quite influential on research agendas (Dicks 2013, Dicks et al. 2013) and perhaps such an exercise could be conducted in Madagascar; bringing together protected area managers and researchers.

HELPING MANAGERS ACCESS RESEARCH RESULTS. Web platforms like ResearchGate and Academia.edu (where researchers share copies of their published work) and Sci-Hub (which uses passwords shared by academics to download and publically archive copies of academic articles) are increasingly offering ways for those without subscriptions to scientific journals to access research results (Bohannon 2016). The conservation community in Madagascar has additionally benefited from the work of those running the Madagascar Environment Justice Network who share particularly relevant articles on an online forum (often with accompanying discussion and debate). Theses from many universities internationally are also increasingly available online; including most theses from the University of Antananarivo defended since 2002. However, our research suggests that many managers are not aware of these ways of accessing research results. Such information could be offered by organisations as part of the training they provide their managers to increase their ability to access research results of interest to them.

WHAT CAN RESEARCHERS DO? Managers are short of time, struggle with internet access and some (though far from all) struggle with reading research published in English or which uses technical language. Therefore, the research community have a clear role to play in improving the accessibility of research results to protected area managers in Madagascar. As part of the terms of their research permits, researchers are required to return results in the form of reports to the relevant ministry, which typically is the Ministry of Environment, Ecology and Forests, in the case of conservation research. However, anecdotal results suggest these often do not make it to the hands of the protected area managers in the sites the researchers worked because either they are not produced or they are not passed on. They are also of variable quality and value to managers because they are produced before the research has been fully analysed, or because they do not explicitly make the management relevance clear. As researchers, we have an obligation to ensure our research is available to be used by society.

Here we present our view, informed by our findings on the barriers to research use by protected area managers in Madagascar, of the steps all researchers should take: (i) Involve managers in the research: Sharing results with potential stakeholders including protected area managers is not something which should happen at the very end of the research process. Researchers should make the effort to discuss the research with managers while the research is underway (ideally even inviting them to the field to get involved in the research). The more potential users of research understand the research conducted, the more likely they are to apply its lessons (Hulme 2014). (ii) Share preliminary results: Researchers should ensure they do a verbal presentation of results (this may be a formal presentation to the protected area team or simply a sit down chat with one or two key people) before they leave the field so any preliminary results can be understood and potentially impact practice as soon as possible. (iii) Ensure final reports are useful and accessible: When producing final reports, researchers should consider the audience and ensure that they make management relevance clear. This may mean producing a specific report aimed at managers in Madagascar, rather than simply using a report produced for funders. Wherever possible they should ensure a copy of their reports gets back to the field sites where they operate. Often data continues to be used in publications for a long period of time after an initial report is published and researchers should make every effort to return these papers ideally with a covering abstract in French where the paper is published in English so managers see how the research conducted in their protected area went on to be used. Most protected area managers in Madagascar have email even if internet access is intermittent. This makes returning reports and papers to protected areas managers much easier. (iv) Make all research open access: Researchers should also be considering about the wider accessibility of articles they publish. Publishing in open access journals such as Madagascar Conservation & Development wherever possible, putting articles up on servers such as ResearchGate or Academia.edu, or in university repositories all increase the value of research to society. There is growing evidence that such practices, perhaps unsurprisingly, also increase the citations a paper receives (Gargouri et al. 2010, Niyazov et al. 2016). As academics are increasingly judged by metrics such as citations (Lane 2010, Burrows 2012), this may act as extra incentive to make research available.

WHAT CAN THE MALAGASY AUTHORITIES DO? Where research permits have been granted for research in terrestrial protected areas, the Ministry collects final reports. These are returned in hard copy to the protected area where the research was conducted. However, such reports may go missing, may not be well archived at the site, and also, may have relevance beyond the site where the research was carried out. For these reasons, we strongly encourage the Ministry to develop an electronic submission and archiving system with a searchable web-interface. Strong incentives need to be put in place to ensure that researchers who have been granted a research permit do return their final reports in both printed and digital forms. For example, new applications should not be granted without a check that previous research reports have been submitted.

Funders of research in many countries are starting to request that raw data is archived to maximise the value of research for future research or management (Molloy 2011). The Malagasy government may consider moving towards requesting that research projects archive data in publicly available repositories. However, it is important to note that data cleaning and preparation for archiving can take many months or even years in the case of biological inventories where taxonomic work is needed. Therefore, it may be difficult to require archiving but it should be explicitly encouraged.

CONCLUSION

Managing a protected area in Madagascar to maintain its incredible ecological value while considering the livelihoods and needs of surrounding populations must be one of the most difficult, but also most important, jobs in conservation. In order to increase efficiency and efficacy, Madagascar's protected area managers therefore need access to the best possible information to inform their decisions. Increasing communication between researchers and protected area managers could increase the applied relevance of research conducted in Madagascar's protected areas. There is much that researchers can do to make their research more likely to be used and if all researchers in Madagascar (whether students or leaders of sizable research projects) were to follow the steps we outline here, we argue that much more of the research conducted in Madagascar could contribute to effective conservation management. This would benefit Madagascar's protected area managers, researchers themselves, and most importantly the protected areas and their local populations.

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SUPPLEMENTARY MATERIAL.

Available online only.

Table S1. Information about the protected areas in Madagascar considered in this work, the IUCN category (cat), size (area), type of organisation (org) leading the management, and the number of respondents who completed the questionnaire (quest) or took part in a semi-structured interview (int).

Supplementary Material 2. Understanding the use of research results in protected area management in Madagascar. A questionnaire.

Figure S3. The location of all the protected areas in Madagascar (green dots indicate protected areas for which we have responses to the questionnaire (left) or the interviews (right). The size of the mark corresponds to the number of responses from a PA (the maximum was 4). Red dots indicate protected areas from which we have no response).

Table S4. Resources which can help managers access research results.

ARTICLE

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An evaluation of the interactions among household economies, human health, and wildlife hunting in the Lac Alaotra wetland complex of Madagascar

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ABSTRACT

In Madagascar, wildlife conservation and human food security and nutrition are deeply interconnected as many people rely on wild foods for sustenance. The Lac Alaotra wetland complex is an ecoregion which is indispensable to both the future food security of Madagascar's people and the conservation of its endemic wildlife. The region is Madagascar's largest rice production area, providing thousands of tons of rice and fish to the residents of one of the world's least food secure nations. The wetland complex also provides habitat to numerous threatened species, including two Critically Endangered mammals found only in the Lac Alaotra wetland complex. Environmental managers must understand how people affect their local environment and how the environment, in turn, affects these people, their livelihoods, and their motivations for future natural resource use. Without an adequate understanding of the complex interactions of local people and their natural environment, it will be impossible to prevent, mitigate, or adapt to future unwanted changes in this complex social-ecological system. We used health assessments of 1953 residents and semi-structured interviews of members of 485 households in 19 communities within the Lac Alaotra wetland complex to investigate human-environmental interactions (including current natural resource use and hunting, and how these behaviors affect local economies and human wellbeing). Our team found that, while rates of wildlife consumption were very low throughout the region, the members of 485 surveyed households ate 975 mammals in 2013, including at least 16 Alaotra gentle lemurs. Thirteen percent of households had consumed wildlife in 2013 and less than 1% of hunted wildlife was sold. Employment rates and annual income were both higher than other regions in Madagascar, and food costs were comparatively low. Nevertheless, 98% of households experienced food insecurity, and coping mechanisms (e.g., reducing portion sizes) appear to disproportionately affect young children and non-working members of households. Half of households did not receive the minimum recommended kilocalories per person per day. We found high rates of child malnutrition consistent with national rural statistics. While wildlife consumption does not appear to have significant economic or health benefits in the communities in the Alaotra wetland complex, high food insecurity significantly increased the number of forest and marshland mammals eaten by households. To improve child nutrition and wildlife conservation, we recommend targeted interventions that improve food security.

RÉSUMÉ

À Madagascar, la conservation de la faune, la sécurité alimentaire et la nutrition humaine sont étroitement liées, car de nombreuses personnes dépendent des aliments sauvages pour leur subsistance. Le complexe des zones humides du lac Alaotra est une écorégion indispensable à la fois pour la sécurité alimentaire future de la population malgache et pour la conservation de sa faune endémique. Cette région est la plus grande zone de production de riz de Madagascar, fournissant des milliers de tonnes de riz et de poissons aux habitants de l'un des pays les plus touchés par l'insécurité alimentaire. Ce complexe des zones humides abrite également de nombreuses espèces menacées, notamment deux espèces de mammifères gravement menacées de disparition qui ne se trouvent que dans les zones humides du lac Alaotra. Les gestionnaires de l'environnement doivent comprendre comment les gens affectent leur environnement local et comment l'environnement, à son tour, affecte ces personnes, leurs moyens de subsistance et leurs motivations pour l'utilisation future des ressources naturelles. En l'absence d'une compréhension adéquate des interactions complexes entre les populations

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locales et leur environnement naturel, il sera impossible de prévenir, d'atténuer ou de s'adapter aux futurs changements qui pourraient être néfastes dans ce système socio-écologique complexe. Nous avons conduit des évaluations sanitaires auprès de 1953 personnes, et des entrevues semi-structurées auprès de 485 ménages dans 19 communautés du complexe des zones humides du lac Alaotra pour étudier les interactions entre l'homme et l'environnement (y compris l'utilisation actuelle des ressources naturelles et la chasse, et comment ces derniers affectent le bien-être). Bien que le taux de consommation de la faune soit très faible dans toute la région, nous avons constaté que les membres des 485 ménages qui ont fait l'objet de nos enquêtes ont consommé 975 mammifères en 2013, dont au moins 16 Hapalémurs du lac Alaotra. Treize pour cent des ménages avaient consommé des animaux endémiques au cours de l'année 2013 et moins de 1% des animaux chassés avait été vendu. Les taux d'emploi et le revenu annuel étaient tous les deux plus élevés que dans les autres régions de Madagascar, et les coûts alimentaires étaient relativement bas. Néanmoins, 98% des ménages ont souffert de l'insécurité alimentaire, et les mécanismes d'adaptation (par exemple, la réduction de la taille des portions) semblaient affecter de manière disproportionnée les jeunes enfants et les membres des ménages qui ne travaillaient pas. La moitié des ménages n'avait pas reçu les kilocalories minimales recommandées par personne et par jour. Nous avons trouvé des taux élevés de malnutrition infantile, cette situation étant conforme avec les statistiques rurales nationales. Bien que la consommation d'espèces sauvages ne semble pas avoir d'avantages économiques ou sanitaires significatifs dans les communautés du complexe des zones humides de l'Alaotra, l'insécurité alimentaire élevée a augmenté de manière significative le nombre de mammifères forestiers et des zones humides consommés par les ménages. Pour améliorer la nutrition des enfants et la conservation de la faune, nous recommandons des interventions ciblées qui améliorent la sécurité alimentaire.

INTRODUCTION

In Madagascar, wildlife conservation, human food security and nutrition are deeply interconnected as many people rely on wild foods for sustenance (Golden et al. 2011, 2016). Madagascar ranks within the ten least food-secure countries in the world (The Economist Intelligence Unit 2016). Poverty and food-price inflation are significant barriers to national food security (EIU 2016). Because of market-based barriers to food access, natural resources serve as a safety net for Malagasy households (Kremen et al. 1999, Golden et al. 2012, 2016, Borgerson et al. 2016), in a country where more than 92% of people live on less than $US 2/day (World Bank 2013) and where diets are lacking in diversity and foods rich in micronutrients and high quality sources of protein (The Economist Intelligence Unit 2016). One especially controversial safety net is the hunting of lemurs for food throughout the island (e.g., Golden 2009, Jenkins et al. 2011, Borgerson 2015, 2016, Golden et al. 2016, Reuter et al. 2016a). This hunting has economic (Golden et al. 2014a) and health benefits (Golden et al. 2011) and in some regions, poverty, poor health, and child malnutrition can best predict an individual's decision to hunt lemurs (Borgerson et al. 2016). For the successful integration of adaptive public health and environmental policy, it will be necessary to understand the use of natural resources and the extent to which humans depend on them on a site-by-site basis.

The Lac Alaotra wetland complex is indispensable to both the future food security of Madagascar's people and the conservation of its endemic wildlife. The region is Madagascar's largest food production area, producing 300,000 tons of rice and 2500 tons of fish (Plan Régional de Développement 2005) to the residents of one of the world's least food secure nations. The complex also provides habitat to numerous threatened species, including two Critically Endangered (CITES 2014) mammals found only in the Lac Alaotra wetland complex: the Alaotra gentle lemur (*Hapalemur alaotrensis*) (Andriaholinirina et al. 2014, Waeber et al. 2017, 2018a,b) and the recently described euplerid *Salanoia durrelli* (Durbin et al. 2010). The human population of the Alaotra region is rapidly growing and has affected the lake and its freshwater marshes through water eutrophication and hypoxia (Lammers et al. 2015), land clearing and erosion (Lammers et al. 2015) and the introduction of invasive species (Andrianandrasana et al. 2005, Rakotoarisoa et al. 2015). Further, land-use practices, including the clearing of vegetation (which increases water evaporation and the erosion of shore sediment) and the diversion of water for the irrigation of rice fields, have reduced the lake to one-third of its original size (Bakoariniaina et al. 2006). Land-users in the Alaotra face difficult decisions when coping with these changes in the environmental system, and adaptation is largely reactive and not proactive (Reibelt et al. 2017a, Stoudmann et al. 2017). Environmental managers must understand how people affect their local environment and how the environment, in turn, affects these people, their livelihoods, and their motivations for future natural resource use. Without an adequate understanding of the complex interactions of the local people of the Alaotra and their natural environment, it will be impossible either for mangers or local residents to prevent, mitigate, or adapt to future unwanted changes in this complex social-ecological system. Here, we present the results of a five-month assessment of communities in the Lac Alaotra wetland complex of Madagascar where we collected data concerning conservation relevant human behaviors in order to understand: (i) the current status of household economics, health and food security; (ii) the current levels of environmental pressure; (iii) whether variation in household socio-economics and health affects natural resource use; and (iv) whether variation in natural resource use has significant human welfare consequences.

METHODS

STUDY SITE. Lac Alaotra and its surrounding freshwater marshes and wetlands cover 43,000 hectares of habitat which border human settlements and degraded lowland sub-humid tropical forests in the northeastern region of Madagascar's high plateau. Our study was conducted in 19 villages within the Lac Alaotra wetland complex. The principal ethnolinguistic group is Sihanaka and the principle economic activity of local people is agriculture, which is supplemented primarily by fishing, wage labor, and sales (this study). Numerous NGOs including Durrell Wildlife Conservation Trust, GERP (The Madagascar Primate Group), and Madagascar Wildlife Conservation have worked extensively in the region, supporting the conservation efforts for the Alaotra gentle lemur (*Hapalemur alaotrensis*) since 1994 and community-based participatory ecological monitoring since 2001 (Andrianandrasana et al. 2005, Ralainasolo et al. 2006). Madagascar Wildlife Conservation manages the 85 hectare Park Bandro on the eastern side of the lake (Rendigs et al. 2015) and Madagasikara Voakajy manages a network of 7 newly created protected areas in the Alaotra-Mangoro region, protecting more than 30,800 hectares (Madagasikara Voakajy 2017).

SURVEY PROTOCOLS. Between August and December of 2014 MAV and TV surveyed 485 households, including 1953 individuals, in 19 communities surrounding Lac Alaotra. They consulted with the local community leaders and then held a local community meeting to discuss the goals of the project before beginning household interviews in each village. During the community meetings, the research was described as an effort to understand the ways in which natural resource use and agricultural activities contributed to human food security, health and general wellbeing.

Households were selected by one of two methods: (i) if a household census existed at the community level (often maintained by the president of the community), then the local research team selected every third household to participate; or (ii) if no household census existed in the community, then the research team selected every third household that they passed in the community. Each head of household consented to participate in the research survey. We interviewed either the male or female head of each household to gather information on household demographics, diet, food security, agricultural labor, livestock raising and diseases, income generation, commercial good ownership, taste preferences, natural resource use, and hunting behavior. Commercial goods included shoes, bicycles, radios, watches, flashlights, and guns. In general, we asked interviewees to recall events over the prior year as this had been demonstrated to be successful with regard to wildlife harvest surveys historically (Golden et al. 2013). Food security was determined using the Coping Strategies Index (CSI) (CARE 2008), a tool which asks household members to report the number of days during the prior week they used various coping strategies to deal with household food insecurity. In addition to questions administered solely to the head of household, we recorded the sex, age (to the nearest year), and occupation of each household member. We also collected data on the health of all available individuals in the surveyed households (1953 individuals within these 485 households), this included specific health information including anthropometric data (height and weight), history of malaria episodes, history of deworming medication, and hemoglobin and blood oxygen level obtained using a portable hemoglobinometer (Rainbow Pulse CO-oximeter from MASIMO). This simple, non-invasive hemoglobinometer uses photospectrometry rather than a blood sample to assess hemoglobin levels. Focus groups were also conducted in each village to determine how to weight the coping strategies used in the CSI (CARE 2008) based on cultural perceptions of the severity of food insecurity. During these focus group meetings, we also recorded information on poultry disease, cost, husbandry, and mortality.

VARIABLE CREATION AND ANALYSIS. All data were analyzed in JMP (www.jmp.com). Simple summary statistics were calculated for most forms of environmental resource use and sociodemographic variables. Thresholds from the Centers for Disease Control and Prevention (CDC) (2000) were used to calculate the prevalence of stunting, underweight, and wasting or low BMI for age in children and young adults age 2–20. We used WHO (2011) guidelines for hemoglobin cut-offs when determining anemia in children and adults. Children under 59 months were considered anemic if their hemoglobin values were less than 11.0, 5–11 year-olds if less than 11.5, 12–14 year-olds if less than 12.0, women 15 years and older if less than 12.0, and men 15 years and older if less than 13.0. Dietary diversity was measured using the Women's Dietary Diversity Score (WDDS) (Kennedy et al. 2010) and nutrient composition and the caloric content of foods were calculated using Stadlmayr et al. (2012). The fatality rates of diseases and illnesses afflicting livestock were calculated by dividing the number of animal deaths reported for a given disease over the prior year by the number reported to have been afflicted by that disease. We used a partition analysis to characterize food-secure and -insecure households. We analyzed the effect of wildlife consumption on child malnutrition and hemoglobin levels using an established generalized linear mixed model where all children were clustered at the level of the household (Golden et al. 2011). The deviation from the minimum recommended hemoglobin level was an untransformed continuous outcome variable that controlled for the age and sex of the individual and wildlife consumption was a log10+1 transformed continuous explanatory variable. We controlled for household income (log10+1 transformed) and food insecurity (roughly normally distributed and determined using CSI methods). Hemoglobin levels and the z-scores for child growth in this population were roughly normally distributed and did not require transformation.

RESULTS

In the 485 surveyed households in the Lac Alaotra wetland complex, mean household size was 3.75 individuals (median 4). Just less than half of the population (41.7%) was less than or equal to 16 years of age and 8.2% were under age 2.

HOUSEHOLD ECONOMY. The principal economic activity of local people was agriculture, which was supplemented primarily by fishing, wage labor, and sales. Household income was high; households earned an average of 1,632,402 Malagasy Ariary (MGA) (or approximately $US544.13 using conversion rates at the time of study) in the prior year (median 1,105,000 MGA ($US386.33); SE 2,255,363 MGA ($US751.79)). This provided an average income of 488,164 MGA ($US162.72) per person during the prior year (median 287,500 MGA ($US95.83); SE 733,634 MGA ($US244.54)). Almost 16% of households reported earning cash income on a consistent daily basis, and more than 99% of households reported cash income in the prior year. Of all economic activities, the highest percentage of households (73.6%) sold rice in the prior year, yet the sale of rice crops supplied only 13.2% of all forms of income earned. Rice production was supplemented with earnings from other crops (23.7% of all income earned: 41.5% of which was from beans), sales of market goods and prepared foods (18.4%), salary and wages earned through services (15.9%), fish and other aquatic animals (14.4%), forest or marshland products (6.9%), livestock products (6.5%), and woven goods (1.1%).

Malagasy people often reside in a seasonal home, or *lasy*, close to their rice fields during the harvest season; however, a minority of the Alaotra population (15.1%) made any use of *lasy* during the prior year. Living in a *lasy* peaked during June at the height of labor demands for swidden agriculture (46.6% of all lasy were occupied during this time). The average *lasy* was a 2.5 hour walk from the center of the community (SE: 1.9 hours) with a maximum distance of 15 hours. Therefore, the average *lasy* was approximately 10.73 km away if we estimate time-distance relationships and expect normal walking speeds (Ralston 1958). This is likely an overestimate due to the challenging terrain.

HEALTH AND FOOD SECURITY. We found a high prevalence of child malnutrition (Table 1) and a mild prevalence of anemia throughout all sub-populations measured in the Alaotra region. Approximately 12.1% of children 2–5 years of age (N=91), 6.6% of children 6–11 years of age (N=271), 9.9% of women 12 and older (N=615) and 8.7% of men 12 and older (N=516) were affected by anemia. Only 9.0% (135 of 1493) of all observed subjects were anemic. We found no significant differences between males and females in their prevalence of anemia.

The most frequently reported mechanisms for coping with food insecurity were to reduce the number of meals eaten in a given day (45% of all incidences of coping strategies used), harvest immature crops (26%), and restrict consumption of food by non-working household members in order to feed working members (14%). Rarely reported strategies included hunting wildlife (5%), eating next years' seed stock (3%), harvesting wild vegetables (2%), borrowing food (1%), eating at friends or families (1%), limiting the portion size of all household members (1%), reducing the portion size of food given to adults in order to feed children (1%), purchasing food on credit (1%), and begging for food (<1%). Only two coping strategies were not reported to have been used during the prior week; these were to reduce the portion size of food given to adults in order to feed children, and to not eat for an entire day and night.

Only 54.8% of people ate the minimum recommended number of kilocalories (kcal) per day during the prior week. This is perhaps not surprising given that CSI results show that 47.3% of households restricted the food consumption of non-working household members to feed working household members an average of 3.42 days over the prior week, or half of all days. The number of kcal consumed per person significantly decreases with household size (F=129.06, R2=0.23, DF=440, p<0.0001). Rice accounted for an average of 52% (± 16.33%) of the daily kcal consumed. Further, the number of cups of rice a person eats per week significantly predicted that individual's kcal consumption (F=1095.09, R2=0.71, DF=457, p<0.0001) and CSI (F=25.56, R2=0.07, DF=358, p<0.0001). Income per person (transformed using $\log_{10}$) significantly predicted that individual's consumption of rice (normally distributed) (F=80.01, R2=0.15, DF=451, p<0.0001). A partition analysis showed that food security was in fact best predicted by the ownership of commercial goods, yearly income, and household size, although these factors only explained 20% of the household variation in food security (R2=0.20, n=360, n splits=3). Food secure households were best characterized by their ownership of more than five commercial goods, having more than one adult (aged 17–39), and a combined income of greater than 1,000,000 MGA per year (highly variable exchange rate, but roughly $US330 at the time of data collection). When controlling for household income, household food security is significantly negatively correlated with child wasting (T=-3.10, P=0.003).

Table 1. Percentages of individuals classified as stunted, underweight, and wasted in villages within the Alaotra wetland complex. (Children are defined as stunted, underweight, or wasted if their height-for-age, weight-for-age, weight-for-height, or BMI-for-age is more than two standard deviations below the CDC (2000) Child Growth Standards median.)

Age range (yrs)	Sex	Sample size (n)	Stunted	Underweight	Wasted
2<5	Male	74	29.50%	29.70%	28.40%
2<5	Female	59	27.10%	22.00%	16.90%
5<12	Male	164	23.80%	15.20%	7.90%
5<12	Female	143	21.00%	15.40%	8.40%
12<20	Male	123	48.00%	14.60%	3.30%
12<20	Female	139	35.30%	14.40%	2.90%
2<20	Male & Female	759	31.40%	17.70%	9.00%

Pork and chicken comprised 57% and 29% (respectively) of all individuals' number one top taste preference for all animal-source foods, including wildlife, and nearly 19% and 17% of all top-ranked food choices (Table 2). Eighty-six percent of measured households ate at least one source of fish or meat in the prior week, and 50% ate the meat of domestic animals. On average, chickens were the most commonly owned domestic livestock, followed by ducks (Table 3). Focus groups in each village reported that chicken meat cost an average of 3,736 MGA per kilogram (just over $US1), and duck meat cost 5,444 MGA per kg (just under $US2). Duck meat was reported to be more expensive than chicken meat because duck husbandry comparatively requires a higher financial and time investment.

Fifty-three percent of households owned chickens which died from disease during the prior year. All deaths were reported to be caused by a disease locally referred to as *barika* or *moafo*. The epidemiology of the disease, including its symptoms and timing (peaking during the holiday season of Christmas through the New Year), is consistent with Newcastle disease. The estimated fatality rate was 79%. Ducks were also reported to be affected by *barika* or *moafo* with symptoms consistent with Duck cholera. The fatality rate for ducks across all diseases was 80%. Four percent of households in the Alaotra had pigs that contracted a disease during the prior year. Locally, this disease was called *pesta* and was characterized by a loss of appetite, being unable to stand, having foamy mouth, being cold to the touch, and vomiting. The fatality rate for *pesta* was 83%. Zebu were affected by *viky* (worms) and *dinta* (flukes). Of the thirty-eight cases where manifestations were severe, only one led to the premature death of the animal.

Table 2. Reported taste preferences of heads of households in the Alaotra wetland complex. Taste preference rankings could not tie (1=most preferred meat, 2=second most preferred, and so on).

	Number of times each animal received a given ranking									
Ranking in Taste Preference	Chicken	Pork	Beef	Goose	Fish (*Tilapia* spp.)	Carnivoran (*V. indica*)	Lemur (*H. alaotrensis*)	Bushpig (*P. larvatus*)	Tenrec (*T. ecaudatus*)	Tenrec (*S. setosus*)
1	21	41	5	0	5	0	0	0	0	0
2	6	15	38	5	6	0	0	2	0	0
3	13	11	20	19	8	0	0	1	0	0
4	23	3	7	25	8	1	2	2	1	0
5	2	4	2	16	31	1	1	1	4	1
6	1	0	0	2	7	1	2	0	8	2
7	1	0	0	1	2	0	0	0	6	2
8	0	0	0	0	0	0	1	0	2	3
9	0	0	0	0	0	0	0	0	0	1
TOTAL	67	74	72	68	65	3	6	6	21	8

Table 3. The range and mean of household pets and livestock assets in communities surrounding the Lac Alaotra wetland complex.

Type of livestock	Cows	Pigs	Ducks	Chickens	Geese	Cats	Dogs
Range (#/household)	0–32	0–50	0–105	0–70	0–50	0–4	0–5
Mean (#/household)	1.41	0.70	3.09	10.07	2.67	0.24	0.48

NATURAL RESOURCE USE. Eighty-five percent of the population relied on firewood for cooking and harvested it themselves daily. Individuals spent a median of 30 minutes (mean of 47.3 ± 37.5 minutes) to collect firewood, and only 3.7% of collected firewood was sold. We found a high dependence on the forest for natural products that can create shelter; 6.3% of households had harvested timber (even if just one piece of wood) and 47.0% had collected thatch roofing in the prior year. While 61.7% of timber was sold, only 4.5% of thatch was sold. Households traveled a median of 60 minutes (mean of 77.6 ± 40.3 minutes) to collect timber and 90 minutes (mean of 107.9 ± 68.7) to collect thatch roofing. There was a low prevalence of local people (5%), who relied on the forest and marshlands for ethnobotanical healthcare (e.g., by collecting plants for the preparation of traditional medicines), but those who used it harvested these traditional medicines at a median rate of two times per week (mean 1.9 ± 1.3). They collected these ethnomedicines at a median distance of 12.5 minutes from the home (mean of 25.0 ± 59.1 minutes). Only 2.5% of households had collected honey in the prior year and honey was collected a median of two hours from their homes (mean of 95.0 minutes ± 36.7). Just over one percent of households had collected precious stones and metals (including sapphires, rubies, and gold); these were collected a median of five hours from the collector's home (mean of 612.0 minutes ± 26.8).

There were distinct gender roles in the collection of some natural products. While firewood was collected by both adult men and women in the household (38.4% and 40.7% respectively), the collection of precious stones and metals, honey, timber, and thatch were predominately male activities (men collected 100%, 90.9%, 88.9%, 61.2% of these products), and the collection of traditional medicinal plants was predominantly a female activity (75.0% of all collection was done by women).

One in eight households (12.8%) ate wildlife during the prior year. Of the 975 mammals eaten by the members of 485 surveyed households, 97.2% were tenrecs, 1.6% were lemurs (specifically the Alaotra gentle lemur; *Hapalemur alaotrensis*), and 1.2% were introduced carnivorans (the Indian civet; *Viverricula indica*) (Table 4). The average household reported eating a median of one forest mammal during the prior year (mean of 2.0 ± 43.4; Table 4). One in ten households (9.9%) ate tenrec meat during the prior year. Of households that ate tenrec meat, each household ate a median of 1.5 tenrecs (mean of 19.7 ± 48.6). Only 2.5% of households ate lemurs during the prior year. Of those households that ate lemur meat, each household ate a median of one lemur (mean of 1.3 ± 0.9) during the prior year. Carnivoran hunting was even less frequent, with 1.2% of households participating, with each household that hunted eating a median of two carnivorans during the prior year (mean of 2.0 ± 0.9). No one surveyed reported eating endemic carnivorans (Euplerids), bats (which were reportedly rarely seen), or tenrecs other than the species *Tenrec ecaudatus* during the prior year.

At least 73.5% of hunting was conducted illegally either because of national prohibitions against hunting (e.g., lemurs) or prohibited equipment (e.g., hunting tenrecs using dogs), according to the most recent updates to legislation (Decree number 2006-400). However, it is important to note that this prior year recall data may include animals that may be legal to hunt but were not hunted during the legal season. The hunting of lemurs is strictly prohibited and the hunting of tenrecs is only authorized during the day, without dogs or other prohibited equipment, between 1 April and 31 May (Ordonnance No 60-126 from Oct. 3, 1960). Most hunting was targeted pursuit hunting (710 of 975 mammals caught).

Only one of 485 surveyed households owned a shotgun and the remaining households predominately used dogs to hunt wildlife. Pursuit hunting was supplemented by snare trapping using natural products (199 animals), and opportunistic hunting (16 animals). Members of households ate 47 forest mammals at the household of a family member or friend during the prior year and purchased only 3 animals (which were bartered using rice for payment, Table 4).

Table 4. The volume of mammalian wildlife consumption in communities within the Lac Alaotra wetland complex, disaggregated by hunting method. The volume of consumption was reported based on the head of household's recall of number of animals consumed during the prior year. (Local people reported an absence of bush pigs (*Potamochoerus larvatus*) in the region. No members of surveyed households ate the meat of bush pigs during the prior year, yet it was listed among preferred foods (Table 2).)

Species	Local name	Total consumption (n)	Pursuit hunting	Trapping	Opportunistic hunting	Eaten with friends or family	Purchased
TENRECS							
Tenrec ecaudatus	Trandraka	947	74.00%	19.00%	1.70%	5.00%	0.30%
Setifer setosus	Sokina	0	-	-	-	-	-
BATS							
Pteropus rufus	Fanihy	0	-	-	-	-	-
EUPLERIDS							
Eupleres goudotii	Fanaloka	0	-	-	-	-	-
Cryptoprocta ferox	Fosa	0	-	-	-	-	-
Galidia elegans	Vontsiramena	0	-	-	-	-	-
Galidictis fasciata	Vontsirafotsy	0	-	-	-	-	-
Salanoia concolor	Vontsira	0	-	-	-	-	-
LEMURS							
Cheirogaleus major	Tsitsihy	0	-	-	-	-	-
Avahi laniger	Fotsife	0	-	-	-	-	-
Daubentonia madagascariensis	Hay-hay	0	-	-	-	-	-
Hapalemur occidentalis	Bokombolo	0	-	-	-	-	-
Hapalemur alaotrensis	Bandro	16	43.80%	56.30%	0.00%	0.00%	0.00%
Eulemur rubriventer	Barimaso	0	-	-	-	-	-
INTRODUCED SPECIES							
Viverricula indica	Jaboady	13	23.10%	76.90%	0.00%	0.00%	0.00%

INTERACTIONS. Forest mammal consumption (the number of forest or marshland mammals eaten by household members during the prior year) was significantly negatively correlated with household food security (R^2=0.15, DF=54, F=5.56, p=0.02). In fact, in a multiple linear regression on the effects of household size, income, food security, and the health of household members (rates anemia), only food security significantly predicted the number of forest mammals that household consumed in the prior year (t=2.35, p=0.02). Unsurprisingly, with very low rates of wildlife harvest locally, we did not find an effect of wildlife consumption on anemia here (generalized linear mixed model, p=0.84).

When investigating the conservation impact of the presence of a protected area, we found that wildlife harvesting in each village increased by approximately one animal per household per year (bivariate linear regression model; r^2=0.30, F=7.13, DF=18, p=0.02) per hour of travel time from a protected area. Forest mammal catch continued to increase (albeit moderately) with increasing distance from the park, even when controlling for distance from the forest (multiple linear regression model; R^2=0.33, F=3.99, DF=18, p=0.04), although it is possible that this difference may be due to reduced reporting near park borders.

DISCUSSION

CURRENT STATUS OF HOUSEHOLD ECONOMICS, HEALTH AND FOOD SECURITY. Madagascar is a highly food insecure country with one of the highest rates of stunting in the world (The Economist Intelligence Unit 2016, International Food Policy Research Institute 2016), and the Lac Alaotra wetland complex is a key region in securing the food security of Madagascar's people (Plan Régional de Développement 2005). We found that employment rates and yearly income were both higher in Alaotra than other regions in Madagascar, and food costs were comparatively low (Golden et al. 2014b, Borgerson et al. 2016). The yearly income of residents of Alaotra was nearly four times that of Betampona (Golden et al. 2014b), and 16% of all households in Alaotra contained a member earning daily wages. Further, incomes may have also risen significantly in the prior decade as households in 2013 reported annual incomes three times those reported in 2005 (Ministère des Finances 2006). Yet 98% of households experienced food insecurity, and coping mechanisms appear to disproportionately affect young children and non-working household members. Half of households did not receive the minimum recommended kilocalories per person per day, and nearly half restricted food consumption by non-working household members. We found high rates of child malnourishment. However, the prevalence of child malnutrition is consistent with, even slightly lower than, that across rural Madagascar (18% stunted, 31% underweight, and 9% wasted in Alaotra vs. 50%, 38%, and 14% nation-wide (WHO 2012, rural Madagascar data)). Rates of anemia were lower than those found in Makira (Golden et al. 2011), but consistent with rates found in Betampona, another area of Madagascar with low rates of wildlife harvest (Golden et al. 2014b).

Consistent with previous studies across Madagascar (Golden et al. 2014b, Reuter et al. 2016a) and in the Alaotra region (Jenkins et al. 2011) the meat of domestic animals was preferred over the meat of wild-caught mammals. People ate the meat from domestic animals more often than those in northeastern Madagascar (Borgerson 2016); 50% of households in Alaotra ate the meat of domestic animals in the prior week. As found in other regions of Madagascar (e.g., Golden et al. 2014b, Rasamoelina-Andriamanivo et al. 2014), poultry were negatively impacted by Newcastle disease, albeit at a slightly lower fatality rate; 79% in Alaotra vs. 96% in Betampona. Newcastle disease outbreaks can have significant impacts on household economies in Madagascar (Rasamoelina-Andriamanivo et al. 2014), and controlling Newcastle disease has been identified as a potential means to both reduce wildlife hunting and improve household nutrition, food security, and economy (Alders and Pym 2009, Golden et al. 2014a). Targeted efforts to identify Newcastle disease early at key node live-bird markets have been recommended for the early identification and control of a Newcastle disease outbreak throughout the Alaotra region (Rasamoelina-Andriamanivo et al. 2014).

CURRENT LEVELS OF ENVIRONMENTAL PRESSURE. Communities in the Lac Alaotra wetland complex were less dependent on forests and marshlands for access to nutritious foods, housing materials, and healthcare than in other areas of Madagascar, and people traveled further to access these resources (Golden et al. 2014b, Borgerson 2016). Overall, few people ate wild mammals during the prior year and those households ate species with high reproductive capacities (and thus high population resilience). As is true in other regions of Madagascar (Razafimanahaka et al. 2012, Golden et al. 2013, 2014a,b, Borgerson 2016, Reuter et al. 2016a), tenrecs were the most commonly hunted forest mammal in the area. *Tenrec ecaudatus* comprised more than 97% of household wildlife consumption by biomass. *T. ecaudatus* is a Least Concern (Stephenson et al. 2016) game species that can be legally hunted in Madagascar, albeit only during open season and without the use of dogs (Decree Number 2006-400, Ordonnance Number 60-126). However, at least 73.5% of all hunting was conducted illegally in the Alaotra region (primarily from using dogs to hunt tenrecs). Particularly concerning, however, was the hunting of Critically Endangered Alaotra gentle lemurs (*Hapalemur alaotrensis*). The surveyed households ate 16 of the remaining population of Alaotra gentle lemurs during the prior year. While population estimates are uncertain, as few as 2500 Alaotra gentle lemurs may remain in the wild (Ralainasolo et al. 2006, Ratsimbazafy et al. 2013, Reibelt et al. 2017b).

The Lac Alaotra wetland complex has notable similarities and differences in comparison to other areas across Madagascar where hunting has been studied. While Razafimanaka et al. (2012) found that more than 70% of respondents in this region had eaten wildlife during the prior year, only 13% of the respondents in this study reported eating wildlife during the prior year. Alaotra residents ate fewer forest mammals per capita (both in total number and in range of species) during the prior year than residents in Betampona (Golden et al. 2014b), Makira (Golden et al. 2013), the Masoala (Borgerson 2016), western Madagascar (Razafimanahaka et al. 2012), or central and north-western Madagascar (Reuter et al. 2016a,b). As a relative percentage of the surveyed households, more than ten times as many households had eaten forest meat in Betampona in the prior year (Golden et al. 2014b) than had in Alaotra.

The techniques used to hunt forest mammals differed in the Alaotra from other regions in Madagascar, but similar to those found by Reuter et al. (2016b) in central and northwestern-Madagascar; hunters in the Alaotra primarily used pursuit hunting methods with dogs, whereas passive snare traps were predominantly used to trap forest mammals in Betampona, Makira, and Masoala (Golden et al. 2014a,b, Borgerson 2016). This difference is likely because most wild meat was that of *T. ecaudatus*, a species most efficiently hunted by dogs, especially in areas with degraded habitat (Golden et al. 2014b, Reuter et al. 2016b).

Deforestation and forest fragmentation can significantly affect local livelihoods (Urech et al. 2015). People within the Lac Alaotra wetland complex, a region of increasing forest fragmentation, were less dependent on the forest for natural products that can create shelter than those in the Betampona forest region (Golden et al. 2014b). Far fewer people collected timber or thatch roofing during the prior year than in Betampona (6% vs. 80%; 47% vs. 90% respectively). Fewer households relied on firewood for cooking than those in Betampona (85% vs. 96%) and household members travelled 1.5–3 times farther to collect this wood (Golden et al. 2014b). Further, Alaotra residents relied far less on forest or marshland resources for healthcare, 5% of households having harvested traditional medicines from the forest at a rate of approximately twice per week, 25 minutes from the home in Alaotra vs. 82% of households having harvested traditional medicines from the forest at a rate of approximately once per week in Betampona. Overall forest resources were less relied upon and individuals travelled further to reach them (e.g., up to five hours each way to collect forest resources of high economic value including precious stones).

Seasonal residences occupied during rice harvest, or *lasy*, were also twice as far away as those in Betampona. *Lasy* were also used by only a minority of residents; proportionally, 40% fewer surveyed residents (relatively) in Alaotra utilized *lasy* during rice harvest than those in Betampona (Golden et al. 2014b). Differences in local ecology may, however, explain much of this variation. People in the Lake Alaotra Wetland complex can also reduce biodiversity by converting marshland (as opposed to forest lands) into irrigated rice fields when confronted with insufficient rice yields (Reibelt et al. 2017b).

CONNECTIONS BETWEEN HOUSEHOLD ECONOMICS, HUMAN HEALTH, ENVIRONMENTAL PRESSURES AND HUMAN WELFARE. Wildlife harvest and consumption does not appear as critical to economic or nutritional wellbeing in the communities in the Lac Alaotra wetland complex as in other regions of Madagascar (Golden et al. 2011, 2014b). The region's financial security, strong access to rice and livestock products, degraded forest ecology, or regional conservation efforts, may explain the low rates of wildlife consumption over the prior year. Yet, food insecurity was still high, and its presence in households was positively correlated with the number of forest mammals consumed. This is consistent with other findings suggesting that improving regional food security and public health outcomes through integrated conservation and development programming may both improve environmental and human health outcomes (Barrett et al. 2011, Golden et al. 2014, Borgerson et al. 2016, Wilkie et al. 2016). Madagascar faces complex and nuanced challenges in achieving food security and reducing malnutrition. The nation has low public expenditure on agricultural research and development and food is comparatively expensive and poor in quality (The Economist Intelligence Unit 2016). Severe inflation has caused food prices to more than triple since the year 2000, and these foods are low in micronutrient availability, protein quality, and diversification (ibid). Thus, it will be necessary to find avenues to secure adequate nutrition in a way that preserves Madagascar's unique biodiversity. Further, because of the strong gender differences in the collection of some natural resources (e.g., 75% of all medicinal plant collection was done by women and 91% of all honey collection was done by men) it will be necessary to ensure that these policies and efforts strive to integrate both men and women into their approaches. To improve child nutrition and wildlife conservation, targeted interventions in the Alaotra could focus on: (1) increased tracking of nutritional outcomes; (2) nutrition-sensitive agricultural policies to increase the focus on, consumption of, and productivity of nutritious crops and small-livestock (especially in remote, hard to access villages); (3) targeted efforts to identify and control Newcastle disease through poultry vaccination; (4) micro-nutrient fortification of key imported food staples such as rice; and (5) efforts to integrate fish-rice paddy aquaculture to offset the short-term reduced nutritional access to wild fish during seasonal fishery closures (Copsey et al. 2009, Wallace et al. 2015); and (6) maintenance of lake water quality (and quantity) to facilitate fish consumption (Lammers et al. 2015). By addressing Alaotra's barriers to food security, policy makers and resource managers can improve both human health and conservation outcomes in this region of key importance to national food security and conservation.

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ARTICLE

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Potential of *Opuntia* seed oil for livelihood improvement in semi-arid Madagascar

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ABSTRACT

The coastal area of the Mahafaly Plateau in southwestern Madagascar is prone to droughts, as well as to other environmental risks, resulting in frequent crop failures, famines, and extreme poverty. Thus, the identification of potential complementary livelihood sources has been identified as a crucial step for the sustainable development of the region. In this contribution, we assess the potential of prickly pear seed oil production as an income alternative for local communities. The prickly pears are cacti in the genus *Opuntia* Mill. and they are highly abundant in the region, particularly as living fences on farmland. From the seeds of its fruit, high-priced seed oil can be extracted. To investigate its economic potential, we inventoried prickly pears in field hedgerows through vegetation inventories and estimated the amount of seed oil that could be produced per household based on field sampling and laboratory analysis. To assess the socioeconomic impact of a potential large-scale project of regional *Opuntia* seed oil production, we conducted interviews with 51 farming households on human *Opuntia* consumption, the utilization of its cladodes as fodder, and other livelihood functions.

Five different prickly pears occur in the research region. We found that two out of these five species are highly important socioeconomically (*Opuntia monacantha* and *O. streptacantha*) and contribute >50% to total food intake during periods of food shortage. Likewise, these species are consumed as a key water source and used as livestock fodder. In contrast, the other three *Opuntia* species are barely eaten by local residents or by livestock (*O. dillenii*, *O. stricta* and *O. phaeacantha*). These species are more spiny, and their fruits are virtually inedible due to a much higher seed content. The combination of low nutritional value and high seed content suggests promising seed oil production potential for these types of *Opuntia*. To avoid competition between human nutrition and the commercialization of local *Opuntia* seeds, sourcing strategies should exclusively target the fruit of the two high seed species. However, investments for oil mills, skilled staff, and adequate logistics would be needed to create local value from this underrated resource in the Mahafaly region.

RÉSUMÉ

La zone côtière du plateau Mahafaly, dans le sud-ouest de Madagascar est caractérisée par un climat sec et aride, et est sujette à des risques environnementaux à l'origine de fréquentes récoltes de moindre qualité, de famines et d'une pauvreté extrême. L'identification de moyens complémentaires a été reconnue comme un étape clé pour le développement durable de la région. Le potentiel de la production d'huile obtenue à partir des graines de figues de Barbarie (*Opuntia* Mill.) a été évalué à titre d'alternative pour générer des revenus par les communautés locales. Les figues de Barbarie sont les fruits de cactus du genre *Opuntia* Mill. qui sont communs dans la région ; les figuiers sont plus particulièrement utilisés pour servir de haies vives pour border les champs. Les graines des fruits contiennent de l'huile qui peut atteindre un prix élevé. Pour étudier le potentiel économique de cette huile, un inventaire des figuiers de Barbarie a été réalisé dans les haies vives bordant les champs, suivi d'une estimation de la quantité d'huile qui peut être extraite des graines par les ménages en procédant à des échantillonnages sur le terrain et à des analyses en laboratoire. Pour évaluer l'impact socio-économique d'un éventuel projet à grande échelle de production d'huile de graines de figues, 51 ménages ont été interrogés sur les différentes utilisations locales des figuiers de Barbarie.

Cinq espèces d'*Opuntia* ont été rencontrées sur la zone d'étude dont deux espèces (*O. monacantha* et *O. streptacantha*) sont importantes d'un point de vue socio-économique. Lors des périodes de pénurie alimentaire, elles représentent plus de 50% de l'apport alimentaire pour les gens de la région. Ces deux espèces sont aussi consommées comme une source d'eau clé et sont utilisées comme fourrage pour le bétail. Les trois autres es-

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pèces d'*Opuntia* sont à peine consommées qu'il s'agisse des gens de la région ou du bétail (*O. dillenii*, *O. stricta* et *O. phaeacantha*). Ces espèces sont plus épineuses et leurs fruits sont pratiquement immangeables en raison d'une teneur en graines beaucoup plus élevée. La combinaison d'une faible valeur nutritive et d'une forte teneur en graines suggèrent un potentiel prometteur pour la production d'huile de graines. Afin de ne pas mettre en péril les valeurs nutritives des figuiers pour les gens de la région avec la commercialisation des semences, les stratégies d'approvisionnement devraient cibler exclusivement les fruits des deux espèces qui présentent le plus de graines. Des investissements, comme ceux destinés aux huileries, un personnel qualifié et une logistique adéquate sont nécessaires pour créer une valeur locale à partir de cette ressource sous-estimée dans la région Mahafaly.

INTRODUCTION

There is an increasing global interest in prickly pear (*Opuntia* Mill.), particularly for the management of dry areas (Gebretsadik et al. 2013). Prickly pears are highly drought resistant due to their CAM physiology (Crassulacean Acid Metabolism, Sáenz et al. 2013), tolerate soil salinity well (Barbera et al. 1995, Ben Salem et al. 1996), are used to combat soil erosion (Nefzaoui and El Mourid 2007) and thrive in harsh environmental conditions in which other fruits and vegetables fail without irrigation (Han and Felker 1997). These beneficiary characteristics of prickly pear gave rise to an international *Opuntia* research and development program by the FAO (Food and Agriculture Organization of the United Nations): the FAO-ICARDA Cactus Network.

Opuntia seed oil is among the most valuable plant oils and it has become a highly attractive resource for the food, cosmetic, nutraceutical and pharmaceutical industries (Feugang et al. 2006, Moßhammer et al. 2006, Liu et al. 2009, Jana 2012, Sáenz et al. 2013, El Mostafa et al. 2014, Guillaume et al. 2015). The current prices for conventional produced *Opuntia* seed oil vary between 275 and 700 €/l, for organic oil between 900 and 1500 €/l (In litt. with 6 international *Opuntia* seed oil trading companies (see Table S8)). It is mainly produced in Morocco, Algeria and Tunisia, commonly based on *O. ficus-indica*. Due to its high share of polyunsaturated fatty acids (especially linoleic acid) and other components (tocopherols, sterols, phenolics), its seed oil is attractive for the cosmetic industry in Morocco (Sáenz 2017). However, the chemical components addressed in *Opuntia* seed oil are not exclusive to *O. ficus-indica*, but are also attributed to other species of *Opuntia. spp.* such as *O. dillenii* and *O. stricta* (antioxidants, polyunsaturated fatty acids, wrinkle-reduction effect; Stintzing and Carle 2005, Hamou 2007, Nazareno and Nefzaoui 2007, Yeddes et al. 2014), among others.

Originating from Mexico, prickly pears were introduced by colonial France to Madagascar and spread rapidly in the semi-arid south of the island (Kaufmann 2001, Middleton 2002). Prickly pears have existed in southern Madagascar for around 100 years and have naturalized (Kaufmann 2004). They are often described as invasive plants, particularly *O. stricta* (Lowe et al. 2000). Such invasive species could potentially threaten the autochthonous biodiversity of Madagascar (Kull et al. 2014). In the southern Malagasy Androy region, Larsson (2004) described *O. stricta* as an invader whereas some surveyed respondents stated that *O. stricta* is negatively impacting both livestock and human health (Larsson 2004).

However, there is no systematic description of prickly pear found in Madagascar. In addition, many prickly pears are often wrongly classified (Kiesling 1998, Binggeli 2003); crossbreedings, landrace strains and hybrids occur in Madagascar (Middleton 2009). Based on historical records and plant material stored in the Paris Museum of Natural History, Allorge and Matile-Ferrero (2011) have shown that the following prickly pears were introduced during the colonial period to Madagascar: *O. cochenillifera*, *O. dillenii*, *O. ficus-indica* and *O. monacantha*. After the eradication of *O. monacantha* due to an insect pest in the 1920s that was introduced and dispersed by the French colonisers (Middleton 1999), around ten other species of Opuntia were introduced to Madagascar in 1925 (Decary 1932).

Traditionally, prickly pears are an important plant for the livestock-based economy of the region: the cladodes of several *Opuntia* species provide dry season food and water for livestock after their thorns are burned; humans can consume the cactus pear fruit (Kaufmann 2004, Larsson 2004). In southern Madagascar, landholders traditionally plant prickly pears around villages, homesteads, cropping fields, and livestock corrals (Kaufmann 2001), occasionally also in fodder plantations (Götter 2016). The importance of prickly pears for Malagasy pastoralists is well documented. The plants increase the carrying capacity of the regional landscape by storing large amounts of water in their cladodes (up to 92% moisture content, Brulfert et al. 1984) and by generating substantial amounts of fodder biomass, complementing more strongly rain-dependent grassland biomass (Kaufmann and Tsirahamba 2006). Thus, some species of *Opuntia* are a key fodder and water source for animal husbandry in southern Madagascar (Middleton 2002, Kaufmann 2004, Larsson 2004). Some authors claim that the rise of pastoralism as a dominating regional livelihood strategy would not have been possible without the introduction of prickly pears used as cattle fodder (Middleton 1999, Kaufmann 2001). Likewise, there is evidence that prickly pear fruits provide an important food resource during the lean period for many farming households in semi-arid Madagascar. This role becomes particularly pronounced during droughts and ensuing food shortages (Kaufmann 2004, Andriamparany 2015, Noromiarilanto et al. 2016).

The human population in southwestern Madagascar is exceptionally poor. Local communities face an annual 'lean' or 'hunger' period (Malagasy: kere) from the beginning of the rainy season (November) to the annual crop harvest (April). During that period, a substantial share of the smallholder farming population runs low on subsistence food resources as well as cash, as many households have to reduce food intake to unhealthily low levels (Noromiarilanto et al. 2016, Hänke et al. 2017). With the next harvest not until weeks or even months ahead, non-farm income sources, livestock sales and the collection of wild plants are crucial to physically survive the lean season (Hänke and Barkmann 2017). One of the wild plants used intensively both by people and for livestock in Madagascar's southwest during the lean period are cactus pears (*Opuntia spp.*), also known in Malagasy as *raketa*. From the seeds of its fruit, one of the most valuable plant oils could be extracted offering an income alternative of substantial potential. Yet, little attention has been paid to the economic potential of *Opuntia*-derived products in Madagascar including the extraction of *Opuntia* seed oil.

Prickly pears have been assessed with regard to fodder quality (Nefzaoui and Ben Salem 2001, Gebretsadik et al. 2013), the chemical composition of their fruit (Tesoriere et al. 2004, Stintzing and Carle 2005, El Finti et al. 2013, Yeddes et al. 2014) and seed oil characteristics (Sawaya and Khan 1982, Ramadan and Mörsel 2003, Ennouri et al. 2005; Liu et al. 2009). In global reports, however, prickly pear seed oil content data show large variations ranging from <4% to >17% (Sawaya and Khan 1982, Coskuner and Tekin 2003, Ramadan and Mörsel 2003, Ennouri et al. 2006, El Mannoubi et al. 2009, Sáenz et al. 2013, Guillaume et al. 2015) making an extrapolation of local seed oil yields difficult. To our knowledge, analyses for fodder, fruits and seed oil of prickly pear found in Madagascar are not available to date. Likewise, little is known about (i) the quantitative abundance of prickly pear in southwestern Madagascar, and (ii) about the importance and exact uses of its different forms.

In this study, we focus on field hedges managed by farmers, where prickly pears often are planted as living fences (SuLaMa Marp 2011, Hanisch 2015). They are highly abundant, and their property rights are well defined, in contrast to e.g., communal land or wild growing prickly pears. Our research objectives are the following: (i) Identifying the different taxa of prickly pear and assess their quantitative abundance in the field hedges. (ii) Assessing the potential competition between traditional uses of prickly pear fruit, particularly during the lean season (contribution to food security, utilization as fodder, economic activities) and seed oil production. (iii) Assessing potential seed oil production per average farming household. This includes a prickly pear inventory, an estimate of fruit quantity per household, the determination of the seed content of the fruit, as well as of the oil content in its seeds. (iv) Determining the overall potential of commercialised prickly pear seeds as an alternative income source, requiring (a) a comparison of the seed oil content in a global context, and (b) consideration of accessible value chains and commercialisation options, including actual and potential uses of the by-products (e.g., fruit pulp, presscake) of prickly pear seed oil.

METHODS

Our study region covered the coastal plain of the Mahafaly Plateau in southwestern Madagascar (see Figure S1). The local population belongs to the Tanalana group. The area is semi-arid and received 200–300 mm rainfall during the years 2010–2015 (Centre National Antiacridien 2015), which is close to the limit of rain-fed arable agriculture (Kaufmann 2004). Moreover, droughts, dry spells and subsequent crop failures have become common in recent years (WFP 2015). The region belongs to the poorest and most disadvantaged areas in Madagascar (INSTAT 2011), which is itself among the ten poorest countries in the world (International Monetary Fund 2015, World Bank 2015). Water sources are scarce and the general infrastructure is weak (SuLaMa Marp 2011). Because of its high salinity, the groundwater is unsuitable for irrigation (Guyot 2002). The regional soils are sandy and of poor quality (low soil nutrients, low organic soil carbon; Andriamparany 2015, Hanisch 2015). Farmers grow cassava, sweet potatoes, maize, millet, sorghum and different leguminousous crops. Malnutrition is common in the area, with famines having occurred frequently in recent years (WFP and FAO 2014, WFP 2015, Noromiarilanto et al. 2016). With severely limited agricultural potential, off-farm income sources are crucial for a sustainable regional development. However, promising alternative income options are scarce in this remote and infrastructurally underdeveloped area of Madagascar (Hänke et al. 2017).

The region harbours unique, endemic biological diversity. The natural vegetation consists of highly specialised dry spiny forest with a plant and animal endemism rate of around 75%–90% (Fenn 2003, Jasper and Gardner 2015) and scattered *samata* trees (*Euphorbia stenoclada*). The level of endemism is among the highest in Madagascar (Fenn 2003, Gautier and Goodman 2003), which has, as such, one of the highest rates in the world (Myers et al. 2000). The research area is located directly west of the Tsimanampetsotse National Park (TNP).

OPUNTIA INVENTORY, SAMPLING AND OIL ESTIMATION. The 51 households were selected as a subset of a stratified random sample of a longitudinal, agroeconomic study conducted in 2014 (Hänke et al. 2017). Household clusters were developed based on Neudert et al. (2015) taking farm size, livestock possessing and wealth into account. We sampled the different household clusters proportionally to account for representativeness. Households were selected from three coastal villages in the sample: Efoetse, Maromatilike and Marofijery. They were selected because (i) they are all close to the national park and, therefore, receive special attention from conservation and development programs (e.g., Madagascar National Parks, World Wide Fund for Nature, and German Development Cooperation (GIZ), and (ii) some farmers had experience in selling prickly pear seeds.

The 51 households have a total of 87 fields whose hedges we inventoried. The prickly pear inventory, as well as complementing household surveys, were supported by three well-trained field assistants, and took place from February to May 2015. The prickly pear inventory consisted of five steps:

(a) Assessment of prickly pear cover in field hedges: To determine the prickly pear cover (in m^2) within the fields' hedges, the length and width of the prickly pear hedges were measured in situ and the prickly pear species was noted. To do this, we randomly selected one third of the 51 households which resulted in a subsample of 17 households, including 29 single fields. To estimate the share of the different prickly pear in the hedges (%), a rule of three was applied by using the spatial cover (m^2 per species) and the total hedge size (m^2). In addition, the total number of prickly pear plant stems was counted in the field hedges, so that we could compare our vegetation inventories with estimates done by interview respondents that were based on the number of stems.

(b) Number of fruit per household: A preliminary analysis of occurring prickly pear had indicated the presence of five taxa. One of them, a prickly pear locally called *rengevoke* (*O. phaeacantha*) was extremely rare and was therefore not considered in this study. Another form of prickly pear locally called *vilovilo* (*O. streptacantha*) was stated to be highly important as a food resource. Therefore, this form was also neglected from the succeeding analyses. In the study area, *O. stricta* var. *stricta* (Malagasy: *mavozoloke* and *raketamena*) is a low growing plant, usually 50–100 cm tall. *O. dilenii* (Malagasy: *boritotse*; synonym: *O. stricta* var. *dilenii*) is slightly taller: around 100–150 cm. *O. monacantha* (Malagasy: *notsoke* and *viromena*), however, grows far higher (up to >3 m). Due to the different growth forms, we applied two different methods for the fruit sampling.

After mapping the occurrence of the different prickly pears cacti, 30 distinct points were randomly placed in the 29 field hedges for each of the three most often occurring prickly pears. The random location of the sampling points was supported by QGIS. At the sampling points, 1 m^2-squares were delineated, and the total number of *O. dilenii* and *O. stricta* fruit were counted. Finally, to estimate the number of fruit from these two prickly pears per household, the average number of *O. dilenii* and *O. stricta* fruit / m^2 were multiplied by the spatial cover (m^2) of *O. dilenii* and *O. stricta* per household. Conversely, for *O. monacantha*, fruit sampling was done for individual plant stems instead of m^2. To do so, the total number of fruit in 30 randomly chosen *O. monacantha* plant stems was counted. Finally, the total number of *O. monacantha* fruit per household was estimated through the number of *O. monacantha* plant stems in field hedges per household, multiplied by the number of fruit per plant stem. Since our in situ analyses covered fruit production during the lean season only, we asked locals how often the different prickly pear produce fruit during the year.

(c) Seed content and seed mass determination: In order to determine the seed content per prickly pear fruit (in mass percent) and dry seed mass (in g_{dm}) per prickly pear fruit, 30 pieces of fruit from *O. dilenii*, *O. stricta* and *O. monacantha* were randomly sampled, freshly weighted, their seeds were extracted, hand washed, and the seeds were freshly weighed. In order to determine the seed content (in mass percent), a rule of three was calculated using seed mass and total weight of the fruit. Subsequently, the seeds were oven dried at 68°C for 24 hours and weighed again in order to determine the dry seed mass (g_{dm}) per piece of fruit. Seed weight (g_{dm}) and seed content (in mass percent) of the three prickly pears were compared with t-tests.

(d) Oil content determination in prickly pear seeds: Preliminary analysis had already indicated an inverse relationship in the relative seed content of prickly pear fruit and human nutritional use. Consequently, it was clear early on that only the two rather inedible, high seed content species would qualify as targets for the commercialisation of prickly pear fruit and seeds. Thus, we chose to conduct a seed oil analysis for only these two varieties (*O. dilenii* and *O. stricta*) that were sourced directly in the study villages. Consequently, we ran a laboratory analysis in order to determine the oil content (in mass percent) in *O. dilenii* and *O. stricta* seeds. A petroleum ether analysis was conducted with an ANKOM XT 15 Extraction System. Through a fatty acid spectrum analysis, the level of linoleic acid was determined and a press-cake analysis for fibre, protein and fat content was conducted (analysis performed by SGS GmbH, Hamburg, Germany).

(e) Extrapolation of the average prickly pear seed oil production per household: To estimate the potential prickly pear seed oil production per average household, first the total number of fruits per household was calculated:

$$\frac{\text{total amount of fruit}}{\text{household}} = \frac{\text{Opuntia spp. cover } (\mathrm{m}^2)}{\text{household}} * \frac{\text{amount of fruit}}{\mathrm{m}^2}$$

Then, the total seed oil (kg)/household was calculated by multiplying the total amount of fruit per household by the seed mass (dry mass) per fruit, as well as the seed oil content in mass percent:

$$\frac{\text{total seed oil (kg)}}{\text{household}} = \frac{\text{total amount of fruit}}{\text{household}} * \left(\frac{\text{seed weight}(g_{DM})}{\text{fruit}} * 1000\right) * \frac{\text{seed oil (mass \%)}}{100}$$

SURVEY. In addition to field inventories and laboratory analyses, we conducted interviews with the 51 farming households. Questions addressed included: Occurrence of prickly pear, fruiting periods and fruiting frequency per year, total number of prickly pear plant stems in their hedges. Prickly pear utilisation: Which varieties are used for human consumption and which as livestock fodder? When are the different varieties eaten by humans? How many? How much do they contribute to overall food intake? What are the reasons for the (non-) consumption of the different prickly pears? Are there negative health impacts for both, humans and livestock? Economic activities involving prickly pear: Sale of fruit, sale of cladodes as fodder, renting out access to prickly pear stands for fodder. Experience with the sale of prickly pear seeds: How much labour is needed for the collection and separation of prickly pear seeds? What would be a fair price? What could be potential conflicts (e.g., competition) arising from the commercialisation of prickly pear seeds?

IDENTIFICATION OF *OPUNTIA* SPECIES. It is challenging to accurately identify the different species of prickly pear: there are around 190 species of which many have not been sufficiently described (Rebman and Pinkava 2001). To make things even more complicated, several landraces, their crossbreeds, as well as species hybrids occur all over the world. Therefore, we asked two *Opuntia* specialists to support species identification based on pictures of the plants, flowers and spines that we provided.

Opuntia domestication began 9000 years ago and, since then, has often been divided wrongly into different species (Kiesling 1998). E.g., *O. ficus-indica* occurs in variable forms, mainly because of extensive selections for new types/varieties for more than 400 years (Helmuth Zimmermann pers. comm.). Indeed, *O. ficus-indica* has been bred and introduced as a spineless form in many parts of the world, however, the plant has gradually converted back to the spiny form through gene recombination and selection (Helmuth Zimmermann pers. comm.). The locally called species *vilovilo* is a spiny *Opuntia* form, that also occurs in South Africa (Obermeyer 1976). It was previously wrongly classified as *O. megacantha* (Kiesling 1998). Lucas Majure (In litt.) identified this species more precisely as *O. streptacantha* belonging to *O. ficus-indica sensu lato*.

RESULTS

OCCURRENCE OF *OPUNTIA* SPP. A total of five different prickly pears were found in the field hedges investigated (see Table S2). One species (*Opuntia phaeacantha*) was extremely rare and was, therefore, omitted from the subsequent analysis. *O. dilenii* was said to produce fruit several times a year and all year long. However, it was not possible for local respondents to state exactly how often. Indeed, we encountered *O. dilenii* plants with no flowers, with flowers, mature, as well as with young fruit at the same time during our fieldwork.

IMPORTANCE OF *OPUNTIA* SPP. FOR HUMAN NUTRITION AND LIVESTOCK FODDER. Concerning nutrition, the respondents listed *Opuntia monacantha* and *O. streptacantha*, as most important for human consumption (Figure 1). According to respondents surveyed, this is due to the low seed content of its fruit. In contrast, *O. dilenii* and *O. stricta* have a high seed content. Our respondents reported that the fruit of these species tastes bad and that consumption results in digestive problems, particularly constipation. Also, *O. streptacantha* is less spiny, and thus its fruit is easier to harvest and consume.

Households collect *O. monacantha* and *O. streptacantha* mainly between October and April, that is, during the lean season. Around 78% of households collect mostly in March, and 12%

mostly in April, which, according to local respondents, is the climax of the lean season where many households run out of food and cash (Hänke et al. 2017). During the lean season, local farmers consume *O. monacantha* and *O. streptacantha* fruit (2.7 ± 0.2; mean ± 1 SE) roughly 2–3 times per day. Between 17 and 27 pieces of fruit are eaten per dish. Seventy-seven percent of the informants said that they eat dishes where *O. monacantha* and *O. streptacantha* are eaten exclusively >10 times per month, and that they contribute to 56.9% ± 2.4% of their total nutrition during the lean period. Moreover, respondents specified that these fruits are also eaten as a water source, as water can become extremely scarce. More than 50 percent of the respondents stated that prickly pear fruit consumption would lead to health problems, with constipation cited most frequently. Likewise, infections caused by the spines during harvesting were mentioned.

As well as for nutrition, *O. monacantha* and *O. streptacantha* were ranked as the most important fodder resources of all prickly pear (Figure 1). To be used as fodder for cattle and goats, the cladodes are separated from the plants, and the thorns are burned off. According to survey respondents, the main constraints to their use as livestock fodder include diarrhoea in the animals, and physical wounds, which can lead to subsequent infections if the thorns are not sufficiently burned off.

ECONOMIC ACTIVITIES AND SALE OF *OPUNTIA* SPP. PRODUCTS. Forty-one percent of respondents confirmed that they regularly sell prickly pear products. However, on average, they consume far more themselves than they sell. The average proportion of own consumption to sale is 88.2% ± 2.3% and 11.9% ± 2.3%, respectively. Exclusively fruits from *O. monacantha* and *O. streptacantha* are sold.

During the dry season, when grasses and herbs are scarce, herders from the Mahafaly Plateau practice transhumance and migrate to the littoral (Feldt 2015). Here, they feed their livestock with the succulent twigs of the dry forest tree *Euphorbia stenoclada* and with prickly pear cladodes (Feldt 2015, Götter et al. 2015). Herders buy access rights to planted cacti areas, and some farmers in the littoral have even started to establish fodder plantations (predominantly *Euphorbia stenoclada* but also prickly pears; Götter 2016). Four percent of the households in our survey sell access rights to prickly pear areas to transhumant herders. The price varies between 135,000 and 187,500 ariary per hectare (42–58€). Also, small zebus and/or goats are occasionally exchanged for access to prickly pear cladodes. Fruit, however, was exclusively sold for human consumption for 13 to 38 ariary a piece (0.004–0.01€, see Table S10).

Experience with the sale of *Opuntia* seeds: Usually, prickly pear seeds are considered as waste by locals and thus discarded. From key informant interviews, we know that a local middleman bought small quantities of *O. dilenii* and *O. stricta* seeds between 2010 and 2013. The seeds were shipped unprocessed, first to Antananarivo, and then to France.

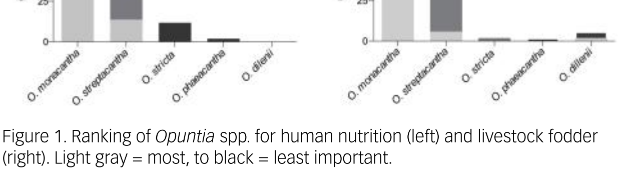

Figure 1. Ranking of *Opuntia* spp. for human nutrition (left) and livestock fodder (right). Light gray = most, to black = least important.

Twenty-six per cent of the villagers surveyed had sold prickly pear seeds to middlemen in quantities of around 5 kg on average per year. In addition to the three villages covered in this study, several additional villages in the southern littoral delivered seeds. Villagers received a fixed price of 3000 Ariary/kg for sun-dried seeds (~0.8€). According to the villagers, a 'fair' price would be 3837 ± 269 Ariary (1.16€ ± 0.08€; mean ± STE) per kg of sun-dried prickly pear seeds.

The villagers harvested the seeds in the following way: (i) the fruit were typically picked with spears, (ii) the fruit was separated from the thorns, (iii) the seeds were separated from the fruit, pulp and juiced by hand, (iv) and the seeds were hand-washed and (v) sun-dried. After being separated from the fruit, the pulp and juice were still consumable according to our respondents. Total labour for the collection and separation of prickly pear seeds was 3.3 ±1.4 hours per kg of sun-dried seeds.

PRICKLY PEAR IN FIELD HEDGES. The average farmer has 1.6 0.1 farm plots with an average plot size of 1.7 ± 0.1 ha (mean ± STE). The farm hedges have an average size of 6015 ± 451 m^2 (0.6 ha) per field, from which 1012 ± 126 m^2 (16.8%; Mean ± 1 STE) consist of prickly pear on average (see SM6). Apart from prickly pears, farm hedges consist predominantly of *Agave sisalana*, *Euphorbia stenoclada*, *Ziziphus spp.* and several bushes. Prickly pear hedges consist, in sum, of 38.2% prickly pear with edible fruit (mainly *Opuntia monacantha*, some *O. streptacantha*), and of 61.8% prickly pear with inedible fruit (*O. dilenii* and *O. stricta*). On average, respondents estimated that a total of 2033 ± 269 prickly pear plant stems can be found in the hedges; according to our inventories it is 2268 ± 608 per household (Mean ± 1 STE) (Figure 2).

SEED MASS AND CONTENT IN *OPUNTIA* FRUITS. Dry seed mass per piece of fruit was significantly higher in *Opuntia stricta* than in *O. dilenii* and *O. monacantha* (t-tests, p<0.001, Figure 4). However, as the total mass per piece of fruit also differed for the different prickly pears, we also analysed the seed content (in mass percent) in fruit. *Opuntia stricta* had a significantly higher seed content than both *O. dilenii* and *O. monacantha*, while *O. dilenii* had a higher seed content then *O. monacantha* (paired t-tests, p<0.001, Figure 3).

FRUIT ESTIMATION AND POTENTIAL SEED OIL PRODUCTION. The analysed *O. dilenii* seeds contained 7.04 mass percent of seed oil, and *O. stricta*, 8.80 mass percent. Households could potentially produce 1.97 kg of *O. dilenii* seed oil, and 12.03 kg/house-

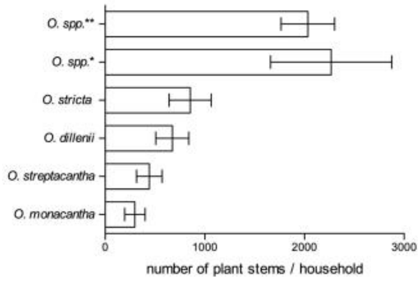

Figure 2. Number of plant stems per household from vegetation inventories compared to self-estimates from respondents, *is the sum of all *Opuntia* spp. below, ** is based on interviews, self-estimates are sums of all *Opuntia* spp. in households´ hedges. Error bars indicate 1 standard error.

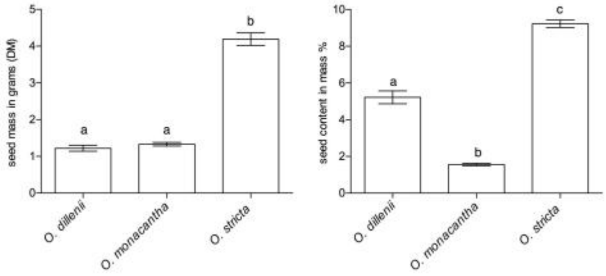

Figure 3. Seed mass and content of *Opuntia* spp. fruits. Error bars indicate 1 standard error; different letters indicate significant differences at p=0.001 in t-tests (left) and paired t-tests in (right) respectively.

hold of *O. stricta*, on average, based on their resources in the field hedges (Table 1). The total number of pieces of fruit per household for *O. monacantha* was estimated based on the total number of plant stems per household (Table 2). However, its seed oil content was not analysed.

DISCUSSION

Decary (1925) claimed that semi-arid Madagascar would be uninhabitable without prickly pears. If lost, a crucial food, fodder and water resource would be absent, resulting in large-scale starvation. However, while Malagasy prickly pears are commonly treated as an undifferentiated group of species commonly referred to by their Malagasy name *raketa* (Allorge and Matile-Ferrero 2011), we find that the different prickly pears fulfil distinct functions for southwestern Malagasy land users. *O. streptacantha* and *O. monacantha* constitute a crucial natural resource for local livelihoods. Particularly during the lean season, these plants contribute a substantial share of total food intake, provide water, and—to a smaller degree—also function as an income source. Likewise, the cladodes of *O. streptacantha* and *O. monacantha* represent a key fodder source for livestock. Without prickly pear, pastoralism could probably not endure in this dry environment (cf. Middleton 1999, Kaufmann 2001). In contrast, *O. dilenii* and *O. stricta* are rarely eaten by humans due to their high seed content and an associated bad taste. Because of their heavy spines they are also less suitable as livestock fodder. Larsson (2004) reports similar findings from southern Madagascar (Androy region).

Table 1. Average yieldable oil potential of *Opuntia dilenii* and *Opuntia stricta* per household (mean values and standard error), based on (a) surface (m^2) per household (n=29) (b), an estimate of the number of fruit /m^2/species in the lean season (n=30 per species), (c) no of fruit per household per species = combing (a) and (b), (d) mass (grams) per piece of fruit (fresh, n=30 per species), (e) seed mass(DM)/fruit, (f) total seed mass(DM) / household= based on (c) and (e), (g) mass percent of oil in seeds, and (h) a final estimate of potential oil production per household based on (f) and (g).

	Opuntia dillenii	Standard Error	*Opuntia stricta* var *stricta*	Standard Error
a. Surface (m^2)/HH	326.62	74.66	443.81	96.3
b. No fruit/ m^2	70.2	3.16	73.47	3.15
c. No fruit /HH	22,929	235.56	32,607	303.39
d.Mass per piece (g)	23.64	0.58	45.83	1.91
e. Seed mass/ piece (g_{DM})	1.22	0.08	4.19	0.17
f. Total seed mass (kg_{DM})/HH	27.97	0.02	136.62	0.05
g. seed oil mass %	7.04	-	8.8	-
h. Seed oil (kg)/HH	1.97		12.03	

Table 2. Total seed mass per household of *Opuntia monacantha*, based on (a) surface m^2 per household, (b) no plant stems per household, (c) number of fruits per plant, (d) number of fruit per household, (e) mass per piece (f) seed mass per fruit g_{DM}.

	Opuntia monacantha	Standard Error
a. Surface (m^2)/HH	414.05	74.64
b. No plant stems/HH	297.8	102.09
c. No fruit/ plant	131	25.4
d. No fruit /HH	39,012	1.896
e. Mass per piece (g)	87.33	3.03
f. Seed mass/ fruit (g_{DM})	1.33	0.05
g. Total seed mass (kg_{DM})/HH	51.89	87.73

WHICH *OPUNTIA* SPP. ARE APPROPRIATE FOR OIL PRODUCTION? Even though the spatial cover of *Opuntia monacantha* is lower than that of *O. dilenii* and *O. stricta*, its total fruit production is comparable. This is due to its size of up to 3–4 m compared to the more stunted growth form of *O. dilenii* and *O. stricta* in southern Madagascar. Considering that *O. monacantha* has a significantly lower seed content at a higher total fruit weight, it is thus more suitable for human consumption, which was also corroborated by the interview respondents.

There could be potential conflicts with a commercialisation of the seeds of *O. streptacantha* and *O. monacantha*, given their high importance for livelihoods particularly during food scarcity. Their contribution to total food intake can reach >50% during the lean period. This is in line with findings from the Androy region, where locals eat up to 50–70 pieces of fruit per person and day during the lean period (Larsson 2004).

While the high seed content species *O. dilenii* and *O. stricta* do not contribute to food security or livestock fodder, they made up >60% of all prickly pears in the fields´ hedges. Although it is conceivable that waste seeds from the consumption of *O. streptacantha* and *O. monacantha* could be used in seed oil production, a Malagasy oil processing company decided to source only 'red' prickly pear fruit (*O. stricta* and *O. ficus-indica*), and not 'green' fruit (species not specified), given their high local nutritional importance (Phileol 2013). Similarly, another Malagasy company is trading oil of *O. dillenii* (Renala 2017).

We found a higher seed oil content in *O. stricta* than in *O. dilenii*. With total seed oil contents of 7.0 (*O. dilenii*) and 8.8 (*O. stricta*; solvent extraction) mass percent, respectively, the values of Mahafaly prickly pear seed oil fall well within the reported ranges of oil yields, which varies between <4% and >17% (Sawaya and Khan 1982, Coskuner and Tekin 2003, Ramadan and Mörsel 2003, Ennouri et al. 2006, El Mannoubi et al. 2009, Sáenz et al. 2013, Guillaume et al. 2015). However, some of this variability may be due to differing maturation times of the fruit (Coskuner and Tekin 2003). Some of the published studies are based on fruits that are bought on European markets (Ramadan and Mörsel 2003), others are taken directly in the field, e.g., in North Africa (Ennouri et al. 2005, Yeddes et al. 2014). Also, most studies measured prickly pear seed oil content using solvent extractions, e.g., with hexane (Sawaya and Khan 1982, Ennouri et al. 2005, El Mannoubi et al. 2009, Ghazi et al. 2013). Yet, if the seed oil were generated through a cold press, seed oil yields would be lower due to higher losses using mechanical oil mills. Oil producers we contacted reported oil yields of around 4–5 mass percent from Malagasy *O. stricta* seeds in test pressings using mechanical mills.

The chemical components addressed in prickly pear seed oil marketing are not exclusive to the most-often studied *O. ficus-indica*, but are also attributed to other prickly pears. One of the components making prickly pear seed oil attractive for the cosmetical industry is its high share of polyunsaturated fatty acids (especially linoleic acid), tocopherols, sterols and phenolics (Sáenz 2017). The shares can vary according to production country and variety, but several studies found linoleic acid to be the dominating fatty acid in prickly pear seed oil, followed by oleic, palmitic and stearic acid. Comparing *O. ficus-indica* seed oils from Morocco, Turkey, South Africa, Tunisia, Chile and Algeria, Sáenz (2017) found shares of linoleic acid between 49.3–64.4%, oleic acid between 15.7–23.5%, palmitic acid between 10.6–13.7% and stearic acid between 3.2–5.4%. Fatty acid shares for Tunesian *O. stricta* seed oil from Tunesia (Ennouri et al. 2005) and *O. dillenii* seed oil from Morocco (Ghazi et al. 2013) confirm that linoleic acid is the dominating fatty acid in *Opuntia* seed oil. In *O. stricta* seed oil from our study area, a linoleic acid share of 66.6% was found, followed by palmitic acid (12.5%), oleic acid (7.9%) and stearic acid (4.5%, which is well in the range of reported fatty acid spectrums.

OPUNTIA PRODUCTIVITY AND OPPORTUNITY COSTS. Our estimates on both plant and fruit numbers was generally in line with the ones of the respondents. If we sum up and transform our calculations of prickly pear fruit production per m^2 to hectares (ha), they show average yields of around 25 tons/ha, which is in the medium range of global reported prickly pear fruit yields. Prickly pears have been shown to provide fruit yields of 13t/ha in Ethiopia (Gebretsadik et al. 2013), 30 t/ha in Italy (GAFÉIAS 2011) and up to 40t/ha in Argentina (Garcia de Cortázar and Nobel 1991).

The prickly pear fruit yield is remarkably high compared to the low agricultural yields in the region, e.g., cassava (0.7–1.0 t/ha; Milleville and Blanc-Pamard 2001, Noromiarilanto et al. 2016), which is the most important subsistence crop in the region. Accordingly, food self-sufficiency has been greatly negative in the past years for local farmers (WFP 2013, WFP and FAO 2014, Noromiarilanto et al. 2016, Hänke et al. 2017). Taking all income sources into account, local farming households earned around 15€ per month in 2015, on average, whereas food sales contributed very little (Hänke et al. 2017). While the sale of livestock can often compensate for food gaps, its sale leads to a gradual depletion of household assets on the long-term (Hänke and Barkmann 2017).

The potential sale of more than 160 kg of seeds (*Opuntia dilenii* and *O. stricta*) per average household would generate >540,000 Ariary a year (155€) if we would apply the 'fair price'. However, total seed production is higher as the calculation is based on a single fruiting period. Both, *O. dilenii* and *O. stricta* give fruit several times a year and they do not only occur in the field hedges. As the fruit needs to be harvested, the seeds extracted, cleaned and dried, there is an opportunity cost in terms of labour spent on these activities. According to respondents' experiences, the complete *Opuntia* seed preparation for 1 kg took 3.3 ± 1.4 hours on average. Opportunity costs are low, however, with regard to (i) the low regional wages, e.g 0.5€ per day for fieldwork or construction work, (ii) the absence of income generating activities and (iii) the low income generated by agriculture in the region (cf. Hänke et al. 2017).

OPUNTIA STRICTA, AN UNAPPRECIATED INVASIVE SPECIES? Globally, *Opuntia stricta* is listed as one of the 100 most dangerous invasive species (Lowe et al. 2000) and studies from southern Madagascar have shown that *O. stricta* is far less appreciated by local communities then other prickly pears (Larsson 2004), which is in line with our findings. The study by Larsson (2004), however, has also shown that *O. stricta* is negatively impacting livestock and human health. Recent attempts to eradicate *O. stricta* plants e.g., in southern Madagascar (Androy region) have been unsuccessful (In litt. with Madagascar National Park Management and World Wide Fund for Nature). Nevertheless, the spiny growth form of *O. stricta* could be one of the reasons making it particularly suitable as living fences, as it protects fields from livestock and intruders. Indeed, *O. stricta* was introduced as living fence in many parts of the world (Foxcroft et al. 2008). Even though it is rarely consumed, it could, thus, still be beneficial for local land managers as a protection from field plots, particularly taking into account the high livestock numbers in the region (Feldt 2015, Hänke and Barkmann 2017).

While survey respondents appreciate *O. stricta* concerning food and fodder far less then *O. streptacantha* and *O. monacantha*, *O. stricta* was most common in the hedges, which may indicate an active management by local farmers. Agricultural fields are anthropogenic managed ecosystems, or social-ecological systems, where human preferences and values play an active role (Berkes and Folke 1998). Still, some respondents in our study regarded *O. stricta* as problematic, particularly since it can colonize agricultural fields. Yet, others stated that "If there is nothing else left, we also eat *O. stricta*". These contrasting views have also been confirmed from other parts of Madagascar, whereas particularly poor people were against eradication attempts of *O. stricta* by conservationists as it contributes to their food security, particularly in times of food scarcity (Middleton 2012). Similarly, research from South Africa has shown that although prickly pears are fought by governmental programs and/or conservationists for biodiversity conservation goals, they can contribute particularly to poor rural livelihoods, which has led to conflicts (Shackleton et al. 2011). Thus, due to opposing interests by different stakeholders, there is little chance of implementing biological control on invasive prickly pears in most countries (Zimmermann 2017).

A VALUE CHAIN APPROACH FOR *OPUNTIA* SEED OIL IN SOUTHWESTERN MADAGASCAR. From a rural development perspective on value addition, one would strive to process prickly pear seeds to the maximum degree possible in the research region itself. Potential income would be lost to the Mahafaly area if only raw, unprocessed seeds were exported. Occasionally, however, it is an economically superior option to export raw materials from countries such as Madagascar, as there are higher import duties associated with processed goods than for raw materials. Fortunately, this consideration does not apply to Madagascar as a least developed country (LCD). Due to the "Everything-but-Arms" agreement between the European Union and several LCDs, import duties are charged neither on prickly pear seeds nor on its seed oil (European Commission 2015).

Most likely, quality considerations place the most challenging constraints on research area-based processing. To maintain the high concentration of antioxidants and unsaturated fatty acids, the oil mill needs to operate in a way that minimises contamination of the seed oil and its exposure to ambient air/oxygen. In turn, this requires an advanced level of technical equipment on the part of the oil mill, skilled staff, and adequate logistics. Historically, Morocco had extensive experience with the production of *Opuntia* seed oil, and the needed requirements were probably easier to fulfil than in our research region. At the country level, however, a small number of enterprises are known to be capable of extracting quality prickly pear seed oil as they extract other fatty and/or essential oils from local plant sources, and commercialise them successfully globally, e.g., Phileol with *Opuntia ficus-indica* and *O. stricta* (Phileol 2013), and Renala with *O. dillenii* (Renala 2017).

A further consideration applies to the type of oil production. Because of the hard seeds and their relatively low oil content, an extraction with solvents has considerable cost advantages. A solvent based extraction with, e.g., hexane, has the disadvantage, however, that this chemical solvent has to be removed from the seed oil after extraction, which becomes excessively expensive for higher grades of purification. Therefore, the quality of chemically extracted, commercial grade *Opuntia* seed oil is regarded as inferior (Naturinstitut 2015). Even if extremely low solvent contents are technically feasible, the market favours seed oils extracted by traditional, i.e., physical/mechanical means. The mechanisms that result in a price premium for purely mechanically produced virgin olive and argan oil are in operation for *Opuntia* seed oil as well. Furthermore, the purity and natural qualities that consumers associate with Madagascar is at odds with chemical extraction from a marketing perspective, targeting the high value use of the seed oil, e.g., in natural cosmetics.

For oils traded in big quantities like for example palmoil, sunflower oil, rapeseed oil, soya bean oil, prices can easily be obtained through databases like FAOstat, Eurostat, UNComtrade, Index mundi, USDA National Agricultural Statistic Services, Statista.com, Destatis or AMIS Market Database. This is not the case for prickly pear seed oil. Six oil traders we contacted all pointed out that prices are not stable and depend on the purity and the quality of the oil. The current prices for conventional produced oil vary between 275–700 €/l, for organic oil between 900–1.500 €/l. Occasionally, prickly pear oil is mixed with cheaper oils and these mixtures are offered as prickly pear oil at a lower price (Oleador 2017).

With local seed oil content of 7.0–8.8%, cactus pear seed processing with mechanical mills generates a substantial amount of presscake. The presscake of *O. stricta* has a low protein (7.2%) and crude fat content (2.4%), but a high fibre content (50.5%) (analysis conducted by SGS Germany GmbH, Hamburg). Due to a fodder scarcity in the project region, especially during the lean period (Feldt 2015), prickly pear presscake could be used to feed ruminants, as they can digest high fibre fodder (Gebretsadik et al. 2013, Sáenz et al. 2013). Another by-product if prickly pear seeds are commercialised is the pulp and juice from its fruit. Juice and pulp could be consumed in the household, sold, or processed to yield jam (Sáenz et al. 2013). This also includes the less appreciated *O. stricta* varieties, since the seeds, reported to cause digestive problems, would be removed. For example, *O. ficus-indica* jams are successfully marketed globally, and can be easily produced through 'low-tech' techniques (Sáenz et al. 2013). The pulp of *O. ficus-indica* fruit contains glucose (35%) and fructose (29%), both in dry weight (El Kossori et al. 1998). Through the fermentation of its sugars, alcoholic beverages can also be produced (Sáenz et al. 2013), such as beer (e.g., Spottzl Brewery Co. and Borderland Brewing Co. for prickly pear beers).

GENDER AND INSTITUTIONAL ISSUES. According to local gender norms, the lower part of prickly pear plants is considered to be a male part, and the upper part a female part (Kaufmann 2004). The preparation of fodder from prickly pear cladodes is an activity conducted by males, while the collection and selling of fruit is a female activity (ibid). If this cultural division of labour were to continue, a commercialisation of prickly pear seeds may strengthen the economic position of women in local households. However, there are recent examples from other fodder plants in the research region that the rules for resource access are changing, i.e., from open access towards increasing privatisation (Götter and Neudert 2015). Three of the surveyed households sold access to prickly pear plantations as livestock fodder. With previously invariant cultural constants becoming more dynamic, the future distribution of benefits from the commercialisation of prickly pear fruit and seeds should be monitored carefully, as there is evidence that men and/or local elites tend to benefit predominantly from market integration in marginal rural communities (Genicot 2002, Basu 2007).

Because of the strongly differing seed content of the fruit, it appears unlikely that a problematically high share of edible prickly pear fruit will be removed from human subsistence consumption in favour of the commercialisation of prickly pear seeds. Although unlikely, it cannot be ruled out completely that local elite households would try to gain preferential access to (privately owned) field hedges and enforce a shift to planting more prickly pear with inedible seeds. However, with sufficiently high seed prices, field owners may find it in their own economic interests to switch to high seed content cactus pears, i.e., *Opuntia stricta*. The two high seed species were already most common in the field hedges. In the worst case, households not owning cactus pear hedges but previously having been granted some access to edible fruit may lose out. At this point, it is impossible to foresee whether the stronger overall economic base in the communities due to the commercialisation of cactus pear seeds could make up for this potential disadvantage.

CONCLUSION

The food security of rural households inhabiting the littoral of the Mahafaly Plateau is chronically low, complementing livelihood sources are lacking and extreme poverty is widespread. Two prickly pears with low seed content in their fruit (*Opuntia streptacantha* and *O. monacantha*) are crucial for human nutrition—and even water uptake—during the annual lean season. Likewise, they represent a key fodder resource. On the contrary, *O. dilenii* and *O. stricta* have a high seed content, making them unsuitable for human nutrition. Their fruits neither contribute to the food security of local households nor are they dedicated as fodder sources for livestock. As the fruit of these two prickly pears grow most abundantly in the living fences of local fields, these two species represent a seed source for seed oil production. Furthermore, the cactus pear fruit yield is remarkably high compared to the low agricultural yields in the region. Our estimates of the average cactus pear seed oil yield per household demonstrate a substantial potential of the collection and pre-processing (cleaning, drying) of cactus pear seeds as an additional income source for local farmers. *O. dilenii* fruit is available throughout the year while *O. stricta* fruit can be harvested from March to August, coinciding with the period where households are harvesting annual crops as well as cassava (Hanisch 2015). Complementing current—often drought-sensitive—income sources, the sale of cactus pear seeds appears to be a potential additional, low-risk component of total household income.

Local processing of the seed oil itself would further upgrade the local value chain, reduce transportation costs, and allow for local use of the press cake. However, financial capital is needed to acquire and operate oil mills, investments in training for local staff is needed, and adequate logistics are required. The more value addition would be done locally, the more livelihood improvements could be brought to some of the poorest rural communities in the world.

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SUPPLEMENTARY MATERIAL

Available online only

Figure S1. Study area.

Table S2. Occurring *Opuntia* spp., their fruiting rates/year, fruit color and fruiting periods

SM 3. *Opuntia phaeacantha, O. streptacantha, O. dilenni, O. stricta* var *stricta, O. monacantha* (left to right).

SM 4. Burning of spines of *Opuntia* spp. cladodes on plantations in the littoral; source: Tobias Feldt.

SM 5. Aerial view of a typical landscape in the coastal area illustrating living fences on farmland.

SM 6. Percentage of *Opuntia* spp. in field hedges.

SM 7. Fruits of *O. streptacantha*, O. stricta var *stricta* and *O. dilenii* (from left to right).

Table S8. Overview of *Opuntia* spp. seed oil prices over the past 10 years, mode of production and origin of oil.

Table S9. Shares of fatty acids in *Opuntia* spp. seed oils. Sources: 1: Sáenz 2017, 2a: Ennouri et al. 2005, 2b: own analysis, conducted by SGS Gmbh Hamburg, 3: Ghazi et al. 2013.

Table S10. Price variation of prickly pear products.

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The use of natural resources to improve household income, health, and nutrition within the forests of Kianjavato, Madagascar

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ABSTRACT

Understanding natural resource extraction in Madagascar is key to developing wider conservation and management strategies that ensure the continued delivery of essential ecosystem services, and the development of health and economic strategies to meet the demands of a growing human population. In the Kianjavato lowland rainforest of southeastern Madagascar, 78% of lemur species, 83% of native carnivoran species, and 67% of frugivorous bat species are threatened with extinction. All three of these groups of mammals are commonly hunted for food in other regions of Madagascar, yet we knew little about current levels of hunting or whether the use of forest resources significantly affects human welfare in this region. We used health assessments of 1267 Kianjavato residents and semi-structured interviews of members of 336 households in 17 communities in Kianjavato to investigate human-environmental interactions. We found high prevalence of child and teenage malnutrition. More than half of the population under 20 years old was stunted, more than half was underweight, and more than one fifth was wasted. Further, one in six residents were anemic. We found that Kianjavato's forests provided essential ecosystem services for its rural communities. As Kianjavato's forests are altered to meet the needs of a growing human population, these direct-use ecosystem services (such as the use of wild animals for food or plants for medicine) are unable to similarly expand to meet the basic needs of the families living in these forests. A worrying proportion of the Kianjavato population depends on forests to meet their healthcare, nutritional, and economic needs, yet they may be failing to do so. All surveyed households (100%) depended on forests to meet their healthcare needs and 40% of the regional economy involved the extraction of finite forest resources (i.e., precious stones). Most households consumed very little wildlife (two animals per household per year) and the great majority (83%) of the forest animals they ate were not threatened with extinction. Forty percent of wildlife were caught illegally. Although hunting is likely not imperiling local wildlife at present, 16% of the Kianjavato population hunts wildlife and 20% are malnourished. The ecosystem services of Kianjavato's forests may currently be insufficient to meet the needs of residents. Therefore, targeted efforts to increase local access to the healthcare system and to improve household nutrition and economy by improving the production and stability of local agricultural products may increase the long-term sustainability of wildlife hunting, household incomes, and regional food security. Efforts such as these that can expand with the growing population to meet future needs may help secure the sustainable use of essential ecosystem services for the long term, improving the health of local people and maintaining the integrity of the forests in which they live.

RÉSUMÉ

Comprendre l'utilisation des ressources naturelles à Madagascar est essentiel pour développer des stratégies de conservation et de gestion plus larges qui permettent à la fois de fournir des services écosystémiques et de développer des stratégies sanitaires et économiques afin de répondre aux besoins d'une population humaine toujours croissante. Dans la forêt tropicale humide de basse altitude de Kianjavato dans le sud-est de Madagascar, 78% des espèces de lémuriens, 83% des espèces de carnivores indigènes et 67% des espèces de chauves-souris frugivores sont menacés d'extinction. Ces trois groupes de mammifères sont généralement chassés dans d'autres régions de Madagascar, mais nous en savons peu sur les niveaux actuels de chasse ou si l'utili-

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sation des ressources forestières affecte significativement le bien-être humain dans cette région. Nous avons conduit une évaluation sanitaire sur 1267 habitants de Kianjavato, ainsi que des entretiens semi-structurés avec des membres de 336 ménages dans 17 communautés de Kianjavato afin d'étudier les interactions entre l'Homme et l'environnement. Nous avons constaté une forte prévalence de la malnutrition chez les enfants et les adolescents. Plus de la moitié de la population âgée de moins de 20 ans souffre d'un retard de croissance, plus de la moitié d'une insuffisance pondérale et plus d'un cinquième d'émaciation. En outre, un résident sur six est anémique. Nous avons constaté que les forêts de Kianjavato fournissent des services écosystémiques essentiels à ces communautés rurales. Comme les forêts de Kianjavato sont altérées pour répondre aux besoins d'une population croissante, ces services écosystémiques à usage direct (tels que la consommation d'animaux sauvages ou des plantes médicinales) ne peuvent plus couvrir les besoins fondamentaux des familles qui y vivent. Une proportion inquiétante de la population de Kianjavato dépend des forêts quant à ses besoins sanitaires, nutritionnels et économiques, cependant ces dernières ne peuvent plus y pourvoir entièrement. Tous les ménages enquêtés (100%) comptent sur la forêt pour la satisfaction de leurs besoins sanitaires. Par ailleurs, l'exploitation de ressources forestières finies (extraction de pierres précieuses) représente 40% de l'économie régionale. La plupart des ménages consommaient très peu d'animaux sauvages (deux animaux par ménage par an) et la grande majorité (83%) des animaux forestiers qu'ils mangeaient n'étaient pas menacés d'extinction. Cependant, 40% de ces animaux forestiers ont été capturés de manière illicite. Certes la chasse ne menace pas actuellement la faune locale mais 16% de la population de Kianjavato reconnaît s'y adonner et 20% souffrent de malnutrition. Les services écosystémiques s'avèrent actuellement insuffisants pour répondre aux besoins des résidents. Il est par conséquent nécessaire de cibler les efforts pour accroître l'accès local au système de santé, ensuite pour améliorer la nutrition et l'économie des ménages (améliorer la production et la stabilité des produits agricoles locaux), et tout ceci dans le but d'augmenter la viabilité à long terme de la chasse, des revenus et de la sécurité alimentaire dans cette région. De tels efforts lorsqu'ils prennent en compte la croissance de la population - et donc ses besoins futurs accrus —peuvent aider à assurer l'utilisation durable des services écosystémiques, à améliorer la santé des populations locales, et en fin de compte, à maintenir l'intégrité des forêts dans lesquelles elles vivent.

INTRODUCTION

Developing nations are working to find a balance between protecting their endemic biodiversity and providing for their growing human populations (Barrett et al. 2011). Madagascar's forests are a valuable resource for rural populations. They provide essential materials for housing (Kremen et al. 1999, Golden et al. 2014a, Borgerson et al. 2018), medicines for adequate healthcare (Rasoanaivo 1990, Rasoanaivo et al. 1992, Novy 1997, Norscia and Borgognini-Tarli 2006, Golden et al. 2012, Randriamiharisoa et al. 2015, Randrianarivony et al. 2017), and a source of food for a diverse diet (Kremen et al. 1998, Styger et al. 1999, Golden et al. 2011, Andriamparany et al. 2015, Borgerson et al. 2016, Golden et al. 2016) in places where adequate alternatives to these resources are often inaccessible, unaffordable, and/or unavailable in sufficient quantity. Government bodies and both public health and conservation NGOs have an opportunity to: (1) create broader management strategies that create positive incentives to promote the use of forest products at rates that remain within their ecologically sustainable limits; and (2) develop alternative health, economic, and food production strategies that can expand to meet the needs of a growing human population in ways that forest resources cannot. Such efforts may secure the integrity of forest ecosystem services for the long term—improving the health of local people and ecosystems for generations to come (Myers et al. 2013, Redford et al. 2014).

The Malagasy people will continue to coexist with and use their forests to support their livelihoods and foster their identity, their culture, and their spiritual systems (Keller 2009, Golden 2014). Yet many animal and plant resources have slow rates of reproduction and/or growth, and in the case of endemic lemurs, their future population viability depends on the survival of adults (Dunham et al. 2008, 2011, Godfrey and Rasoazanabary 2011). In these cases, over-extraction can contribute to reducing the population to levels that make them vulnerable to extirpation and eventual extinction. Previous research has focused on the use of forest resources surrounding Madagascar's national parks. Incentive and livelihood-based management strategies in the communities on Madagascar's national parks' borders have also been implemented with a primary goal of securing the ecosystem-focused management plans within park borders. However, most of Madagascar's people, and over 90% of Madagascar's land area, exist outside of these protected areas. Understanding the pressures of natural resource extraction outside of the national park system, and its impacts on local health and wellbeing, will be key to developing broader national level management strategies that ensure both the continued delivery of essential direct-use ecosystem services and the conservation of Madagascar's treasured native and endemic wildlife.

The Kianjavato forest of southeastern Madagascar is an area of lowland rainforest home to six species of endemic carnivorans, nine species of lemurs, and more species of bat (14) than any other eastern lowland site in Madagascar (MEFT 2008, Goodman et al. 2014). A portion of these forests fall within a mixed-use New Protected Area, the Forest Corridor Ambositra-Vondrozo (COFAV). Seventy-eight percent of Kianjavato's lemur species are threatened with extinction (two species are Critically Endangered; *Prolemur simus* and *Varecia variegata*), as are 83% of its native carnivoran species and 67% of its frugivorous bat species (IUCN 2016). All three of these groups of mammals are commonly hunted for food in other regions of Madagascar (Jones et al. 2008, Golden et al. 2011, 2014a,b, Jenkins et al. 2011, Borgerson 2015, 2016, Reuter et al. 2016a,b), yet we know little about current levels of hunting in this region or whether this exploitation has significant consequences for human welfare. Without an adequate understanding of the complex interactions between the people of the Kianjavato region and their natural environment, it will be difficult for local people, natural resource managers, and public health officials to prevent, mitigate, or adapt to future unwanted ecosystem changes.

Here, we present the results of a four-month assessment of communities in the Kianjavato region of Madagascar. We collected data concerning conservation-relevant human behaviors in order to understand the ways in which Kianjavato's forests provide resources that improve the wealth, health and nutrition of the Malagasy people who live in this region. It is our hope that these data aid public health and conservation specialists in creating broader data-based management strategies that both promote the sustainable use of forest resources, and develop alternative health, economic, and food production strategies that can expand to meet the needs of the people and ecosystems of Kianjavato.

METHODS

STUDY SITE. Kianjavato is within the Vatovavy-Fitovinany region of southeastern Madagascar. The Vatovavy-Fitovinany region is home to a primarily rural population of at least 1,104,675 people (54.7 individuals per square kilometer) (MEFT 2008) mainly from the Antaimbahoaka ethnolinguistic group (this study). The principal economic activity of local people is agriculture, which is supplemented primarily by livestock raising, forestry, and fishing (MEFT 2008). Literacy is low, with only 41.5% of the adult population being able to read and write. Vatovavy-Fitovinany (the region comprising Kianjavato) has stronger transportation infrastructure compared to other remote eastern regions of Madagascar. The region can be accessed by a regional airport as well as by railway, three national highways and several large rivers (ibid).

The Vatovavy-Fitovinany ecosystem is characterized by wooded grasslands and pseudo-steppes (61.5% of all land area), agricultural land (22.5%), and forest lands (12.9%) (MEFT 2008). Within this region, Kianjavato is a low elevation humid evergreen forest with an annual rainfall of 1,800 mm (FOFIFA weather station 2011, Manjaribe et al. 2013). The region is home to 105 plant species endemic to Madagascar (two are endemic to the region) and 220 nationally endemic animal species (nine are endemic to the region) (MEFT 2008). A portion of the Kianjavato forests fall within the COFAV protected area (IUCN Category VI), but all are subject to national laws regarding water and forest resource management. Both the Kianjavato Ahmanson Field Station (KAFS; operated by the Madagascar Biodiversity Partnership) and the Conservation Credit Program (which includes the Education Promoting Reforestation Project; Manjaribe et al. 2013) are working in the region to support research, forest conservation, and local livelihoods.

SURVEY PROTOCOLS. Between January and April 2014, we surveyed 336 households, including 1267 individuals, in 17 communities in the Kianjavato region. All surveys were completed by the MAHERY team, which is not involved in local natural resource management. We consulted with the local community leaders and then held a local community meeting to discuss the goals and possible implications of the project before beginning household interviews in each village. During the community meetings, the research was described as an effort to understand the ways in which natural resource use contributed to human health and general wellbeing.

We interviewed either the male or female head of each household to gather information on household demographics, agricultural labor, livestock raising and diseases, income generation, commercial good ownership, forest resource use, and hunting behavior. Commercial goods included shoes, bicycles, radios, watches, flashlights, and guns. In general, we asked interviewees to recall events over the prior year. Households randomization was conducted per methods in Borgerson et al. (2018). The head of each household consented to participate in the research survey. In addition to questions administered solely to the head of household, we also collected data on the health of all available individuals in the surveyed households (1267 individuals within these 336 households). We recorded the sex, age (to the nearest whole year), occupation and educational obtainment of each household member. We then collected specific health information including anthropometric data (height and weight), a history of malaria episodes, a history of deworming medication, and a hemoglobin and blood oxygen level using a portable hemoglobinometer (Rainbow Pulse CO-oximeter from MASIMO) (644 individuals). This simple, non-invasive method uses photospectrometry rather than a blood sample to assess hemoglobin levels.

VARIABLE CREATION AND ANALYSIS. Simple summary statistics were calculated for most forms of environmental resource use and socio-demographic variables. Thresholds from the Center for Disease Control and Prevention (CDC) (2000) were used to calculate the prevalence of anemia from levels of hemoglobin in children and adults and the prevalence of stunting, underweight, and wasting (children <5 years old) or low BMI for age (children >5 years old) in children and young adults age 2–20. Children were defined as stunted, underweight, or wasted if their height-for-age, weight-for-age, weight-for-height, or BMI-for-age is more than two standard deviations below the CDC (2000) Child Growth Standards median. Children under 59 months were considered anemic if their hemoglobin values were less than 11.0, children who were between the ages of five and 12 (5<12) were anemic considered anemic if their hemoglobin values were less 11.5, children age 12 to 15 (12<15) if less than 12.0, women 15 years and older if less than 12.0, and men 15 years and older if less than 13.0. The fatality rates of diseases and illnesses afflicting livestock were calculated by dividing the number of animal deaths reported for a given disease over the prior year by the number reported to have been afflicted by that disease. To examine if endangered animals were more likely to be reported as eaten in another person's home (instead of hunted by the participant) we performed a Chi Square on IUCN threatened status and hunting methods (both nominal categorical variables). We analyzed the relationship between wildlife consumption, child malnutrition, and hemoglobin levels using an established generalized linear mixed model where all individuals were clustered at the household level. Hemoglobin was an untransformed continuous outcome variable that controlled for the age and sex of the individual, wildlife consumption was a $\log_{10} +1$ transformed continuous explanatory variable, and household income ($\log_{10} +1$ transformed) was controlled for as a continuous variable. Hemoglobin levels and the z-scores for child growth in this population were roughly normally distributed and did not require transformation.

RESULTS

The 336 surveyed households in the Kianjavato region were comprised of a mean of 3.77 individuals (median 3). Almost half of the population (47%) was less than or equal to 16 years of age and 7% were under age two. Participants were primarily of the Antaimbahoaka ethnolinguistic group (66%), followed by Betsileo (11%), Merina (10%), Tanala (9%), and Tandroy (4%).

HOUSEHOLD ECONOMY. All households reported farming as their primary employment. Forty-two percent of households declined to answer whether they had received cash income during the prior year. The preponderance of precious stone mining and sales (an often-illegal behavior) likely explains the high prevalence of respondents declining to answer questions about income generation, a behavior we have not found common in other regions of Madagascar. Households that reported their cash income earned a median of 50,000 Malagasy Ariary (MGA) (US$21.74) (mean of 411,740 ± 708,938 MGA or US$179.02 ± US$308.23) during the previous year or a median of 16,667 MGA per person (US$7.22) (mean 148,903 ± 365,299 MGA or US$64.74 ± US$158.83). One-tenth of households had sold amethysts, emeralds, corundum, or crystals during the prior year and the money earned from the sale of precious stones supplied 39.0% of all reported cash income (the highest percentage out of all reported income-earning categories). Of the households whose members had sold precious stones during the prior year, half had sold emeralds (providing 43.8% of total income from the sale of precious stones; with a median earning of 1,500,000 MGA per household), over a quarter (27.8%) had sold corundum (34.4% of precious stone income; median household earnings of 3,000,000 MGA), 16.7% had sold amethysts (21.1%; 3,000,000 MGA), and 5.6% had sold crystals (0.6%; 200,000 MGA).

Chickens were the most commonly owned domestic livestock, followed by ducks (Table 1). On average, adult chickens were sold in this region for 12,000 MGA (or US$5.22). All households which owned chickens had some of their flock die from disease during the prior year. All deaths were reported to be caused by a disease locally referred to as *barika*. The symptoms of the disease were consistent with Newcastle disease and the estimated fatality rate was 31.0%.

A minority of the Kianjavato population (13.0%) made use of *lasy*, a seasonal home close to rice fields, during the prior year. For those residents that used *lasy*, this use peaked during April at the height of labor demands for swidden agriculture (43.2% of all lasy were occupied during this time). The average *lasy* was a 3.75 ± 2.10 hour walk from the center of the community with a maximum distance of 15 hours. Therefore, the average *lasy* was approximately 16.36 km away if we estimate time-distance relationships and expect normal walking speeds (Ralston 1958).

HEALTH. Malnutrition was a profound issue (Table 2). Of all measured households, 52.5%, 71.25%, and 22.5% contained stunted, underweight, and wasted children, respectively. We found no significant differences between male and female children in their nutritional status. Nearly one in five (128 of 646) subjects was anemic. Men were significantly more likely to be anemic than women (X^2: DF=1 (628), $R^2=0.03$, $p<0.0001$; 54.30% of men (total number of men sampled = 341) vs. 45.70% of women (total number of women sampled = 287)).

Table 1. The range and mean of household livestock assets in Kianjavato communities.

Type of livestock	Cow	Pig	Duck	Chicken	Goose
Range (#/household)	0–15	0–14	0–40	0–70	0–14
Mean (#/household)	1.28	0.43	3.79	8.02	0.53

Table 2. Percentages of individuals categorized as stunted, underweight, wasted, or anemic in villages within the Kianjavato region. (* Sample sizes of children under five (one individual) and children 6-12 (11 individuals) are too small to report independently, so all ages of children under 20 have been collapsed into a single group for analysis. The finger-cuff used at this time to measure hemoglobin using photospectrometry was difficult to use on children with small fingers, and heights and weights were only recorded for individuals whose hemoglobin was measured. This issue has since been resolved. ** One individual whose hemoglobin was measured declined to have their weight or height measured.)

Age range (yrs)	Sample size (n)	Stunted	Underweight	Wasted	Anemic
2–20*	89	52.8%	69.7%	22.5%	20.0%
21–55	486**	-	-	-	19.6%
> 55	69	-	-	-	21.7%

NATURAL RESOURCE USE. Respondents reported a very high reliance on the forest for healthcare. Nearly all (99.7%) households harvested traditional medicines from the forest at a median frequency of two times per week (mean of 2.20 ± 0.83 times), collected at a median distance of 30 minutes (mean of 47 ± 140 minutes) from the home. Ninety-one percent of the population relied on firewood for cooking. Individuals walked a median of 30 minutes (mean of 46 ± 94 minutes) each day to collect firewood, and none of this wood was sold. None of the interviewees had collected honey during the prior year. Local people reported high bee mortality attributed to a pervasive disease. There were distinct gender roles in the collection of natural products. While the collection of traditional medicinal plants was predominantly a female activity (85.0% of all collection was done by adult women), firewood was primarily collected by adult men in the household (83.0% of collection).

Sixteen percent of households had consumed wildlife in the prior year (3.0% had in the prior month). Of the 755 forest mammals that surveyed households consumed during the previous year, 46.0% were tenrecs, 31.5% were bats, 12.7% were lemurs, 6.6% were bushpigs, 2.9% were euplerids, and 0.3% were introduced carnivorans (Table 3.) Assuming the average un-processed weights of species (Goodman 2012), the surveyed households caught a total of 553 kilograms of meat during the prior year (median of 0 kg and mean 1.7 ± 6.9 kg per household; range 0–58kg). Only 7.4% of households ate tenrec meat (these households each ate a median of six tenrecs or 6.6kg of tenrec meat during the prior year), 5.7% of households ate lemurs (two lemurs; 1.26kg), 4.5% ate bats (five bats; 1.31kg), 4.2% ate the meat of bushpigs; and 2.1% ate carnivorans (one native euplerid and one introduced viverrid carnivoran; 8.0kg). Bushpig meat was often purchased in pieces weighing roughly 1–2kg per piece. Of the 16.0% of households that reported eating wild meat during the prior year, they ate a median of six forest mammals (mean of 14.5 ± 15.7).

One out of every six forest mammals eaten during the prior year was threatened with extinction; 1.3% were Critically Endangered, 11.0% were Endangered, 5.2% were Vulnerable, 28.6% were Near Threatened, and 53.9% were Least Concern (IUCN 2016). IUCN status did not significantly affect the number of animals that respondents reported eating in their own or another person's household. According to the most recent updates to legislation (Decree number 2006-400), at least 40.2% of hunting was conducted illegally either because of national prohibitions against hunting (e.g., lemurs) or prohibited equipment (e.g., hunting tenrecs using dogs). Individuals recalled their hunting over the prior year, and did not specify the calendar month in which they caught each animal. This prevents the identification of the illegal hunting of game species that were caught outside of their legal hunting season (i.e., tenrecs, euplerid carnivorans, and bats).

Approximately two percent of surveyed households owned a firearm (range 0–8 guns per household). Local Malagasy predominately reported eating wildlife at the households of friends and/or family (419 animals). This consumption was supplemented by targeted pursuit hunting (total of 153 animals) using nets (110), dogs (35), and thrown rocks (8). Opportunistic hunting (total of 118 animals) using found objects (97) and dogs (21) was also common.

Table 3. The volume of mammalian wildlife consumption in communities within Kianjavato, disaggregated by hunting method. (* IUCN (2016) CR, Critically Endangered; EN, Endangered; VU, Vulnerable; NT, Near Threatened; LC, Least Concern. **P. larvatus was reported by the number of occasions this animal was consumed rather than the number of individuals, as it was frequently purchased as weighed pieces of meat (approx. 1-2kg) or eaten at friends' homes. The associated price is therefore also per piece and not per animal.)

Species	Type of animal	IUCN status*	Hunting regulations	Total number eaten (n)	Eaten as a guest (%)	Opportunistic hunting (%)	Pursuit hunting (%)	Trapping	Purchased	Price per animal (MGA)
Tenrec ecaudatus	Tenrec	LC	Seasonal	282	58	24	12	0	6	1,824
Rousettus madagascariensis	Bat	NT	Seasonal	216	46	0	53	0	1	1,000
Microcebus jollyae	Lemur	EN	Prohibited	83	45	55	0	0	0	-
Setifer setosus	Tenrec	LC	Seasonal	61	95	0	0	0	5	2,000
*Potamochoerus larvatus***	Bushpig	LC	Unrestricted	50	24	0	0	0	86	2,684**
Pteropus rufus	Bat	VU	Seasonal	22	41	23	36	0	0	-
Hapalemur griseus	Lemur	VU	Prohibited	9	100	0	0	0	0	-
Prolemur simus	Lemur	CE	Prohibited	8	100	0	0	0	0	-
Fossa fossana	Carnivoran	VU	Seasonal	6	100	0	0	0	0	-
Hemicentetes semispinosus	Tenrec	LC	Seasonal	4	100	0	0	0	0	-
Galidictis fasciata	Carnivoran	VU	Seasonal	4	100	0	0	0	0	-
Cheirogaleus major	Lemur	LC	Prohibited	3	100	0	0	0	0	-
Varecia variegata	Lemur	CE	Prohibited	2	100	0	0	0	0	-
Viverricula indica	Carnivoran	LC	Unrestricted	2	100	0	0	0	0	-
Eulemur rufifrons	Lemur	NT	Prohibited	1	100	0	0	0	0	-
Cryptoprocta ferox	Carnivoran	VU	Restricted	1	100	0	0	0	0	-
Salanoia concolor	Carnivoran	VU	Seasonal	1	100	0	0	0	0	-
Eulemur rubriventer	Lemur	VU	Prohibited	0	-	-	-	-	-	-
Daubentonia madagascariensis	Lemur	EN	Prohibited	0	-	-	-	-	-	-
Avahi peyrierasi	Lemur	VU	Prohibited	0	-	-	-	-	-	-
Galidia elegans	Carnivoran	LC	Seasonal	0	-	-	-	-	-	-
Total				755	55	16	21	0	8	-

Purchasing wildlife (total of 60 animals) and trapping (total of five animals) was less common. Wildlife was purchased for a mean 7200 MGA (US$3.13) per kilogram (range 1380–17,530 MGA per kilogram).

INTERACTIONS. Households that contained individuals who sold precious stones during the prior year earned significantly more than those that did not (T-test: t=7.78, DF=18.34, p<0.0001; 1,821,111 ± 831,737 MGA (US$791.79 ± US$361.62) vs. 265,943 ± 508,780 MGA (US$115.63 ± $221.21)). They also owned more commercial goods (T-test: t=1.73, DF=17.49, p=0.05; 5.75±7.10 vs. 2.84 ± 3.57). Members of these households also ate more wild animals than those that did not sell stones (T-test: t=2.30, DF=17.67, p=0.03; 8.89 ± 7.57 animals per household vs. 1.87 ± 12.84). Specifically, they ate more bushpigs and lemurs (T-tests: t=1.68, DF=17.37, p=0.05; 0.89 ± 1.97kg of bushpig per household vs. 0.11 ± 0.86kg, and t=1.73, DF=17.29, p=0.05; 1.94 ± 4.21 lemurs per household vs. 0.22±1.64) and fewer native carnivorans (euplerids) (t=-2.37, DF=317, p=0.02; 0.00 ± 0.00 euplerids per household vs. 0.04 ± 0.28). Household size and age demographics, the consumption of introduced carnivorans and bats, and the proportion of children that were categorized as stunted, underweight or wasted, were similar between households that did and did not sell precious stones during the prior year.

Household income seemed to be unrelated to participation in wild meat consumption and to the presence of wasted or anemic children in the household. Yet, households without stunted and underweight children had significantly higher incomes (T-test: t=-2.42, DF=49.39, p=0.02, 438,919 ± 735,099 MGA vs. 120,286 ± 341,140 MGA per year; t=-1.90, DF=24.30, p=0.04, 531,682 ± 866,319 MGA vs. 168,333 ± 386,504 MGA per year). We did not find a relationship between wildlife consumption (the grams of forest mammal meat eaten by household members during the prior year) and anemia or stunting at this site. However, the amount of wildlife a household ate (in grams) was significantly positively correlated with child wasting and the severity of low body mass (generalized linear mixed model: R2=0.11, DF=2, F=5.56, p=0.005, R2=0.11, DF=2, F=5.11, p= 0.008). Children were significantly more underweight and wasted within households that ate wild meat than in those that did not (T-tests: Weight t=-2.19, DF=26.31, p= 0.04, mean z-score -4.33 ± 3.63 vs. 2.40 ± 2.80; Wasting t=-2.37, DF=28.19, p=0.02, mean z-score -1.50 ± 1.98 vs. -0.34 ± 1.70). Because these data are cross-sectional, the tests are not designed to show a causal linkage. However, it is likely that inadequate access to food leads certain households to rely more heavily on wild meats.

DISCUSSION

We found that the communities surrounding Kianjavato's forests relied on natural resources for wealth, nutrition, and especially healthcare in a country where adequate alternatives to these resources are often inaccessible, unaffordable, and/or unavailable in sufficient quantity. The trade of precious stones was associated with higher household wealth, and greater wealth appeared to improve children's health and nutrition. However, these effects were perhaps unconnected: the children in households that traded stones were no healthier than those in households that did not sell these mineral resources. While members of households who sold precious stones were also more likely to eat wild meat, wild meat consumption was unrelated to household wealth. Perhaps the most striking finding was that nearly every household collected medicinal plants from the forest. Whether or not this activity positively affected health outcomes cannot be determined from our data, but its prevalence strongly suggests that these natural resources are important for community healthcare.

KIANJAVATO FORESTS AND HOUSEHOLD ECONOMY. The sale of amethysts, emeralds, corundum, and crystals supplied nearly 40% of all reported cash income during the prior year. Households that contained individuals who sold precious stones in the last year also ate nearly five times as many wild animals than those that did not. These findings differ from those in other regions of Madagascar, such as Alaotra, where people who were employed by a large-scale industrial nickel mine ate less wild meat than those who were not employed by the mine because of top-down incentives (Randriamamonjy et al. 2015). Formal industrial nickel mining in Alaotra was structured as a contractual engagement that benefitted the welfare and income of local residents with policies to prevent hunting, which led to either reduced consumption of wildlife or a significant fear of reporting it (Randriamamonjy et al. 2015). There are two commercial formal mining operations that employ local residents in the Kianjavato region. The mining reported by surveyed households in Kianjavato was not part of either commercialized formal activity, but rather an informal, artisanal and potentially illegal activity. It is possible that the interviewees in this study who were comfortable enough to report their open sale of high-value gemstones may also be more willing to report other sensitive information, such as the consumption of wildlife. It is also possible that informal gem collection at this site increased the amount of time spent in forests searching for these stones, allowing additional occasions for the opportunistic capture of wildlife, or increased income to facilitate the purchase of the comparatively expensive wild meat in the region.

KIANJAVATO FORESTS AND NUTRITION. Nearly one sixth of households in Kianjavato consumed forest meat during the prior year (16%). The majority of the wildlife consumed was not threatened with extinction (83%) but was often illegally caught (40%). While this demonstrates broad non-compliance with conservation policies, illegal catch is less than that of the Alaotra wetland complex (Borgerson et al. 2018), the Makira Natural Park (Golden et al. 2014b), or Masoala National Park (Golden et al. 2014b, Borgerson 2016, Borgerson et al. 2016) despite a general lack of law enforcement in the region (officials are often stationed far from the study area). Natural resource use in the forests of Kianjavato has notable similarities and differences from other areas in Madagascar. The people of Kianjavato ate less wildlife than those across other regions of Madagascar, including that of Moramanga, Port Berge, or Mahabo (Razafimanahaka et al. 2012), Betampona (Golden et al. 2014a), Masoala (Borgerson 2016), the Alaotra-Mangoro region (Jenkins et al. 2011), or sites across central and northwestern Madagascar (Reuter et al. 2016a), but ate more wildlife than those in the Alaotra wetland complex (Borgerson et al. 2018). Because we did not survey the density of wildlife in this study, we do not know what effect the availability of wildlife had on this consumption. However, within forest mammal groups, the percentages of households that consumed lemurs, carnivorans, bats, or bushpigs were within the ranges—albeit on the far lower end—of those found in other regions of Madagascar (Golden et al. 2013, 2014a,b, Reuter 2016a, Borgerson 2016, Borgerson et al. 2018).

One concerning finding was the consumption of the Critically Endangered lemur species, *Prolemur simus*. Assuming a minimum population size of 500 individuals (Wright et al. 2008, IUCN 2016), surveyed households ate as much as 1.6% of the remaining population during the prior year. These lemurs were eaten by a very small number of households (N=4), so small scale-targeted incentive-based conservation efforts may be particularly effective for this species.

As in other regions of Madagascar, tenrecs were the most common animal eaten in Kianjavato (Razafimanahaka et al. 2012, Golden et al. 2013, 2014a,b, Borgerson 2016, Reuter et al. 2016a). However, the percentage of households that ate tenrecs during the prior year was smaller than any other documented region (7% in Kianjavato, compared to 10–91% in the sites across central and northeastern Madagascar, Alaotra, Betampona, Masoala, and Makira (ibid)).

Unlike other regions in Madagascar, local Malagasy reported eating the majority of wildlife when they were guests within the households of friends and family. We suspect people reported eating wildlife at the household of a friend or family member as a tool to provide accurate information to the interviewer without incriminating themselves. Most residents of Kianjavato (when not reporting eating wild animals as guests) preferred pursuit hunting using nets or opportunistic hunting using found objects. This also differs from other areas of Madagascar. Hunters in both Alaotra (Borgerson et al. 2018) and sites across central and northwestern Madagascar (Reuter et al. 2016b) primarily use pursuit hunting methods with dogs, whereas passive snare traps are predominantly used to trap forest mammals in Betampona, Makira, and Masoala (Golden et al. 2014a, Borgerson 2016).

While wildlife was rarely purchased (60 animals or 8% of all consumption), the percentage of wild meat purchased was higher than most other research sites in Madagascar (Golden et al. 2013, 2014a,b, Borgerson et al. 2018) but lower than in central and northwestern Madagascar (Reuter et al. 2016a). Wild meat was purchased at a price per kilogram far higher than that of Makira or Masoala in eastern Madagascar (Golden et al. 2014b) or that of sites across central and northwestern Madagascar (Reuter et al. 2016b); but prices were comparable to that of Mahabo in western Madagascar (Randrianandrianina et al. 2010).

Child malnourishment was more severe in Kianjavato than other sites in Madagascar: 53% stunted, 70% underweight, and 22% wasted (WHO 2012, rural Madagascar data). The prevalence of anemia was also high, with 20% of surveyed individuals being affected. Interestingly, we found no gender differences in the prevalence of stunting, underweight, and wasting in children, but found that males were significantly more likely to be anemic than females. The consumption of wild meat was correlated with child malnourishment within a household. Increasing the availability and affordability of nutrient-rich foods and promoting efforts that improve local food security may reduce the hunting of wild species, keeping it within sustainable limits (Wilkie et al. 2016). Previous research has shown that food insecurity can significantly increase the number of forest mammals a household eats (Borgerson et al. 2017, 2018) and that poor health can best predict a person's decision to illegally trap threatened lemurs (Borgerson et al. 2016). The subsistence consumption of forest animals can provide substantial economic and health benefits to Madagascar's rural poor (Golden et al. 2011, 2014a), which explains the psychology around this often-illegal behavior. Yet given the overall low levels of wild meat consumption at this site, and that the consumption of wild meat was not associated with lower childhood anemia or better growth at this site, the forests of Kianjavato may currently be unable to provide an adequate safety net for households experiencing malnutrition and food insecurity.

KIANJAVATO FORESTS AND HEALTHCARE. Ethnobotanical medicines can provide essential healthcare services for treatments that might otherwise be delayed or altogether avoided because of their prohibitive cost or inaccessibility (Golden et al. 2012, Pattanayak and Sills 2001). For example, in southwestern

Madagascar 235 plant species are used to treat 76 categories of illness (Randrianarivony et al. 2017), and in northeastern Madagascar 241 plant species are used to treat 82 categories of illness, providing an economic benefit equivalent to 43–63% of annual household income (Golden et al. 2012). Kianjavato residents relied on forest resources for healthcare more than other regions of Madagascar and they travelled farther distances to reach these presumably valuable resources (Golden et al. 2012, Borgerson et al. 2018). Nearly 100% of households harvested traditional medicines from the forest (compared to 5% in Alaotra, 82% in Betampona, and 94% in Makira), at a rate of approximately twice as often as in Betampona and a distance twice as far from the home as in Alaotra (Golden et al. 2012, 2014b, Borgerson et al. 2018).

CONCLUSIONS

Forests provide essential ecosystem services that improve the wellbeing of the rural communities that live within them (Ickowitz et al. 2016, Milner-Gulland 2012, Redford et al. 2014, Rowland et al. 2017, Sunderland et al. 2013). Yet, as forests are altered to meet the needs of a growing human population, certain direct-use ecosystem services (such as the use of wild animals for food or plants for medicine) are unable to similarly expand to meet the basic needs of the families which live in these forests (Wilkie et al. 2016). A worrying proportion of the Kianjavato population hunts wildlife, is malnourished, and depends on forests to meet their healthcare needs, yet they may be failing to do so. The ecosystem services of Kianjavato's forests may currently be insufficient to meet the needs of residents. Therefore, targeted efforts to increase local access to the healthcare system, household nutrition, food security, and economy while restoring wide-scale environmental conditions are urgently needed. Efforts to improve the stability and accessibility of health, economic, and nutritional services, that can expand with the growing population to meet future needs, may help secure the sustainable use of the remaining essential ecosystem services for the long term, improving the health of local people and maintaining the integrity of the forests in which they live.

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SUPPLEMENTARY MATERIAL

Figure S1. The Study Region.

S2. Survey Materials.

ARTICLE

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Rabies in primates: are aggressive pet lemurs a risk to humans?

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ABSTRACT

Non-human primates harbor zoonotic pathogens including the rabies virus (*Rabies lyssavirus*). Though the chances of rabies transmission from primates is low, guidelines currently recommend a post-exposure prophylaxis for unvaccinated persons. In Madagascar, lemurs have been described as carriers of the rabies virus, but a discussion about the risk of rabies transmission to humans from lemurs, particularly in the context of in-country ownership of lemurs, has not been studied. We use qualitative and quantitative data collected from household surveys (n = 271 interviewees who had seen a pet lemur across 12 urban towns), web-based surveys (n = 229), and the literature (publications using data collected by the Institute Pasteur of Madagascar over the last century) to examine the context in which the rabies virus could be transmitted from lemurs to humans. Though only a few wild and pet lemurs in Madagascar have tested positive for rabies, post-exposure treatment is sometimes also sought out following aggressive incidents with lemurs. Many interviewees (22 ± 6%, mean ± 95% confidence interval CI) across 12 towns indicated that pet lemurs they had seen, had a history of aggression. Some lemur owners appear to be aware that their pets could transmit the rabies virus and seek veterinary care to prevent this. The public health burden of rabies is relatively low in Madagascar and despite some anecdotes in the literature, it appears that lemurs are rarely the source of rabies when humans become infected. However, this case study highlights the lack of data and publications regarding the public health implications of human-lemur contact in Madagascar.

RÉSUMÉ

Les primates non-humains hébergent des pathogènes zoonotiques incluant le virus de la rage (*Rabies lyssavirus*). Bien que les risques de transmission de la rage par les primates soient faibles, les lignes directrices recommandent actuellement une prophylaxie post-exposition pour les personnes non vaccinées. À Madagascar, les lémuriens ont été décrits comme porteurs du virus de la rage, mais une discussion sur le risque de transmission de la rage à l'Homme par les lémuriens, en particulier dans le contexte de la propriété locale des lémuriens, n'a pas été étudiée. Nous utilisons des données qualitatives et quantitatives collectées à partir d'enquêtes auprès des foyers (n = 271 interviewés ayant vu un lémurien dans 12 villes), des enquêtes en ligne (n = 229) et de la littérature (publications utilisant des données collectées par l'Institut Pasteur de Madagascar au cours du siècle dernier) pour examiner le contexte dans lequel le virus de la rage pourrait être transmis par les lémuriens aux humains. Bien que seuls quelques lémuriens sauvages et animaux de compagnie à Madagascar aient été testés positifs à la rage, un traitement post-exposition est parfois également recherché suite à des agressions par des lémuriens. De nombreuses personnes interrogées (22 ± 6%, moyenne ± Intervalle de confiance IC à 95%) dans 12 villes ont indiqué que les animaux de compagnie qu'ils avaient vus avaient des antécédents d'agression. Quelques propriétaires de lémuriens semblent être conscients que leurs animaux de compagnie peuvent transmettre le virus de la rage et demander des soins vétérinaires pour éviter cela. La rage constitue une charge relativement faible pour la santé publique à Madagascar et malgré quelques anecdotes dans la littérature, il semble que les lémuriens soient rarement la source de la rage lorsque les humains sont infectés. Cependant, cette étude de cas souligne le manque de données et de publications concernant les implications / conséquences du contact entre humains et lémuriens sur la santé publique à Madagascar.

INTRODUCTION

Non-human primates (NHPs) are known to harbor a large diversity of zoonotic pathogens and they are often targeted for zoonotic disease surveillance (Levinson et al. 2013). For example, studies have shown that NHPs in all regions of the world can be carriers of the rabies virus (*Rabies lyssavirus*) (Gautret et al. 2014). The rabies virus, an agent of a lethal encephalitis, is responsible for around 55,000 human deaths every year (World Health Organization 2010). In Africa, rabies causes ~24,000 human deaths per year with 4 out of every 100,000 people at risk (World Health Organization 2010). Rabies in humans is almost always fatal once clinical signs develop (National Health Service 2017).

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When humans interact with NHPs (e.g., via pet ownership, tourism encounters, in the process of capturing an animal for bushmeat) there are opportunities for the exchange of pathogenic organisms (reviewed by Muehlenbein 2017), such as the rabies virus. Though the chances of rabies transmission from primate bites or scratches are low (Health Protection Agency 2013), when bites/scratches occur, guidelines typically recommend a post-exposure prophylaxis (PEP) for unvaccinated persons (Health Protection Agency 2013). In these cases, the World Health Organization (2010) recommends the provision of both a vaccine and the rabies immunoglobulin in response to severe injuries (e.g., transdermal bites or scratches; licks on broken skin or mucous membrane) and just the vaccine in response to minor injuries (minor scratches or abrasions without bleeding) from wild animals. A 2014 review (Gautret et al. 2014) concluded that, "a large number of international travelers sustain NHP-related injuries during their trips" (p 6). The study hypothesized that "underreporting of rabies in NHPs is likely to be significant" (p 4).

In Madagascar, the rabies virus is found across the entire island (Morvan et al. 1993, Reynes et al. 2011). Dogs and cats are the two-most commonly suspected vectors for rabies transmission to humans in Madagascar; in 1998, dogs were suspected as the source of potential rabies exposure in 93% of consultations in which a person received PEP treatment for rabies (n = 5,165 people in Madagascar; Zeller et al. 1999). In cases where animals are tested for rabies (after a human receives PEP treatment following an interaction with the animal), cattle, pigs, and dogs test positive more than 50% of the time for rabies (Andriamandimby et al. 2013). Some wild animals in Madagascar have been noted as potential rabies carriers for humans (including bats, Andriamandimby et al. 2013) and the risk from these animals is recognized by entities like the Center for Disease Control (2017).

Madagascar's endemic primates – the lemurs – can be infected with the rabies virus (this having been experimentally confirmed prior to the 1930s, Girard 1930: 15; cited by Jennings 2009; one lemur – out of 26 lemurs tested – tested positive for rabies, Zeller et al. 1999; four laboratory confirmed cases in lemurs in 1994 in Madagascar, Tsiresy 1995 cited in Gautret et al. 2014). It has been hypothesized that lemurs could contract rabies from feral and pet dogs, before transmitting the virus to humans (Coulanges et al. 1974), but it is not clear that this is a frequent occurrence. Wild lemurs rarely come into contact with domestic or feral dogs, where they might contract rabies (Coulanges et al. 1974). However for pet lemurs, it was previously though that captive/pet lemurs are kept away from humans (i.e., in a cage) or well supervised (i.e., away from dogs) (Coulanges et al. 1974) but more recent research indicates that 28% of lemurs seen in captivity are kept as habituated animals (i.e., not restrained) with more freedom of movement than caged or restrained lemurs (Reuter and Schaefer 2016).

The potential transmission of rabies from lemurs to humans has been studied only as an aside to the study of rabies transmission to humans from dogs, cats, bats, and cattle (e.g., Coulanges et al. 1974, Zeller et al. 1999, Reynes et al. 2011, Andriamandimby et al. 2013). The risk of humans contracting rabies from lemurs has been considered very low (Coulanges et al. 1974). However, human-lemur contact, where rabies transmission might occur, is common in the context of illegal pet lemur ownership within Madagascar's tourism industry (Reuter and Schaefer 2016, Reuter and Schaefer 2017a). In Madagascar, which was visited by 222,000 tourists in 2014 (World Tourism Organization 2014), there are thousands of lemurs kept in illegal captivity (Reuter et al. 2016). In many cases, these lemurs are kept for the purpose of money-making from the tourism industry (Reuter and Schaefer 2017a). For example, tourists might pay money to take a photo with a lemur or feed a lemur a banana, or lemurs might be kept as an 'added value' attraction at restaurants and/or hotels (Reuter and Schaefer 2017a). As such, many tourists will encounter captive, semi-captive, or habituated but wild lemurs (at hotels, restaurants, in private and public reserves, national parks, and in other public areas such as on the beach) where human-lemur interactions are often encouraged (Reuter and Schaefer 2017a).

In some cases, captive lemurs are reportedly aggressive with their human owners or with tourists (Reuter and Schaefer 2017b). It is through these aggressive incidents, which can result in bites and scratches, that the rabies virus could be transmitted. Unfortunately, even when aggressive incidents are not due to rabies (i.e., not due to heightened aggression during the so-called 'furious rabies' stage, Coulanges et al. 1974), the inability to know with certainty whether a lemur is infected with rabies means that humans are encouraged to seek PEP treatment whenever these types of incidents occur (Coulanges et al. 1974). Interactions with NHPs result in numerous tourists needing to receive preventative post-exposure treatment every year. In France, of the 424 patients visiting a rabies clinic (including people returning from travels abroad), almost 20% were injured by nonhuman primates, including lemurs (Gautret et al. 2010).

It is clear that gaps in our knowledge remain with respect to rabies transmission to humans via lemurs. Prior review papers on the disease ecology of wild lemurs do not mention rabies (e.g., Junge and Sauther 2006). In addition, no publication has focused exclusively on rabies transmission from lemurs to humans and as noted below, the publications on the topic (e.g., published by, or with data from, the Institute Pasteur of Madagascar [IPM]) are difficult to access. For example, a global review on the rabies virus in NHPs (Gautret et al. 2014) found little information on this topic from Africa and cited just one conference presentation on the subject for Madagascar (Tsiresy 1995; having apparently not come across any of the IPM publications). Therefore, given the large and increasing number of tourists visiting Madagascar (World Tourism Organization 2014), and the high number of lemurs being kept in captive conditions where they are encouraged to directly contact humans (Reuter et al. 2016), there is a need to revisit the issue of disease transmission between humans and lemurs.

METHODS

QUANTITATIVE DATA. The data presented in this paper include information collected from household surveys as well as data from IPM publications (from the years 1898 to 2016).

Household surveys. Data were collected in 12 towns (Table 1) in central, southern, and eastern Madagascar in July to August 2016 (see Reuter et al. 2018 for full methods on survey administration). Data collection took place in both urban and rural areas using 627 household surveys. We used stratified random sampling within towns and interviewed no more than one adult per household to ensure independent sampling. Interviews were anonymous, no identifying information was collected, and respondents received no compensation for their participation. Interviews took an average of ~10 minutes. Verbal informed consent was received, and interviews were conducted by a 2-person team composed of one international project leader and one trained Malagasy translator (see Acknowledgements). Questions were asked in the local Malagasy dialect with the semi-structured nature of the interview allowing for clarifying questions to be posed in French or Malagasy as needed. A full list of interview questions can be found in Reuter et al. (2018), and included (among other questions): (i) Have you seen a pet lemur? (ii) Was the lemur aggressive? If yes, how? (iii) Do you know how pet lemur ownership ended? Following Reuter et al. (2016), we did not provide interviewees with a definition of a 'pet lemur' though the researchers' definition of what constitutes a pet lemur can be found in Reuter et al. (2016). We excluded lemurs seen in zoos or reserves.

International standards for research ethics were followed and research was approved by an ethics oversight committee (Institutional Review Board, University of Utah). Research followed all national and local laws pertaining to the survey of adults in Madagascar. Research was authorized by locally elected officials in every town and commune in which research took place. This research required no government permits.

Data published by the Institute Pasteur of Madagascar. Since 1901, the Institute Pasteur of Madagascar [IPM] has provided rabies services to the public in Madagascar. IPM reported the first lemur suspected as being the vector of rabies in 1910 (Girard 1930: 905 as cited in Jennings 2009). Since 1939, anti-rabies services have been provided to the Malagasy public nationwide via the Center for Anti-Rabies Treatment (CTAR) within the IPM. CTAR supplies rabies vaccines to all anti-rabies treatment centers in Madagascar, provides rabies treatment to humans free of charge, and tests animals suspected of being the source of the rabies virus. In many cases, the IPM's annual reports provide a historical record of the number of rabies cases treated nationally each year in Madagascar, as well as the number of cases that are attributed to lemurs (both wild and captive); however, the most recent annual reports do not include this level of detail.

We present information taken from the annual reports for IPM (via the IPM website) or where data from the IPM had been published by other authors in secondary literature (Table S1). Many of the IPM reports are accessible only via the archives in Madagascar or in Paris, France and are not available through interlibrary loan; therefore, much of this information is not in the public domain. We present what information we have been able to access through the above-noted, online literature search.

Analysis. For household surveys, as there may be greater variation between than within towns, interviewees were used as subsamples within each study site for most analyses and towns were used as replicates; therefore, when results are presented as mean values with 95% confidence intervals, towns are used as replicates.

QUALITATIVE DATA. In addition to the quantitative data reported, above, we present some qualitative information recorded from 229 web-based surveys about pet lemurs in Madagascar (administered in 2015 and 2016). The methods and a broader investigation into the results of the surveys have been published in Reuter and Schaefer (2016, 2017a,b). These web-based surveys asked people to provide different pieces of information about the pet lemurs that they had seen in Madagascar; in some instances, respondents provided detailed information about the context of lemur ownership. Select quotes from respondents are provided, below.

RESULTS

PARAMETERS OF THE DATASET. In 2016, household interviews across the 12 towns yielded 271 individuals who had seen a pet lemur (Table 1). These individuals provided information on whether the pet lemurs were known to be aggressive.

IPM data taken from primary and secondary publications included relevant information from the years 1898 to 2016 (Table S1). These data indicate that nationally, 566 people in 1960 (Source C, Table S1), and at least 4,022 people per year from 1998 onwards (Sources E and F-N, Table S1), received PEP rabies treatment following potential exposure to the virus (Figure 1a). Most

Table 1. The proportion of respondents across 12 towns who reported about a pet lemur that had been/was aggressive towards humans.

Town (French name)	Number of people interviewed	Number of people who had seen a pet lemur	Percent of respondents indicating that the lemur had a history of aggression
Ambositra	99	44	23%
Anakao	40	33	6%
Andasibe	53	3	33%
Antananarivo	54	11	27%
Antsirabe	51	22	32%
Beforona	54	6	33%
Efotse	9	8	13%
Fianarantsoa	84	50	32%
Tôlanaro (Fort-Dauphin)	50	31	10%
Moramanga	60	23	26%
Toamasina (Tamatave)	50	23	17%
Toliara (Tulear)	23	17	12%
Total	627	271	22 ± 6%

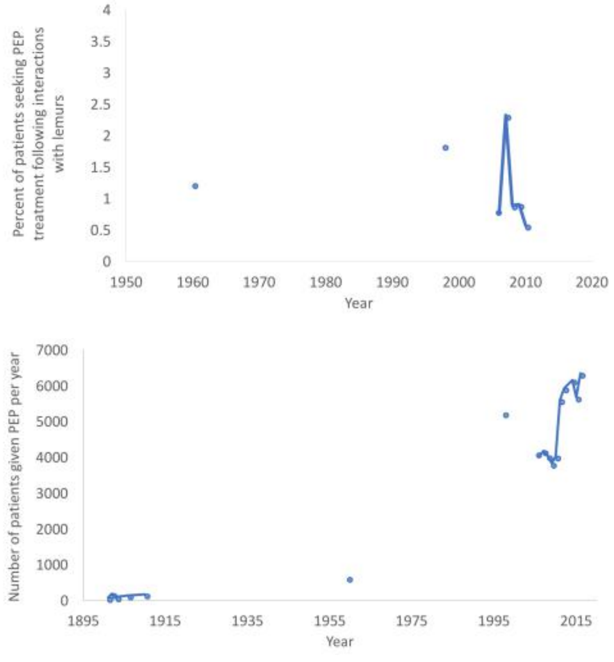

Figure 1. The number of patients given PEP rabies treatment by IPM following potential exposure to the virus, at a national level (a) and the percent of rabies patients who received PEP treatment because of an interaction with a lemur (whether captive or wild) (b). Note that data for figure (b) were not available for all years where data for figure (a) could be found. Lines are drawn between points where there are two or more continuous years of data available. † For (a), data taken from Sources B, C, E, and G-P (Table S1). For (b), data taken from Sources C, E, G, H, I, J, and K (Table S1).

Figure 2. Photographs submitted to the Pet Lemur Survey showing a typical human-lemur encounter by a tourist (a), a scar on the hand of a pet lemur owner in Madagascar from a lemur bite (b), and two different habituated pet lemurs (owned by two different owners) interacting with domestic dogs (c,d).

individuals (63% in 1902, 58% in 1910, 77% in 1960, and between 90% - 97% from 2006 to 2015; Sources B, C, E, G-O, respectively in Table S1) received their PEP treatment in the greater Antananarivo area.

TRANSMISSION FROM DOGS TO LEMURS. We do not have quantitative data on how often lemurs come into contact with feral or domestic dogs (Figure 2). However, there are several anecdotes collected via the web-based surveys that help clarify how pet lemurs might be exposed to the rabies virus from feral and pet dogs, and subsequently infect humans.

Several respondents to the web-based survey described lemurs being kept on leashes where they could not escape village dogs (Figure 2). One respondent wrote: "They kept [the lemur] tied to a post with a rope around his middle because he often tried to bite the children and the dogs." Another wrote: "There were several [lemurs] at a home in the village which were tied with rope around their waists with only a couple of feet allowance to move (no cage). [The lemurs] had frequent diarrhea…They were incredibly stressed and had no way to hide or get away from people, dogs, etc."

In other instances, lemurs – even on leashes – had relatively friendly relationships with some, but not all, dogs. "One adult lemur was kept on a leash. The place also had a dog that the leashed lemur would try to leap at, but with the (short) leash on, it would just fruitlessly jump over and over and over and over again, swinging like a pendulum, while the dog stood just out of range. I did see the lemur at night once snuggled closely with another dog, so…maybe it just didn't like this one particular dog or it wanted to wrestle. Humans could go up and hold and pet the lemur and the lemur would be calm, but when the dog appeared, the lemur would go crazy after the dog again." The anecdotes provide evidence that some pet lemurs could conceivably be bitten/bite a dog and then, in turn, bite humans.

LEMURS AS CARRIERS OF THE RABIES VIRUS As part of their rabies. surveillance services, IPM conducts rabies tests on animals when the patient being given PEP or being treated for rabies can identify the animal suspected of being the source of the viral infection. IPM records indicate that ~150 lemurs were tested for rabies since 1898 (total number of lemurs tested is unclear given overlaps in the year-ranges considered by different sources; Table S2). Of the lemurs tested, only one lemur (between 1994 and 1998) tested positive for rabies (another publication noted that four lemurs in Madagascar were laboratory confirmed to have rabies in 1994, though it is not clear whether these were the same lemurs tested by IPM, Tsiresy 1995 as cited in Gautret et al. 2014). In addition, between 1910 and 1913, seven lemurs were recorded as testing positive for rabies but Coulanges et al. (1974) has hypothesized that six of these individuals should be considered false positives. The reasoning provided in Coulanges et al. (1974) is that no lemurs had been found to be positive for rabies between 1954 and 1973 and that, therefore, 6 or 7 of these earlier 'positive' tests likely were incorrect, as they were all made by one observer during 1910 and 1913. In comparison, dogs that have bitten or scratched humans (and where the human seeks rabies treatment), test positive between 42% to 69% of the time (Table S2).

Some pet lemur owners appear to be aware that lemurs can be carriers of the rabies virus. In the web-based survey, one veterinarian in central Madagascar indicated that "at the vet clinic, we have some clients from the South who bring lemurs to vaccinate against rabies…even if having pet lemurs is against the law, as a clinic, we cannot refuse to treat them." However, not all owners are able to find veterinarians who are willing or knowledgeable enough to treat their pet lemurs. One entity in Madagascar (visited in 2016 as part of our household surveys) that had two lemurs on the premises without permits (although they were caring for lemurs that had been kept as pets initially by someone else) indicated that they had difficult time securing veterinarian care for their lemurs (see Reuter et al. 2018 for more information).

TRANSMISSION FROM LEMURS TO HUMANS. To transmit the rabies virus to humans, lemurs must lick, bite, or scratch humans and such aggressive interactions were reported in our survey. In our household surveys, 22 ± 6% (± 95% CI, n = 12 towns as replicates) of respondents who had seen a pet lemur reported that the pet lemur had a history of aggression (Table 1). A few respondents (n = 11 individuals) provided additional context for the lemur's aggression: the lemur was aggressive towards individuals that were not its owner (n = 4); the lemur had bitten adults and children (n = 2); the lemur was aggressive when outside a cage and/or is caged because it is aggressive (n = 2); the lemur became aggressive during reproductive season (n = 1); the lemur became aggressive when it matured into an adult (n = 1); and the lemur was aggressive when someone accidentally stood on its tail (n = 1).

Lemurs are rarely cited as a potential source for rabies when humans seek PEP treatment in Madagascar. In 1960, 1.24% of the individuals treated at IPM cited lemurs as the reason for needing PEP rabies treatment (Figure 1b). From 2006 to 2010, this percentage ranged between 0.57% in 2010 to 2.32% in 2007 (Figure 1b). Both wild and pet lemurs have been cited as the reason for needing PEP rabies treatment, with 23% to 61% of people noting that the lemur was a pet (Table S3).

The lemurs' owners are not the only ones that are affected. One tourist, who had visited an "island where [lemurs] are being fed bananas by tourists" reported in our web-based survey that the lemurs were "quite aggressive." The respondent further noted:

"my husband was bitten (later requiring rabies shots) and I was scratched."

DISCUSSION

In this paper, we use rabies as a case study for examining how disease transmission might take place between lemurs and humans in Madagascar. Though the risk from rabies is low, we use quantitative and qualitative data to elaborate on how transmission of the rabies virus from lemurs to humans might take place. The risk of rabies transmission from lemurs to humans is not unique to Madagascar; nine other African countries have primates that carry rabies (Gautret et al. 2014). However, what is unique about the case of lemurs in Madagascar, at least for the African continent, are the in-depth data that have been collected over the past century in Madagascar by the IPM (Jennings 2009). These data, combined with our surveys on captive lemurs in Madagascar, provide an interesting case study for examining the potential risk of rabies in the context of pet primate ownership.

RABIES IN MADAGASCAR. There are approximately four to ten confirmed cases of human rabies each year in Madagascar with most cases in urban areas, especially near the capital of Antananarivo. Rabies cases in rural areas are likely underreported (Andriamandimby et al. 2013). In 2016, there were 6,338 people given PEP rabies treatment following potential exposure to the rabies virus (Institut Pasteur de Madagascar 2017). The primary vector of rabies in Madagascar is typically roaming dogs (Jennings 2009; Sources G-P in Table S1). It has been noted that the human victims of rabies are often children, because they play outdoors and therefore come into contact with dogs, the disease's main carrier (Jennings 2009). The Center for Disease Control (2017) notes that children are at risk because they "tend to play with animals, might not report bites" and "their smaller stature…makes severe bites to high-risk areas, such as the face and head, more likely." However, partly because of nationwide vaccination efforts and the provision of PEP before clinical signs appear, the number of deaths every year are low.

RABIES AND LEMURS. It appears possible that lemurs could get rabies from both dogs (Coulanges et al. 1974), fossa (*Cryptoprocta ferox*), and potentially other animals known to carry rabies. In terms of lemur contact with dogs, there is evidence of feral and domestic dogs making inroads into areas where wild lemurs would roam. For example, 41% of domestic dogs around the Ranomafana National Park had reportedly killed a wild animal, sometimes on a weekly basis (Valenta et al. 2016). Regarding fossa, a man in Ihosy contracted rabies from a fossa bite in 2007 (Institut Pasteur de Madagascar 2007). The sample taken from this fossa was tested by the Institute Pasteur Paris, which determined that it was "very close to the canine rabies strains in Madagascar" (Institut Pasteur de Madagascar 2007). It is therefore feasible that lemurs could also contract rabies from fossa prior to passing the virus along to humans.

Nevertheless, the percentage of lemurs carrying the rabies virus appears to be very low (Table S2) though few lemurs have been tested. For example, IPM records indicate that only ~150 lemurs have been tested for rabies since 1898 (Table S2), which is much lower than the number of people who thought they might have been exposed to rabies from a lemur (Table S3) and much lower than the number of animals tested by IPM in total (Table S2). It was noted that in the past, the number of animal specimens tested by IPM was low though efforts were made in 1997 "to encourage veterinarians to ask for rabies diagnosis in suspicious animals free of charge" (Zeller et al. 1999: 59). Most annual IPM reports still make mention of the difficulties around collecting, transporting, and testing samples and also continue to note that few samples from areas outside of Antananarivo are tested (e.g., Institut Pasteur de Madagascar 2016, 2017). A recent IPM annual report noted that veterinarians often do not have the resources to send samples for testing (Institut Pasteur de Madagascar 2007) even though the testing itself is a free service.

RABIES TRANSMISSION FROM LEMURS TO HUMANS. There is a potential for both wild and pet lemurs to transmit rabies to humans. There are numerous reports in the literature of international tourists to Madagascar seeking PEP rabies treatment upon returning home following being bitten by a lemur (Folb and Cooke 2006, Gautret et al. 2010). There are many anecdotes of highly habituated, wild lemurs in national parks (and private/public reserves) jumping onto tourists in search of food (e.g., lemurs in the Ankarana National Park, KER pers. obs.). In the Bradt travel guide, an anecdote regarding an infant-carrying, female *Lemur catta* who bit a tourist in self-defense (Bradt 2007: 124) is used to illustrate the value of seeking rabies vaccinations prior to travel for 'peace of mind', and because medical treatment may be difficult to obtain.

While the data collected by IPM show that people more frequently seek PEP rabies treatment following interactions with wild lemurs (rather than to pet lemurs, Table S3), captive lemurs could still contract rabies and transmit it to humans. In 1993, a rabies case was described in the IPM dataset that involved a captive ring-tailed lemur (*L. catta*) at a tourism resort that had been in contact with many dogs suggesting that the virus was transmitted from dog to lemur (Zeller et al. 1999). As another example, a well-known lemur researcher was quoted as stating that, "the chances [of being infected by rabies from a lemur] are so small that I wouldn't dream of getting rabies shots after a lemur bite…the chance of a rabid dog catching a lemur which then got away seem not worth worrying about – except in one circumstance. If the lemur was hand-raised, either a current pet or a pet released into the wild, it may attack a human without provocation" (Bradt 2007: 124). The threat of rabies transmission from pet primates to humans is not limited to lemurs. For example, a study of U.S. soldiers stationed in Afghanistan found that over a 4-month period, 8 of 10 bites from NHPs requiring preventative rabies treatment were from pet monkeys (Mease and Baker 2012).

IMPLICATIONS

The number of lemurs that have tested positive for rabies is extremely low, and therefore the risk of humans contracting rabies from lemurs does not appear to be high. Yet, Madagascar is somewhat unique in that injured travelers attending a rabies treatment center in France for PEP treatment were five times more likely to be seeking treatment due to an encounter with a primate in Madagascar compared to North Africa, the rest of sub-Saharan Africa, Latin America, and the Middle East (n = 424 injured travelers attending a rabies treatment center in Marseille, France between 1994 and 2007, Gautret et al. 2010).

There are several factors that could potentially lead to an increase in the number of cases of humans contracting rabies from both wild and pet lemurs in the future. First, the amount of contact between wild and pet lemurs and dogs could increase. Increasing human population of Madagascar (2-3% increase/year, United Nations 2017) could be accompanied by an increase in the number of dogs on the island (as the African human population increases, so does the dog population, Cleaveland 1998). An increase in Madagascar's dog population could lead to increased contact between dogs and wildlife (Cleaveland 1998). Dogs in Madagascar are known to venture into forests and sometimes attack wild animals (Valenta et al. 2016), which could result in an increase in the number of wild lemurs contracting rabies. Second, lemurs could become more susceptible to diseases in the future. Madagascar's increasing human population size could lead to further habitat degradation, thereby placing stress on the lemurs and making them more susceptible to diseases such as rabies (Junge and Sauther 2006). Given that the rabies virus appears to have been introduced to Madagascar around 1840 (Jennings 2009), lemurs may have little immunity to the virus, and lemurs in general are highly susceptible to new diseases (Junge and Sauther 2006). Third, lemur-human contact could increase in the future. The increasing population in Madagascar could bring more people into contact with lemurs (Junge and Sauther 2006). In addition, an increase in the number of tourists visiting Madagascar could place more humans in contact with lemurs as tourists pay to feed lemur and/or take photos with lemurs (Reuter and Schaefer 2017a). A study of all Danish travelers traveling to rabies-endemic countries from 2000 to 2012 indicated that increases in the use of Pre-exposure prophylaxis (PrEP) and PEP could be explained by the increased rate of traveling, and not by an increased awareness of rabies risk or more bites per traveler (Christiansen et al. 2016).

The number of travelers exposed to rabies by NHPs and receiving PEP has been increasing (Gautret et al. 2014). The Danish study also found annual increases of 8.2% and 8.8% of PrEP and PEP usage, respectively, from 2000 to 2012 (Christiansen et al. 2016). In other studies, bites from NHPs, including lemurs, accounted for up to 20% of international travelers seeking PEP rabies treatment, with most being injured from bites (Gautret et al. 2010). Additionally, Riesland and Wilde (2015) suggest that, of people seeking treatment for rabies, tourists are bitten by NHPs more often when compared to locals. In one survey of 3,845 tourists at four international locations for primate-based tourism, most tourists knew they could get diseases from wild primates and yet still touched or fed primates when given the opportunity (Muehlenbein 2017). In Madagascar there are likely thousands of human-lemur interactions by tourists every year (e.g., Reuter and Schaefer 2016, 2017b) despite travel guidelines advising against the touching of these animals. For example, the Consulate General of France specifically advises that both residents and expatriates living in Madagascar should not touch cats, dogs, and lemurs because of the risk of rabies (Le Brun and Randrianarison 2014).

Since Madagascar's population is increasing, it would not be surprising if the number of pet lemurs (estimated at 28,000 between 2010 and 2013; Reuter et al. 2016) also increased, though no data on whether pet lemur ownership has increased, decreased, or remained stable exist. Our household surveys indicate that aggression towards humans, including bites and scratches, is not uncommon (approximately 22% of individuals who had seen a pet lemur reported it was aggressive) which could potentially increase the rate of rabies transmission. Though the risk of getting rabies from lemurs may currently be low, individuals should still take prophylactic precautions (Coulanges et al. 1974; Christiansen et al. 2016).

FUTURE RESEARCH

It has been noted that the "animal trade for the purpose of exotic pet ownership will continue to facilitate the emergence of infectious diseases" (Muehlenbein 2017: 35). We suspect that this is also true for lemurs in Madagascar. It is likely that lemurs are carriers for other viruses that are of greater public health concern than the rabies virus, but the data needed to evaluate their role in transmitting those diseases likely do not exist. For viruses alone, lemurs were "directly implicated" in an outbreak of the Chikungunya in Madagascar in 2005–2006, described as "an amplifying reservoir host" for Yellow Fever, and carry the human-mediated herpesvirus (reviewed by Barrett 2011). Notably, changes in the environment – such as is expected with climate change – are anticipated to change lemur (Brown and Yoder 2015) and parasite distributions (including viruses, Barrett 2011). Therefore, additional research is needed to better inform the impacts of pet lemur ownership on the transmission of diseases between humans and lemurs.

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SUPPLEMENTARY MATERIAL

Available online only

Table S1. The primary and secondary sources from which IPM data were collected, including information on the information source, the year(s) for which this source provided information, and the type of information taken from this source.

Table S2. The number and percent of animals that tested positive for the rabies virus in tests conducted by the Institut Pasteur de Madagascar (IPM, samples typically sent to IPM by veterinarians). These lemurs were tested by the IPM because the animals were suspected as being rabies virus carriers (i.e., a human receiving PEP treatment from IPM indicated that the specific animal was the reason for seeking treatment).

Table S3: Information collected from patients about whether the lemur in question (i.e., the lemur which caused a person to receive PEP treatment at IPM) was a wild or pet lemur, as well as what happened to the lemur in question. Descriptions of lemurs are translated from the French language directly from IPM reports (noting that the IPM reports provided no further information about how lemurs were categorized into these different descriptions).

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Dryland tree data for the Southwest region of Madagascar: alpha-level data can support policy decisions for conserving and restoring ecosystems of arid and semiarid regions

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ABSTRACT

We present an eco-geographical dataset of the 355 tree species (156 genera, 55 families) found in the driest coastal portion of the spiny forest-thickets of southwestern Madagascar. This coastal strip harbors one of the richest and most endangered dryland tree floras in the world, both in terms of overall species diversity and of endemism. After describing the biophysical and socio-economic setting of this semiarid coastal region, we discuss this region's diverse and rich tree flora in the context of the recent expansion of the protected area network in Madagascar and the growing engagement and commitment to ecological restoration. Our database, DTsMada (short for Desert Trees of Madagascar), is part of a larger 'work-in-progress', namely an eco-geographical database on desert and dryland trees of the world. DTsMada draws heavily on the Catalogue of the Vascular Plants of Madagascar (MadCat) project, in which floristic, ecological and endemism parameters are compiled, together with available conservation status assessments based on IUCN Red List criteria. Both are projects within the plant systematics database, Tropicos®, developed at Missouri Botanical Garden and maintained on the Garden's website. To highlight the need for greater study of the interactions between biological, bioclimatic, and anthropogenic determinants of current and potentially changing biogeographical patterns and community dynamics in the tree strata of vegetation in the study area, we consider four contrasting groups of native trees: *Adansonia* spp. (Malvaceae), *Pachypodium* spp. (Apocynaceae), *Baudouinia* spp. (Fabaceae), and all 11 species in the 4 genera of Didiereaceae in Madagascar. We discuss DTsMada as a prototype dataset of alpha level information vital for effective conservation, landscape planning, sustainable use and management, and ecological restoration of degraded arid and semiarid ecosystems, in Madagascar and elsewhere.

RÉSUMÉ

Nous présentons un ensemble de données éco-géographiques sur les 355 espèces d'arbres (156 genres, 55 familles) présentes dans les fourrés et forêts épineux de la frange côtière aride et semiaride du Sud-ouest de Madagascar. Cette région possède un des assemblages d'arbres de climat sec les plus riches (en termes de diversité spécifique et d'endémisme), et les plus menacés au monde. Après une description du cadre biophysique et de la situation socio-économique de cette région, nous présentons cette flore régionale dans le contexte de la récente expansion du réseau de des aires protégées de Madagascar et de l'engagement croissant dans le domaine de la restauration écologique. Notre base de données DTsMada (raccourci de « Desert Trees - Madagascar », en anglais) s'inscrit dans le cadre d'une base de données éco-géographique plus large que nous développons, regroupant les espèces d'arbres des régions arides et semiarides du monde entier, avec un accent particulier mis sur leur utilisation dans la conservation, gestion et restauration écologique. Nombre des informations présentées dans DTsMada proviennent du projet MadCat (Catalogue des plantes vasculaires de Madagascar) qui regroupe des données floristiques et écologiques, et les statuts d'endémisme et de conservation des espèces végétales, basés sur les critères de l'UICN.

Ces deux projets font partie de la base de données taxonomique Tropicos®, du Jardin Botanique du Missouri. Pour souligner le besoin de disposer de plus d'études pour comprendre : les interactions entre les facteurs biologiques, bioclimatiques et anthropiques qui affectent la biogéographie et les dynamiques des communautés dans les strates arborées de la végétation dans la région étudiée, qu'il s'agisse de la situation actuelle ou celle d'un futur qui sera éventuellement modifié, nous considérons quatre groupes bien différents d'espèces d'arbres in-

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digènes : *Adansonia* spp. (Malvaceae), *Pachypodium* spp. (Apocynaceae), *Baudouinia* spp. (Fabaceae) et les 11 espèces dans les 4 genres de la famille des Didiereaceae du Sud-ouest de Madagascar. Nous traitons DTsMada comme prototype d'une base de données de niveau alpha, vitales pour la conservation, la planification, le développement durable, la gestion et la restauration écologique des écosystèmes arides et semiarides de Madagascar et d'ailleurs.

INTRODUCTION

Seasonally-dry, inter-tropical forests, woodlands, and thickets are among the most highly threatened and least well-studied terrestrial ecosystems on Earth (Sunderland et al. 2015). They are as rich or richer in both plant and animal species and more productive than other dryland ecosystems and many mesic ones (Aronson et al. 2005), yet their importance—for both biodiversity conservation and delivery of ecosystem services—is often underestimated. The drylands—including the hyperarid, arid, semiarid, and dry-subhumid biomes that occupy >40% of the Earth's land surface (Reed and Stringer 2016)—are often treated as if they have little lasting value to people. This in turn tends to lead to a spiral of degradation leading to potentially catastrophic consequences for over two billion people who live in these regions (Reynolds et al. 2007, Lal et al. 2012).

There are two underlying factors that contribute to degradation. Firstly, the unsustainable extraction of woody biomass and palatable fodder through a process called 'artificial negative selection' (Burkhart 1976). The most desirable timber trees are progressively harvested and removed, thus leading to replacement by less desirable individuals of the species, and more generally to species of inferior ecological quality and timber value compared to the ones removed through selective extraction. Similarly, the hardest-wooded trees that people can exploit are generally extracted for charcoal production first—e.g., *Baudouinia rouxevillei* in southwest Madagascar—while soft-wooded trees (such as Baobabs) are left behind until people have no other choice left but to use them for fiber and wood. Similar patterns of extraction generally apply to forage and fodder consumption, especially when population density is high and people are very poor (Randriamalala et al. 2016). Secondly, the impact of the 'shifting baseline syndrome' proposed by fisheries scientist Pauly (1995), a term coined to describe the gradual lowering of expectations of the quality and quantity of fishery resources with each new generation of people. Although conceived and applied in relation to ocean fish stocks over the past 100 years (Pauly 1995), arguably it applies to dryland ecosystem trees and other valuable resources as well. Many dryland ecosystems and arboreal formations in southwestern Madagascar and elsewhere, were once much more abundant and diverse than they are today (Felger et al. 2001, Le Floc'h and Aronson 2013).

Relative to its size (587,000 km²), Madagascar has a remarkable array of bioclimates which were the subject of an intensive study by Cornet (1974), and vegetation types (Moat and Smith 2007). The island is rich in number of species and in the level of endemism recorded in all groups of organisms. Of the ca.11,400 described species of vascular plants in the country, 95% are angiosperms, and among these, almost 96% are indigenous, with only ca. 400 non-native, naturalized species known. Of the indigenous angiosperm flora ca. 84% have been recorded recently as endemic (Callmander et al. 2011, Rabarimanarivo et al. 2014). However, every year between 50 and 100 new plant species are described, and it is projected that 2,200 or more species of higher plants endemic to Madagascar remain to be described (Phillipson, unpubl. data), which would bring the total number of described species to more than 13,600, with vascular plant species endemism for Madagascar close to 90% (Phillipson 1994, 1996, 2006, Lowry II et al. 1997). Relatively little is known about either historical or contemporary impacts of human land and resource use on the flora and vegetation in Madagascar. In contrast, wild animal-plant interactions have received some attention from evolutionary ecologists working on broad time scales (Gautier et al. 2012). For example, Bond and Silander (2007) suggested that various branch and foliage characteristics present in over 20 plant lineages endemic to Madagascar may have evolved as anti-browsing adaptations and for dispersal by elephant birds or aepyornids and other large herbivores now long extinct. Grubb (2003) suggested that the spines covering the stems of most or all Malagasy Didiereaceae, and whose length parallels leaf length, are an evolutionary adaptation to protect the leaves against arboreal primates. They noted that members of the same family in Africa have no spines. More recently, Crowley and Godfrey (2013) found that giant lemurs may have played a key role in the evolution of spines in this group of plants.

The southwestern dry forests and spiny thickets are everywhere highly fragmented due to over-exploitation of wood, bark and fiber by local people, especially for charcoal production, which remains the main source of cooking fuel in Toliara, and other cities throughout the country (Vieilledent et al. 2018). Harper et al. (2007) estimated that at least 28% of the surface area of forest and spiny thicket was lost between 1950 and 2000, and that in 2000 only 4 million hectares of this vegetation still existed, of which less than half occurred in the coastal area on which we focus in this paper (Figure 1).

Prior to 2003, less than 3% of southwestern Madagascar was included in the national network of protected areas. In that year, former President Ravalomanana launched the so-called Durban Vision process to increase the area in Madagascar available for biodiversity management three-fold, from 17,000 km² to over 60,000 km² (ca. 10% of Madagascar's total land area) within 10 years (Virah-Sawmy et al. 2014). The subsequent program to implement the vision process, through the *Système d'Aires Protégées de Madagascar* (SAPM), has resulted in the formal establishment of 85 additional protected areas by government decrees issued in April and May 2015, as well as significant additions to existing areas. The total number and surface area of the protected area network has been extended to 122 sites covering just over 71,000 km² (Gardner et al. 2018). Four long-established protected areas in southwestern Madagascar contain areas of dry spiny forest and thicket. These are the Andohahela National Park and the Beza Mahafaly Special Reserve, Tsimanampesotse National Park, the area of which has been recently dramatically increased from 432 km² to 2,627 km², and the much smaller (63 km²) Cap Sainte Marie Reserve (Figure 2). In addition, this vegetation type is also represented in certain of the newly established protected areas in the southwest (SAPM 2018) (Figure 2).

The objective of this paper is to present a database of a poorly-studied tree flora that will be part of a worldwide study and an on-line database linked to it, that will cover dryland and desert trees of the world. The global database we are building, and this specific component of it, which we call DTsMada (short for Desert

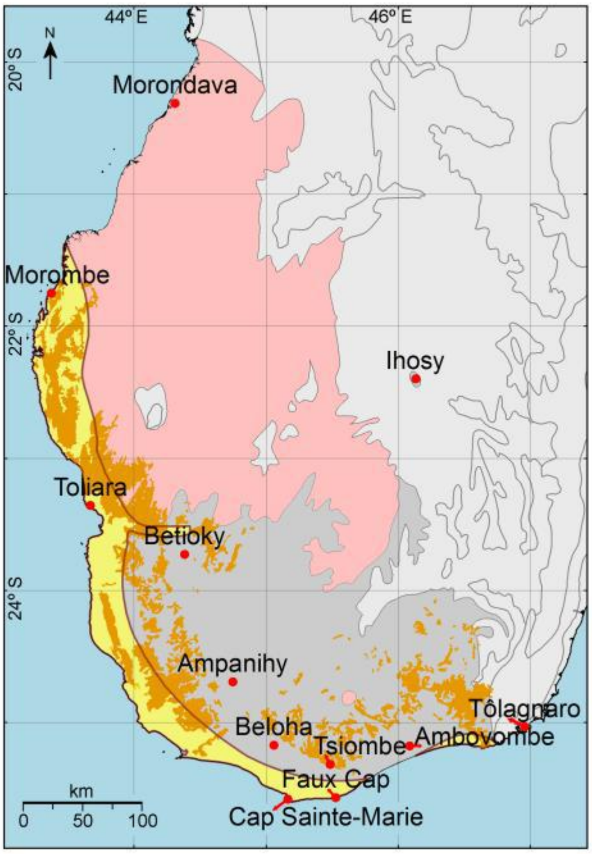

Figure 1. The Semiarid (yellow with brown outline), Lower Subarid (grey), and Upper Subarid (pink) zones in the Dry Southwest region of Madagascar (Cornet 1974). (The scattered areas indicated with orange shading correspond to the ca. 4 million ha of extant spiny forest-thicket in the region (Moat and Smith 2007))

Trees of Madagascar), represent alpha-level information for those engaged in conservation, planning, ecological restoration, and long-term ecosystem management in megadiverse areas not only in Madagascar (Birkinshaw et al. 2013), but also in drylands worldwide. Such databases can provide information in a systematic fashion, and insights, to assist fundamental and applied research, including intentional community reassembly (Verdu et al. 2009, Castillo et al. 2010) through planning for protection and natural regeneration, and active interventions aimed at ecological restoration.

METHODS

STUDY AREA. Here we consider the tree flora of the coastal strip of southwestern Madagascar, which is the driest part (mean precipitation 350–450 mm per annum) of the country, with a notably erratic distribution of rainfall, seasonally, annually and spatially (Donque 1975). This area corresponds to the *Étage sous aride* 3 of Cornet (1994), modified by Schatz (2002) to Subarid 3. Coastal fog contributes additional moisture here (Dewar and Richard 2007), but its role has not been well studied. The formations found here include 'dry spiny forest-thicket', 'degraded dry spiny forest', and 'coastal bushland', as mapped in the Atlas of the vegetation of Madagascar (Moat and Smith 2007). While there are many NGOs and a number of community-based conservation, restoration, and sustainable development projects in Madagascar, especially in the humid, eastern part of the country (Roelens et al. 2010, Birkinshaw et al. 2013), far less attention is being paid to the unique and highly threatened ecosystems in the drier regions (Waeber et al. 2015). This contribution is part of an on-going study and database we are assembling on dryland trees of the world (Le Floc'h and Aronson 2013). We consider the ecology, diversity and distribution, conservation status, horticultural and silvicultural prospects, and the various uses by people of dryland trees to be essential information for all who work for conservation, ecological restoration, and long-term, sustainable ecosystem management in Madagascar, and elsewhere.

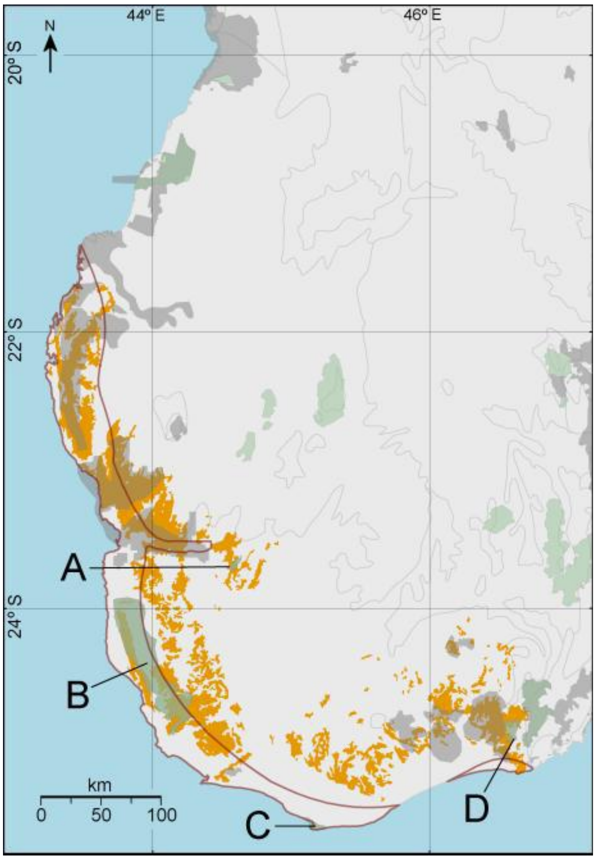

Figure 2. Protected areas in southern Madagascar. (Long-established protected areas in southern Madagascar (shaded green) harboring spiny forest-thicket (shaded orange): A. Bezà-Mahafaly Special Reserve; B. Tsimanampesotse National Park (including recent southeastern extension); C: Cap Sainte Marie Reserve; D. Andohahela National Park (Parcelle II). Newly delimited or proposed protected areas (shaded grey) (Source: SAPM 2018))

The soils of southwestern Madagascar are not diverse, reflecting the relatively simple geology of the region, generally comprising of superficial lithosols and regosols (Cornet 1974). The most conspicuous geological features in the region are the tertiary limestone outcrops that extend from Morombe in the northwest of the region to the extreme south, and which form a series of plateau areas separated by the main river basins draining from the highlands and western slopes of the interior to the southwest coast—namely from south to north the Menarahandra, Linta, Onilahy, Fiherenana, and Mangoky rivers. A generally narrow coastal strip to the west of the limestone outcrops represents a series of ancient, so-called 'aepyornien' dunes (Du Puy and Moat 1996), consisting of consolidated calcareous sandstones derived from the limestone plateau. To the north of Toliara, the Mikea area and at certain sites south of this city, an extensive coastal dune system, varying in width from five to 50 km, overlies the calcareous sandstone formations that reach the surface further inland. In the south, the Karimbola plateau with its calcareous lithosols abuts the rugged basaltic territory of the Androy people, which is adjacent to the volcanic formations that abruptly delimit the dry southwest region from the more humid areas of Madagascar to the east.

Only two of the four long-established protected areas mentioned above harbour dry spiny forest and thicket fall within our study area (Tsimanampesotse National Park and Cap Sainte Marie Reserve). However five of the new protected areas established in 2015 (Gardner et al. 2018) contain dry spiny forest and thicket and lie largely within our study area. These include: (1) Mikea, between Morombe and the Manombo River, (2) Ranobe PK32, between the Manombo and Fiherenana Rivers, (3) Tsinjoriake, between the mouth of the Onilahy River and Toliara, and (4) Amoron-i Onilahy, along the lower Onilahy basin.

Today spiny thicket, deciduous forest and woodland form a highly fragmented patchwork in southwestern Madagascar, but they were formerly more abundant and had much stronger ecological connections across the region and to the much larger dry bioclimatic region to the north that encompasses most of the western half of Madagascar (Moat and Smith 2007, Vieilledent et al. 2018). The two dominant groups of the forest canopy today are tree Euphorbias, and members of the four genera of Didiereaceae occurring in Madagascar, (*Alluaudia*, *Alluaudiopsis*, *Didierea*, and *Decarya*) all of which are to a large degree endemic to this region. Vegetation cover is quite variable, with poorly studied correlations to soils, available nutrients in the soils, and substrate types (Moat and Smith 2007). Mills et al. (2012) suggest that woody plants in particular are sensitive to nutrient status of soils in arid and semiarid regions.

In his seminal treatment of the bioclimate of Madagascar, which recognized a total of 29 bioclimatic units mapped across the whole of Madagascar, Antoine Cornet distinguished a subarid (*subaride*) region in southwestern Madagascar (Cornet 1974). With only 350–650 mm mean annual precipitation, this region represents the driest of the five major bioclimatic 'levels' (*étages*) he recognized. Within the subarid region, Cornet (1974) recognized three bioclimatic 'sub-levels' (*sous-étages*) based on increasing hydric deficit. The term 'subarid' (or sub-arid) is rarely used in English, as compared to 'semiarid', a term widely employed by the FAO and other UN agencies, and which has a similar meaning. A semiarid zone is formally defined as having an aridity index of 0.20–0.50 (i.e., annual precipitation divided by evapotranspiration, which is often denoted as P/ET) (Cornet 1974). These conditions prevail only in the driest part of Cornet's subarid region, the predominantly coastal area of 16,200 km² that is the main subject of this article (Figure 1), and is dominated by southwestern dry spiny thicket (Moat and Smith, 2007).

For simplicity, we use the term 'semiarid' in the context of our study area, which serves to distinguish it from the remainder of Cornet's subarid region, and henceforth refer to it as the 'semiarid zone' (Table S1). The two larger, less arid and predominantly inland areas recognized by Cornet in his subarid region do not have truly semiarid climates, and for these we retain the term subarid. We shall refer to the less arid, northernmost area as the 'upper subarid zone' and the southern area, which has a more gradual transition to the semiarid zone as the 'lower subarid zone (Figure 1) within Cornet's *Étage Subaridé*.

The semiarid zone consists of the sandy littoral strip along the southwestern coast and the lowest elevation portion of the limestone escarpment leading up to the Karimbola plateau. It stretches from the mouth of the Mangoky River, just north of the town of Morombe, located about 220 km north of Toliara, to Cap Sainte Marie (alias Cape Vohimena) at the southernmost tip of Madagascar. From there it extends east to the Manambovo River near the town of Tsiombe, then beyond to the mouth of the Ranofotsy River, just south of Andohahela National Park, 25 km west of Tôlagnaro (alias Fort Dauphin). That small area in the southeast constitutes an isolated rainshadow semi-desert with exceptionally high local endemism.

An important feature of the region is its erratic rainfall. Rainless periods can persist for as long as 12 months, during which a significant water deficit accumulates for most plants, and the entire annual precipitation is often concentrated in one or two short heavy rainstorms. The coastal strip is the driest portion of the region but it is a zone where the contribution of fog to total precipitation is significant, even during the generally dry months April to October (Donque 1975). Cornet (1974) had access to data from eight stations in the dry southwest when preparing his bioclimatic map; only three are situated within the semiarid zone. A more recent synthesis of data was provided by Oldeman (1990) (Table S2). Still, reliable long-term data on weather and climate are lacking.

Plant species diversity and endemism: Focusing on the diversity and endemism of vascular plant species of the semiarid zone, based on data extracted from the Madagascar Catalogue (2018), a total of 930 native vascular plant species in 107 plant families have been recorded, of which roughly 23% are endemic to the area. Summary data on the diversity of the better represented families is provided in Table 1.

Considering global tree diversity, a striking feature is the large number of taxonomic groups to which they belong including tree ferns, Gymnosperms and within the angiosperms—six families of monocots and 75 families of dicots (Thomas 2014). The range of

Table 1.Number of genera and species recorded in the semiarid zone of southwestern Madagascar for families with four or more tree species recorded in the zone, and number of species currently regarded as endemic to the zone, following the taxonomic classification of The Angiosperm Phylogeny Group (2016).

Family	Genera	Species	Endemic species
Anacardiaceae	4	9	5
Apocynaceae	2	6	1
Asteraceae	3	4	1
Bignoniaceae	5	6	0
Boraginaceae	3	11	2
Burseraceae	1	19	7
Capparaceae	5	8	2
Celastraceae	7	8	3
Combretaceae	1	8	3
Didiereaceae	4	11	6
Ebenaceae	1	7	0
Euphorbiaceae	5	26	6
Fabaceae	25	78	19
Malvaceae	9	33	4
Meliaceae	4	5	1
Moraceae	2	10	1
Pedaliaceae	1	5	1
Phyllanthaceae	6	8	0
Rhamnaceae	4	6	1
Rubiaceae	9	10	0
Rutaceae	5	7	2
Sapindaceae	8	11	3
Sapotaceae	2	4	0
Solanaceae	1	4	2
Xanthorrhoeaceae	1	5	2

life forms and life history strategies among trees is also large, notably in dryland ecosystems where drought, nutrient status in soils, and unpredictable weather and climate provide strong selection pressure on desert trees and all other forms of organisms. This is particularly true in the drylands of southwest Madagascar.

Dryland trees: In our global database project, and for the dry southwest Malagasy tree flora considered here (Figure S1), we find it necessary to develop our own definition of dryland trees given that none of the numerous definitions presented used previously seems entirely satisfactory for our study areas. We use elements from the definitions offered by Shreve and Wiggins (1951), Bernhardt (2000), Felger et al. (2001), and Schatz (2000, 2001) to complement the following definition: In the context of drylands, trees are long-lived plants that develop at least one sturdy long-lived trunk, from one to 20 meters or more in height. There may be additional vertical stems, but after cutting, burning, or browsing, it may be difficult or impossible to distinguish which stem was initially the main stem.

This definition includes longevity and the presence of a single, primary trunk, whether tall or short, as opposed to the multi-branching life forms found in shrubs. Even in the absence of human impacts, many dryland trees—like some montane and arctic tundra trees—never attain five meters in height. Examples abound in the drylands of Africa and Madagascar, in genera such as *Acacia*, *Adenium*, *Aloe*, *Commiphora*, *Cyphostemma*, *Euphorbia*, and *Moringa*. Similarly, in many groups of Australian trees, lignotubers and other underground organs have evolved to allow trees to survive drought, fire, and severe grazing (Nicolle 2006).

To underscore the spectrum of life forms and taxonomic groups in which they occur, we use names such as 'monocot tree', 'dwarf tree', 'bottle tree', or 'arboreal cactus' when a dryland tree deviates from standard notions of trees. Dwarf trees, candelabra tree euphorbs, and monocot trees—those without lignified stems—can be recognized as special category of desert trees. In the evolutionary ecology of desert and dryland trees, succulence also merits special attention as it occurs in leaves and young stems, but also in tree trunks (and roots), producing a condition called pachycaul (alias bottle trees). In the dry southwest and other drylands, there are also many other adaptations to drought and unpredictability observed in trees (and other plants) such as ultra-rapid leaf shedding during drought, and thorns or spines.

In preparing the distribution maps presented in this article, we followed Cornet (1974) and Schatz (2000) for bioclimatic regions, and for vegetation cover and protected areas, we followed Moat and Smith (2007), and supplemented their maps by other recent unpublished data. For species distribution, we used the Tropicos® database. Regarding taxonomy, we followed the on-going Catalogue of Vascular Plants of Madagascar project (http://www.tropicos.org/project/mada) and APG IV (The Angiosperm Phylogeny Group 2016).

DATA SAMPLING AND ANALYSIS. The second lead-author has conducted numerous field trips in southwest Madagascar over the past 28 years. Shorter trips devoted to this study have been undertaken by the first and third authors since 2002. Field observations of the information used to complete the various fields in the database for the trees included were supplemented by consultation of the Catalogue of the Plants of Madagascar database (Madagascar Catalogue (MadCat) 2018), literature searches, and careful review of herbarium specimens of the taxa considered for the MadCat database, in the herbaria at the National Museum of Natural History in Paris, France, and at the National Herbarium at Tzimbazaza, Antananarivo, Madagascar, as well as the Royal Botanic Gardens Kew, UK, and Missouri Botanical Garden, USA.

Included in DTsMada are data regarding species distribution, bioclimate, habitat categories and endemicity derived from the Madagascar Catalogue (2018). Additionally, we note endemicity to the semiarid zone, based on MadCat, and our study of herbarium specimens and field observations. We also note presence or absence of a series of eco-physiological features thought to be of functional and adaptive significance, based on herbarium specimens and our own field observations. These include: the pachycaul (swollen trunk) life form (e.g., *Adansonia*), stem succulence (e.g., *Didiereaceae*), leaf succulence (e.g., *Aloe*), and the presence of spines or thorns. Further, we note the presence of unusual bark characteristics such as peeling (e.g., most Commiphora), and leaf duration (deciduous, evergreen or semi-deciduous). Data for conservation risk assessments for some taxa have been obtained from the IUCN Red List of Threatened Species (IUCN 2015) and the Red List published by the IUCN Madagascar Plant Specialist Group (2011) (Table 2). Assessments published in 1998 used earlier criteria that are no longer regarded as valid (e.g., examples of criteria 1, 2, 3), with some of the assessments still being provisional, i.e., having not yet been validated by the IUCN Red List authority. Additional adaptive traits recorded in the DTsMada database include sexual system (hermaphrodite, monoecious or dioecious), long distance dispersal syndromes, e.g., anemochory, the ability to coppice, the type of habitat(s) where the species is most commonly found, and height range (m) at maturity.

RESULTS AND DISCUSSION

The semiarid zone harbors 355 documented tree species in 156 genera and 55 families in a total area of approximately 16,200 km². Endemism is also high: a total of 316 (89.0%) of the tree species recorded from this zone are endemic to Madagascar, and 76 species (21.4% of the tree flora) are restricted to the zone, and a further 111 are confined to the dry southwest. Therefore, based on our results, 187 (52.7%) of the 355 tree species identified in our study area are regional endemics. Furthermore, two genera (1.2%) are strictly endemic to the semiarid zone (*Alluaudiopsis* and *Salvadoropsis*), a total of 12 genera (7.7%) are endemic to the dry southwest, and 38 genera (24.4%) of the 156 present are endemic to Madagascar (Table 3). More than half (52.7%) of the tree flora in the broader subarid region as a whole (sensu Cornet 1974) is endemic to that region and more than a fifth is endemic to the semiarid zone.

In order to illustrate some of the biogeographical patterns and life history traits that occur in the arboreal flora of the semi-

Table 2. IUCN risk of extinction assessment categories for 117 evaluated Malagasy endemic tree species of the dry southwest region of Madagascar. (Sources: IUCN website www.iucnredlist.org; IUCN Madagascar Plant Specialist Group (MPSG) 2011. CR: Critically Endangered; EN: Endangered; VU: Vulnerable; NT: Near Threatened; LC: Least Concern)

Source	Year published	CR	EN	VU	NT	LC	Total
IUCN	1998	1	3	4	1	1	10
IUCN	2004		2	2		7	11
GSPM	2011	5	26	21	16	18	86
IUCN	2012		1			2	3
IUCN	2014		2	1	1	3	7
	Totals	6	34	28	18	31	117

Table 3. Summary of the data available from the Madagascar Catalogue for the 355 known species of trees of the semiarid zone of southwestern Madagascar. (Data include three levels of endemism: endemic to (i) Madagascar as a whole, (ii) to the dry southwest region, and (iii) to the coastal semiarid zone. Data for selected morphological traits are also shown indicating correlation of each to degrees of endemism. Note that nearly 30% of assessed species were considered to be Endangered (EN), and 58.1% as Vulnerable or higher risk, including a significant portion that are Endangered or Critically Endangered)

	Madagascar	dry southwest	semiarid zone
endemic species	316	187	76
non-endemic species	39	168	279
Percent endemism	89.0%	52.7%	21.4%
Number of pachycauls	26	17	10
Percent of endemic flora	8.3%	9.1%	13.2%
Number of leaf succulents	17	15	9
Percent of endemic flora	5.4%	8.0%	11.8%
Number of armed species*	45	32	15
Percent of endemic flora	14.2%	17.1%	19.7%

arid zone, we now present four case studies of three genera with many endemic species, each in a different, widespread tropical family, and the four Malagasy genera of Didiereaceae.

CASE STUDY 1. The genus *Adansonia* (Malvaceae): *Adansonia* comprises eight species, of which six are endemic to Madagascar (Cron et al. 2016). Like *Pachypodium*, this iconic group shows a clear distribution pattern in various dry areas of sub-Saharan Africa and Madagascar, but with a single species, *A. gregorii* F. Muell., endemic to the Kimberley ranges in northwestern Australia (Baum 1995, Baum et al. 1998, Leong Pock Tsy et al. 2009). As discussed by Raveloson et al. (2014), Baobabs are comparable to lemurs in their iconic value and the importance of strengthening educational and conservation measures for their protection and integration in far-seeking programs of conservation and sustainable development. To this call to action, we would add a third component, namely ecological restoration.

Adansonia za is widespread throughout the subarid and dry bioclimatic regions of Madagascar. *A. grandidieri* occurs mostly in the central-west part of the country (around Morondava), but just extends into the semiarid zone. *A. rubrostipa* is coastal in distribution and is certainly the best represented species within the semiarid zone (Figure 3). The other three Malagasy species, *A. suarezensis*, *A. perrieri*, and *A. madagascariensis*, are concentrated in the north and northwest, and do not occur in the dry southwest. It seems that *A. digitata*, the most widespread Baobab having a vast range in Africa, was intentionally introduced to Madagascar from sub-Saharan Africa where it is native, and is cultivated, never wild, in Madagascar, India, and Australia (Baum 1995, Pettigrew et al. 2012). However, in southern Oman and Yemen it appears to have been introduced more than 1000 years ago, and now occurs as an escape from cultivations in a few localities (Aronson et al. 2017).

In Madagascar as in Africa, *Adansonia digitata* shows polyploidy and its distribution is linked to villages, both active and abandoned (Leong Pock Tsy et al. 2009). *Adansonia* species in general tend to be left uncut by people clearing areas for agriculture because their wood is of little use for construction, firewood, or charcoal, and because the trunks are a valuable source of moisture for livestock in periods of prolonged drought when stems can be cut and fed to animals. The tree has many other domestic uses as well, including fiber from the bark used for various purposes. Furthermore, there are strong ritual or spiritual uses and connotations associated with this widespread, iconic group of bottle trees (Leong Pock Tsy et al. 2009). As a result the trees are exposed to human-mediated evolutionary pressures and opportunities that may result in the patterns of hybridization brought to light by Leong Pock Tsy et al. (2013).

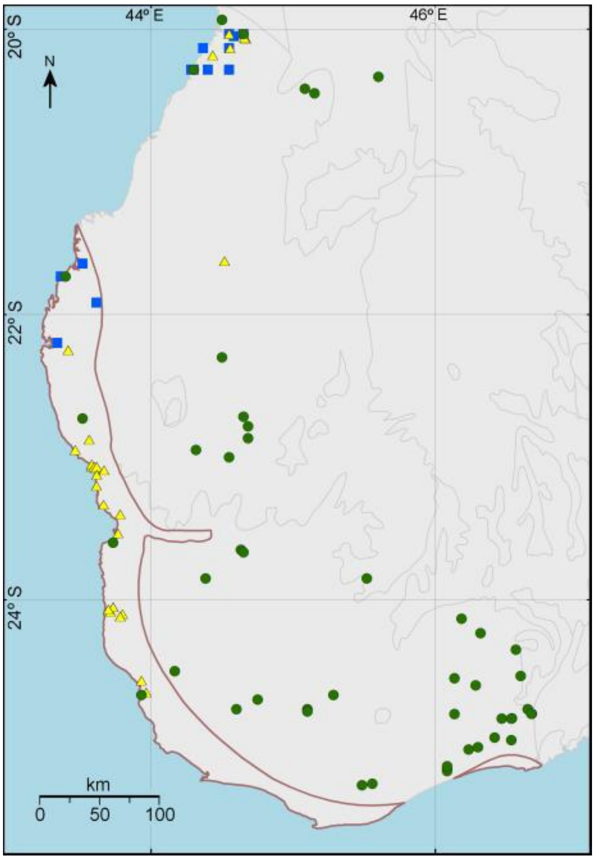

Figure 3. Known occurrence in the Dry Southwest Region of the three endemic species of *Adansonia* - *A. grandidieri* (blue squares), *A. rubrostipa* (yellow triangles), and *A. za* (green dots) that enter the Semiarid Zone (purple outline).

CASE STUDY 2. The genus *Pachypodium* (Apocynaceae): The 25 species of the pachycaulous genus *Pachypodium*, like those of *Adansonia*, are mostly concentrated in Madagascar. According to Rapanarivo and Leeuwenberg (1999), no less than 20 species are endemic to Madagascar while five occur in Angola, Mozambique, South Africa, Swaziland, and Zimbabwe. The genus shows an extraordinary amplitude of life forms and habitats, ranging from nearly prostrate shrubs in granitic hills of central Madagascar to succulent trees 4–6 m tall in the canyons of the Gariep river (*P. namaquanum*), near the South African border with Namibia. In Madagascar, five species enter the semiarid zone (Figure 4). These include four trees—*P. geayi*, *P. lamerei*, *P. meridionale*, and *P. mikea*, and also the shrubby species, *P. cactipes*.

Three of the four arborescent species of *Pachypodium* in Madagascar occur in the semiarid zone yet extend into the subarid region as a whole, while a single species, only recently discovered, is endemic to the coastal areas of the zone between Toliara and Morombe, where it is partially sympatric with the other tree species (Lüthy 2005). The well-known dwarf species *P. brevicaule* is endemic to quarzite outcroppings in central Madagascar and does not occur in the dry southwest. *Pachypodium brevicaule* and other species are much sought after as ornamentals for the horticultural trade, which has led to over-harvesting and reduction of its range. The natural populations of certain species have also

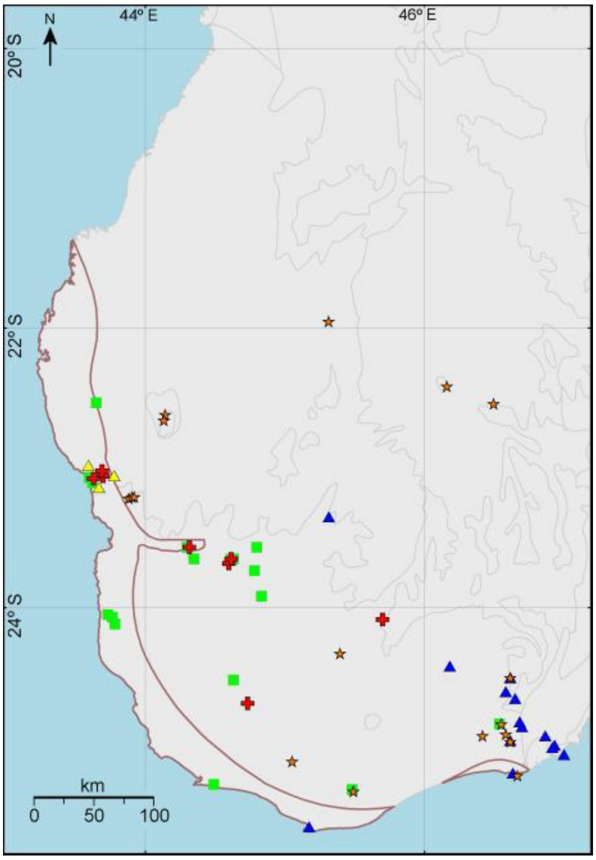

Figure 4. *Pachypodium*: of the 20 species in Madagascar, only five enter the Semiarid Zone: four are trees - *P. geayi* (green squares), *P. lamerei* (gold stars), *P. mikea* (yellow triangles), and *P. meridionale* (red crosses), and one a shrub, *P. cactipes* (blue triangles), only *P. mikea*, a narrow endemic, is strictly restricted there.

been modified due to translocation within Madagascar and illegal commerce overseas (Sajeva et al. 2007). All Malagasy species of the genus are listed in CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora)—three in Appendix I, and all others in Appendix II (Sajeva et al. 2007).

CASE STUDY 3. the four Malagasy genera of Didiereaceae: We consider the Didiereaceae, which are similar in appearance to various primitive cacti and are grouped with them in the order Caryophyllales (The Angiosperm Phylogeny Group 2016). In Madagascar, there are 11 species in four genera—*Alluaudia*, *Alluaudiopsis*, *Decarya*, and *Didierea*. Until recently, this family was considered to be endemic to Madagascar, however based on molecular studies (The Angiosperm Phylogeny Group 2016), it now also includes 11 African species in three genera formerly placed in Portulacaceae—*Ceraria* (six species), *Calyptrotheca* (two species), and *Portulacaria* (three species). Notably, all these African taxa are mainly shrubs—or rarely small trees—many with broad distributions. In contrast, most of the 11 taxa in Madagascar are unequivocally trees, all are endemic to the island and all occur within the semiarid zone, to which five species are endemic. In fact, only two species, *Alluaudia humbertii* and *A. dumosa*, occur beyond the subarid region, having outlying populations in the center-south of the country near the town of Ihosy (Figure 5). Among the four Malagasy genera, *Alluaudiopsis* appears to be the most ancient (Applequist and Wallace 2000) and, as in *Adansonia*, various episodes of polyploidization within the genus seem to have occurred.

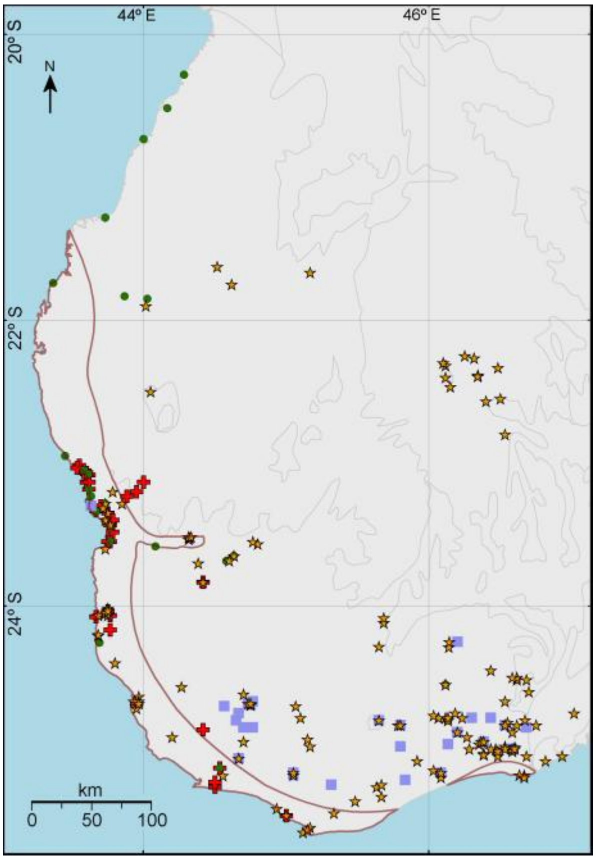

Figure 5. Distribution of Didiereaceae in Madagascar, comprising 11 species in 4 genera: 6 species of *Alluaudia* (gold stars); 2 species of *Alluaudiopsis* (red crosses); 1 species of *Decaryia* (blue squares); 2 species of *Didierea* (green dots).

Like the well-known Spekboom of southern Africa (*Portulacaria afra*), many Malagasy Didiereaceae can be reproduced from cuttings or, for those species where it is possible, stancheons (i.e., very large cuttings, typically 50–200 cm long). These rooted cuttings can grow quickly and serve as dense living fences (Figure S2). This is true especially for *Didierea madagascariensis* and *Alluaudia procera*. Additionally, *Alluaudia ascendens* produces relatively sturdy wood that is cut into wide, thin boards used as sheathing to cover exterior walls of houses (Schatz 2000). It is possible that the distribution of some or all of these trees was modified and extended by intentional use and transport by people. Moreover, the thick stems of several species are used for firewood, and young leaves of some species are highly palatable to livestock. *Didierea madagascariensis* is a fast-growing, pioneer colonizer of sandy habitats that could be of particular value in ecological restoration and rehabilitation.

CASE STUDY 4. *Baudouinia* (Fabaceae): This is a hardwood tree that once was more abundant. *Baudouinia rouxevillei* H. Perrier, a small to medium-sized tree, with wood that is highly prized by wood-workers. It is restricted to a small area of the Mahafaly Plateau between the Fiherenana River in the north and the Itambono corridor southwest of Betioky, where it occurs in low, deciduous woodland and scrubland on limestone 100–300 m above sea level. Historically, it was an offence to cut the wood, as it was reserved for the King; the translation of the local name—*Manjakabetany*—means 'King's wood' or 'King of the Earth' (Du Puy 2002). Yet that taboo was insufficient. Already in

2002, it was considered "rare and endangered due to its restricted distribution and over-collection for its ornamental wood" (Du Puy 2002: 71). We wonder if that combination of factors might not be a feature relevant for many tree species in the region, in this small genus and many others. Attention has recently been drawn by Ranaivoson et al. (2015) to a worrisome situation regarding *Tamarindus indica*, another multi-purpose legume tree of the southwest semiarid region that for centuries, according to these authors, was a sacred tree among the local Mahafaly people, strictly protected from cutting by taboos (*fady*). However, in recent years people started to disregard the taboos, and cut down the trees for firewood, to the point where the species is now disappearing.

The shifting baseline syndrome (cf. Pauly 1995) and artificial negative selection forces in direct relation to shrinking stocks and loss of functional biodiversity also exists with regard to trees and other useful plants in arid and semiarid areas in general. It is suggested that hardwood trees in the genera *Albizia*, *Dalbergia*, *Diospyros*, *Operculicarya*, and *Baudouinia* are especially at risk. Thus, species of special concern include *Albizia aurisparsa* (Drake) R. Vig., *A. mahalao* Capuron, *Dalbergia xerophila* Bosser & Rabevohitra, *Dichrostachys venosa* Villiers, and *Diospyros sakalavarum* H. Perrier. Further research on preferences and uses of trees by local people in the dry southwest of Madagascar would no doubt be of great value, such as the study performed recently in the Analalava area, near Foulpointe, eastern Madagascar by Lavialle et al. (2015).

CONCLUSIONS

In a surprising number of Earth's vast drylands, highly diverse arboreal floras still occur and provide the infrastructure for multilayered woodlands and shrublands such as those of the dry southwest of Madagascar. These provide multiple services to people and other forms of life (Le Floc'h and Aronson 2013). We argue that the social-ecological and economic roles of these tree (and shrub) species must be re-evaluated. To rectify this situation, reliable up-to-date data are needed to enable us to understand biodiversity and biogeographical patterns and interdependence between the taxa present, and the ecosystem functions in different habitats. On-line, interactive databases are thus invaluable tools to provide a summary of current knowledge and knowledge gaps facilitating targeted research to improve the knowledge base.

Our primary goal here has been to contribute to the knowledge base necessary for developing and implementing coordinated, science-based, and far-sighted conservation, planning, management, and restoration programs in drylands worldwide, seeking to strengthen sustainable local economic development and human wellbeing, combat desertification and ecosystem degradation and initiate restorative processes at ecosystem, landscape, and bioregional levels. The importance of native dryland trees and the assemblages they form—or once formed in areas where there has been environmental degradation—has been underestimated and under-studied, or else forgotten since most trees were removed long ago. We also note that at the national scale in Madagascar, many new priority conservation areas have been proposed or are already in different stages of formal recognition. Obviously, it will take time for effective management of the new protected areas to be established, and for on-site protection and management to become truly effective. We hope that this contribution and the database we have assembled will be of use.

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SUPPLEMENTARY MATERIAL

Available online only

Figure S1. Spiny forest-thicket in the Dry Southwest region of Madagascar.

Figure S2. Use of Semiarid Zone trees by local communities.

Figure S3. Exemplary taxa and morphological adaptations.

Table S1. Summary of names used by Cornet (1974), Schatz (2000) and the present authors for each biogeographic area.

Table S2. Climatic data for the driest stations of the coastal zone of the Dry Southwest region of Madagascar.

Table S3. Ecogeographical database for the dry southwest Malagasy tree flora.

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Miscellaneous behavioural observations of Malagasy birds

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ABSTRACT

Madagascar possesses a unique avifauna characterized by high endemism rates at species and higher taxonomic levels, but little is known about the behaviour, diets and interspecific interactions of many species. We present a number of opportunistic observations of Malagasy birds collected during 2012–2015, including a foraging association between Hook-billed vanga *Vanga curvirostris* and White-breasted mesite *Mesitornis variegatus*, aggressive interaction between a fledgling Madagascar cuckoo *Cuculus rochii* and its Common jery *Neomixis tenella* host, records of carnivory in Green-capped coua *Coua ruficeps olivaceiceps* and frugivory in Lafresnaye's vanga *Xenopirostris xenopirostris*, an unusual aggregation of Alpine swift *Tachymarptis melba* around a telecommunications tower, entrapment of Madagascar mannikin *Lepidopygia nana* in a spider's web, and anti-predator behaviour (mobbing) of potentially predatory reptiles in Souimanga sunbird *Nectarinia souimanga*, Madagascar magpie robin *Copsychus albospecularis*, Madagascar paradise flycatcher *Terpsiphone mutata*, Common newtonia *Newtonia brunneicauda* and Crested drongo *Dicrurus forficatus*.

RÉSUMÉ

L'avifaune de Madagascar est unique, caractérisée par des taux d'endémisme élevés aux niveaux des espèces, genres, familles et ordres. Cependant, nous connaissons encore mal les comportements, les régimes alimentaires ou encore les interactions interspécifiques de nombreuses espèces. Sont présentées dans cette note une série d'observations opportunistes collectées au cours de la période 2012–2015, incluant : i) une interaction lors de la recherche de nourriture entre un Vanga écorcheur *Vanga curvirostris* et une paire de Mésite variée *Mesitornis variegatus*, ii) une interaction agressive entre un oisillon du Coucou de Madagascar *Cuculus rochii* et son hôte, une Petite éroesse *Neomixis tenella*, iii) la prédation d'un lézard (*Tracheloptychus madagascariensis*) par un Coua à tête verte *Coua ruficeps olivaceiceps*, iv) la frugivorie par un Vanga de Lafresnaye *Xenopirostris xenopirostris*, v) une agrégation inhabituelle des Martinets à ventre blanc *Tachymarptis melba* autour d'une installation de télécommunication, vi) le piégeage d'un Capucin de Madagascar *Lepidopygia nana* dans une toile d'araignée (*Nephila* sp.), et vii) le harcèlement des reptiles incluant des serpents (*Ithycyphus miniatus*, *Acrantophis madagascariensis*) et un caméléon (*Furcifer pardalis*) par le Souimanga malgache *Nectarinia souimanga*, le Shama de Madagascar *Copsychus albospecularis*, le Tchitrec malgache *Terpsiphone mutata*, la Newtonie commune *Newtonia brunneicauda* et le Drongo malgache *Dicrurus forficatus*.

* * *

Madagascar possesses a unique avifauna characterized by high levels of endemism at species and higher taxonomic levels. One-hundred-and-six out of 256 regularly occurring species are endemic, while 40 genera and six families are restricted to Madagascar and the neighbouring Comoros archipelago (Safford and Hawkins 2013). Unfortunately, the paucity of researchers and publishing observers on the island means that little is known about the behaviour, diets and interspecific interactions of many species, yet an improved understanding of species ecology may be useful for conservation efforts as well as for academic reasons. Here, we contribute to filling this gap with a series of opportunistic field observations, largely concerning endemic species, collected during the period 2012–2015 from around Madagascar (additional behavioural observations can be found in Gardner et al. 2011; Gardner and Jasper 2014). Herein we follow the taxonomy adopted by Safford and Hawkins (2013).

ASSOCIATION BETWEEN WHITE-BREASTED MESITE *MESITORNIS VARIEGATUS*, MADAGASCAR BLUE VANGA *CYANOLANIUS MADAGASCARINUS*, AND HOOK-BILLED VANGA *VANGA CURVIROSTRIS*. At 1111h on 29 April 2015, south of Campement Anilotra (Campement des Anglais) in Ankarana National Park (E049° 06′ 27″, S12° 54′ 37″, Diana Region), we encountered a mixed flock containing Madagascar blue vanga, Crested drongo *Dicrurus forficatus* and Red-tailed vanga *Calicalicus madagascariensis*. We tried to elicit a response

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from a Madagascar blue vanga with the use of call playback (using a recording from Huguet and Chapuis 2003), but the call instead triggered a duet by a nearby pair of White-breasted mesite, and this duet was in turn answered by a duet from a distant pair of conspecifics. In total we played the call of Madagascar blue vanga three times and each time it elicited a duet from the White-breasted mesite pair.

Having been obscured by dense undergrowth, the White-breasted mesites came into view after several minutes as they foraged in the leaf litter. They were followed at a distance of about 2 m by an adult Hook-billed vanga, which hopped through the undergrowth, perching in shrubs and lianas at a height of about 1 m, constantly observing the mesites foraging beneath. We observed the birds for approximately 10 min, during which time the vanga remained close to the mesites and watched their movements closely (though sometimes distracted by us), and regularly emitted a muted version of its 'whistle' call. It also emitted a soft, cat-like 'meow' call and a number of bill snaps, often in response to the singing of the mesites. However, we did not see the vanga descend to the ground to take prey, or capture any prey in the vegetation.

The three species of mesite (Mesitornithidae) forage in pairs or small groups in areas of thick leaf litter on the forest floor, slowly and deliberately searching amongst fallen leaves for invertebrates. They may be followed by a range of birds which take invertebrates flushed by their actions. For example, groups of Subdesert mesite *Monias benschi* are frequently followed by Crested drongo (85/174 mesite group encounters, Seddon 2001) and more rarely by Lafresnaye's vanga *Xenopirostris xenopirostris* and Madagascar hoopoe *Upupa marginata* (1.2% and 0.8% of group encounters, Seddon and Tobias 2013). Species known to follow groups of White-breasted mesite include Crested drongo, Madagascar paradise flycatcher *Terpsiphone mutata*, Madagascar magpie robin *Copsychus albospecularis*, Long-billed tetraka *Bernieria madagascariensis* and Rufous vanga *Schetba rufa* (Langrand 1990, Eguchi 1998, Hawkins 2013). However, this behaviour has never been observed in Hook-billed vanga. Since this species consumes vertebrates much more frequently than other vangas (Schulenberg and Hawkins 2013a), we speculate that the bird may have been hunting for *Brookesia* dwarf chameleons (Chamaeleonidae), which forage within leaf litter and were said to be common in that area by our guide.

CARNIVORY BY GREEN-CAPPED COUA *COUA RUFICEPS OLIVACEICEPS*. On 6 April 2014 at 0931h, at the Arboretum Antsokay (E043° 45′ 18″, S23° 24′ 53″, Atsimo Andrefana Region), we observed an adult Green-capped coua predating a Madagascar girdled lizard *Tracheloptychus madagascariensis* (Gerrhosauridae) (Figure 1). The lizard was captured on the ground in an area of bare sand.

The nine extant species of *Coua* are omnivorous, feeding on insects and other invertebrates, plant matter (fruits, flower buds, seeds, tree gum), small reptiles (skinks, geckos, chameleons) and the eggs of reptiles and birds (Milon et al. 1973, Goodman et al. 1997, Safford and Hawkins 2013). However, this is the first record of vertebrate carnivory in either subspecies of *Coua ruficeps* (Safford and Hawkins 2013). The only remaining coua species not known to consume vertebrates is the Running coua *Coua cursor* (Safford and Hawkins 2013); but this may simply reflect a lack of observations.

Figure 1. Green-capped coua *Coua ruficeps olivaceiceps* predating a Madagascar girdled lizard *Tracheloptychus madagascariensis*, Arboretum Antsokay, southwest Madagascar, 6 April 2014. (Photo: Louise Jasper)

AQUATIC HABITAT USE BY VERREAUX'S COUA *COUA VERREAUXI*. On 18 April 2013 at 1004h, we observed an adult Verreaux's coua in aquatic vegetation on a small tributary of the Onilahy River, south of the spring known as Andoharano (E043° 46′ 56″, S23° 32′ 36″, Atsimo Andrefana Region) (Figure 2). The bird appeared to be foraging within a dense, 1.5 m tall bed of the fern *Acrostichum aureum*, but when disturbed by the approach of our vessel it flew into the spiny thicket vegetation on the slopes of the limestone plateau on the opposite bank. Verreaux's coua is endemic to the South Malagasy Spiny Forest Endemic Bird Area (Stattersfield et al. 1998), which covers the driest region of the country and contains few wetlands. The habitat adjacent to the wetland, into which the coua flew, was typical of the species – described as "spiny thicket on and around limestone outcrops of Mahafaly Plateau and close to coast, often dominated by plants in the families Didiereaceae and Euphorbiaceae" (Goodman 2013a). However, we are not aware of any previous records of the use of aquatic vegetation by this species.

UNUSUAL INTERACTION BETWEEN FLEDGLING MADAGASCAR CUCKOO *CUCULUS ROCHII* AND ITS COMMON JERY *NEOMIXIS TENELLA* HOST. On 30 December 2012 at 1121h, between Talatakely and Vatoharanana in Ranomafana National Park (approx. E047° 25′ 30″, S21° 16′ 34″, Haute Matsiatra Region), we observed an interaction involving a fledgling Madagascar cuckoo and its host, a Common jery (Figure 3). The host perched next to the cuckoo and began feeding it, but within 1 sec the cuckoo had

Figure 2. Verreaux's coua *Coua verreauxi* using aquatic vegetation (a bed of the fern *Acrostichum aureum*), Onilahy River, 18 April 2013. (Photo: Louise Jasper)

Figure 3. Sequence of images showing the temporary capture of a Common jery *Neomixis tenella* host by a fledgling Madagascar cuckoo *Cuculus rochii*, Ranomafana National Park, Madagascar, 30 December 2012. (Photos: Louise Jasper)

grasped the jery by the leg with its bill. The host immediately began struggling, unbalancing the cuckoo from its perch. However, the cuckoo retained its grip on the jery while dangling suspended from the branch. After 4–5 sec of continued struggle, the cuckoo released its grip on the branch and fell, at which point the jery escaped.

We are aware of only one comparable incident, in which a Common cuckoo *Cuculus canorus* grasped the head of its host, a Dunnock *Prunella modularis*, as it delivered food to its gape, and killed it (Hens 1949). Both incidents likely represent 'overenthusiastic' attempts to grasp food by the cuckoo parasites, rather than predation attempts upon their hosts (N. B. Davies 2017, pers. comm.).

UNUSUAL AGGREGATION OF ALPINE SWIFT *TACHYMARPTIS MELBA*. On 28 May 2012 at 1137h, LDJ observed a flock of at least 215 Alpine swift flocking around the emitters of a telecommunications pylon in the village of Belalanda (E043° 38' 42", S23° 17' 48", Atsimo Andrefana Region) (Figure 4). The birds appeared to be attracted to particular panels which they flew towards feet first, although they did not land. Magnification of the images reveals no clouds of insects around the tower, and there were no nests on the structure.

There is evidence that electromagnetic radiation can interfere with bird orientation (Engels et al. 2014), however most research has focused on low frequencies (<50 kHz) rather than the high frequencies (typically >900 kHz) used in telecommunication signals (C. Meier 2018, pers. comm.). The Alpine swift is a presumed resident in Madagascar which forms nesting colonies on cliffs and buildings elsewhere in its range. However, its nesting sites in Madagascar remain unknown (Safford 2013a). We are not aware of any information on maximum flock sizes of this species in the southern hemisphere though 200+ individuals appears to be unusually large: in Europe flocks of more than 1000 individuals have been observed (C. Meier 2018, pers. comm.).

MOBBING OF CHAMELEON BY SOUIMANGA SUNBIRD *NECTARINIA SOUIMANGA*. At 1120h on 14 April 2015, on the southernmost limestone karst (*tsingy*) outcrop of the Ankarana Massif (E048° 59' 06", S13° 03' 45", Diana Region), we observed two adults and one juvenile Souimanga sunbird mobbing a large panther chameleon *Furcifer pardalis* (Chamaeleonidae; total length <38 cm, Glaw and Vences 2007). All three birds were alarm calling from branches to the side of and behind the chameleon, and flew above and around it for several minutes, but did not approach it from the front. Safford (2013b) notes that Souimanga sunbird is aggressive and may relentlessly mob predators, singly or in groups. Our observations show that Souimanga sunbirds recognize large chameleons as potential predators, however we are aware of only one record of a chameleon (*Furcifer oustaleti*) predating birds in Madagascar (García and Vences 2002).

Figure 4. Flock of Alpine swift *Tachymarptis melba* flying around emitter of telecommunications tower in Belalanda, southwest Madagascar, 28 May 2012. (Photo: Louise Jasper)

SNAKE MOBBING BY COMMON NEWTONIA *NEWTONIA BRUNNEICAUDA*, MADAGASCAR MAGPIE ROBIN *COPSYCHUS ALBOSPECULARIS*, MADAGASCAR PARADISE FLYCATCHER *TERPSIPHONE MUTATA* AND SOUIMANGA SUNBIRD *NECTARINIA SOUIMANGA*. On 20 March 2015 at 1202h at Baie des Sakalava (E049° 23' 28", S12° 16' 41", Diana Region), LDJ was alerted by the alarm calls of Madagascar magpie robin and Souimanga sunbird to an area of shrubby vegetation within a patch of degraded coastal thicket. On closer approach she found a mixed aggregation including Common newtonia, Madagascar magpie robin, Madagascar paradise flycatcher and Souimanga sunbird, mobbing an adult-sized *Ithycyphus miniatus* (Lamprophiidae; total length <170 cm, Glaw and Vences 2007). The snake was initially moving across the ground before climbing into a bush after several minutes: all four bird species continued to alarm call vociferously from distances between 1 m and 5 m, though none physically approached the snake. The snake continued to hunt for over 30 min during which Madagascar magpie robin and Souimanga sunbird continued to alarm call persistently, with Common newtonia and Madagascar paradise flycatcher also continuing to alarm though more intermittently. During this time the snake caught and consumed a probable House mouse *Mus musculus*, and was closely approached by three human observers, but the birds continued to alarm throughout. Although none of these species are noted as known snake prey items (Safford and Hawkins 2013), our observations suggest that all recognize snakes as potential predators.

FRUGIVORY IN LAFRESNAYE'S VANGA *XENOPIROSTRIS XENOPIROSTRIS*. On 25 November 2012 at 0631h, LDJ observed a male Lafresnaye's vanga eating the fruit of *Commiphora lamii* (Burseraceae) in degraded coastal spiny thicket south of the village of Anakao (E043° 38' 35", S23° 40' 11", Atsimo Andrefana Region) (Figure 5). The bird picked the ripe fruit with its bill, but then held it against a branch with its foot in order to remove and eat the fleshy aril before dropping the seed (as described for White-headed vanga *Artamella viridis* eating the red arils of *Commiphora guillaumini* fruit, Böhning-Gaese et al. 1995): it was observed feeding on the fruit continuously for about five minutes. Since the seeds were neither destroyed nor swallowed but dropped around the tree, the bird is unlikely to function as either a seed predator or a seed disperser.

Members of the Vangidae are primarily insectivorous, though the larger species take vertebrates and "a few species consume at least some fruit" (Schulenberg 2013a). Species recorded eating fruit include Madagascar blue vanga, Chabert vanga *Leptopterus chabert* (including red arils of *Commiphora* fruit), Bernier's vanga *Oriola bernieri* and White-headed vanga (Benson et al. 1977, Böhning-Gaese et al. 1995, 1999, Schulenberg 2013b, Schulenberg and Hawkins 2013b): our observation is the first record of frugivory in the genus *Xenopirostris*. The 44 Malagasy species of *Commiphora* are widespread in the country's dry regions (Schatz 2008, Gostel et al. 2016). The oily, energy-rich arils are consumed by birds including the Lesser vasa parrot *Coracopsis nigra*, Greater vasa parrot *C. vasa*, Common jery and now three species of vanga, as well as a lemur (Verreaux's sifaka *Propithecus verreauxi*), and the ant *Aphaenogaster swammerdami* (Böhning-Gaese et al. 1995, 1999).

Figure 5. Male Lafresnaye's vanga *Xenopirostris xenopirostris* eating fruit of *Commiphora lamii*, Anakao, 25 November 2012. (Photo: Louise Jasper)

MOBBING OF BOA BY CRESTED DRONGO *DICRURUS FORFICATUS*. On 29 December 2014 at Anjajavy Lodge (E047° 13' 40", S14° 59' 27", Sofia Region), LDJ observed a Crested drongo mobbing a large (total length <320 cm, Glaw and Vences 2007) Madagascar ground boa *Acrantophis madagascariensis* (Boidae) that was lying motionless against a log. The bird aggressively mobbed the snake in flight, approaching to within approximately 1 m, and emitted a loud, metallic alarm call that we had not previously heard.

The Crested drongo is a very aggressive bird that frequently mobs raptors and other large birds (Safford 2013c), as well as a captive Ring-tailed lemur *Lemur catta* (van Someren 1947). However, we are not aware of any records of this species mobbing snakes. The Madagascar ground boa is a predominantly terrestrial ambush predator, and thus unlikely to predate a mid-stratum sally gleaner such as the Crested drongo.

ENTRAPMENT OF MADAGASCAR MANNIKIN *LEPIDOPYGIA NANA* IN SPIDER WEB. At 1740h on 17 June 2015, about 15 min after sunset, we witnessed a Madagascar mannikin fly into, and become trapped within, the web of a golden orb spider, *Nephila* cf. *inaurata*, in a hotel garden in urban Morondava (E044° 16' 05", S20° 17' 59", Menabe Region). The web was suspended between two trees at a height of approx. 3.5 m. The bird struggled frantically to escape and the large, female spider immediately began to approach it, reaching out to touch it with its forelegs. After about 15 sec the bird escaped the web and was able to fly away apparently unharmed.

Entrapment of birds in spider webs is a relatively rare event, a recent review revealing only 69 reports involving 54 bird species in 24 families: of these, four involved members of the mannikin family, Estrildidae (Brooks 2012). Of those in which the spider was identified, 50% (n=23) were in the genus *Nephila*. Results suggest that birds may survive if they escape the web before being wrapped in silk by the spider (n=8), but otherwise invariably die unless released (Brooks 2012).

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ESSAY

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La place pour le concept d'État gardien en droit de l'environnement dans l'encadrement du secteur minier à Madagascar

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ABSTRACT

In environmental law, the concept of custodian state generally assumes that the state is the guarantor of the interests of present and future generations, and of the implementation of the objective of intra- and intergenerational equity for sustainable development. The state is expected to protect people's rights to a healthy environment and to safeguard the natural heritage in order to transmit it as a legacy to future generations. In the context of the mining sector in Madagascar, researchers have shown that the state's role tends to be redefined so as to limit itself to facilitating mining investments, to the detriment of rights and public interest protection. In Madagascar, successive policies and strategies have displaced the state from regulation and management of its own natural resources. According to the principles of neo-liberal economy, its disengagement from the regulation of mineral resource exploitation would allow the development of favorable conditions to improve resource management and to reduce environmental impacts. However, this leaves little room for maneuver to ensure the protection of social and environmental rights that may be affected by the development of this sector. The article reflects on this contradictory situation, its origins and its stakes in Malagasy environmental law.

RÉSUMÉ

En droit de l'environnement, le concept de l'État gardien postule d'une manière générale que l'État est garant des intérêts des générations actuelles et futures, donc de la mise en œuvre de l'objectif d'équité intra et intergénérationnelle du développement durable. L'État est supposé protéger les droits des populations à un environnement sain et sauvegarder le patrimoine naturel en vue de le transmettre en héritage aux générations à venir. Or, dans l'encadrement du secteur minier à Madagascar, des chercheurs ont démontré que le rôle de l'État tend à être redéfini de façon à se limiter à faciliter l'investissement minier, au détriment de la protection des droits et de l'intérêt public. À Madagascar, les politiques et stratégies successives ont écarté l'État de la réglementation et la gestion de ses propres ressources naturelles. Suivant les principes néolibéraux, son désengagement de l'encadrement de l'exploitation des ressources minières permettrait le développement de conditions favorables à l'amélioration de la gestion des ressources et à la diminution des impacts environnementaux. Cela lui laisse toutefois peu de marge de manœuvre pour promouvoir la protection des droits sociaux et environnementaux pouvant être affectés par le développement du secteur minier. L'article propose un début de réflexion sur cette situation contradictoire, ses origines et ses enjeux en droit de l'environnement malgache.

INTRODUCTION

Ce texte revêt une dimension prospective ; il s'agit d'un questionnement qui met à jour certaines idées demandant encore à être creusées. C'est à cette réflexion prospective que le lecteur est invité à travers cet essai dont l'objectif est de soulever des questions sur le rôle de l'État malgache dans la protection de l'environnement et sa capacité à assumer ce rôle dans l'encadrement du secteur minier. Il convient de noter que la conception de la protection de l'environnement que nous adoptons dans ce texte englobe une dimension sociale indissociable, que l'on retrouve d'ailleurs dans la plupart des textes en droit de l'environnement. Les deux aspects (environnemental et social) étant étroitement imbriqués, lorsque nous évoquons la protection de l'environnement, cela implique aussi notamment la protection des communautés locales.

La réflexion s'appuie sur les processus sélectifs de libéralisation mis en place à Madagascar sous l'impulsion de divers acteurs, particulièrement les réformes successives dans le secteur de l'environnement et des ressources naturelles, notamment les ressources minières. En effet, la politique minière malgache de 1998 a été lancée dans le contexte de la mise en œuvre du programme de désengagement partiel de l'État de certains secteurs économiques entamé dans les années 1980, et du Projet de réforme du secteur minier (PRSM) promu et appuyé par la Banque Mondiale de 1998 à 2002 (Banque Mondiale 2003). Le PRSM mettait en place un ensemble de réformes du cadre légal et réglementaire du secteur minier, avec pour objectif la redéfinition et la limitation du rôle de l'État dans ce secteur, pour mieux offrir un

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environnement légal favorable et incitatif aux investisseurs (Sarrasin 2006).

Les recherches menées par le Groupe de recherche sur les activités minières en Afrique (GRAMA) et le Centre interdisciplinaire de recherche en développement international et société (CIRDIS) de l'Université du Québec à Montréal ont souligné l'impact de telles réformes en termes de réduction de l'espace de décision de l'État, de fragilisation de ses capacités de suivi et de contrôle, et son aptitude à apporter des mesures correctives (Campbell 2010). Par ailleurs, le transfert d'une part des fonctions et responsabilités de l'État en matière sociale et environnementale vers des acteurs privés n'est pas sans conséquence sur l'intérêt public, la protection des droits sociaux et environnementaux et les objectifs d'équité intra et intergénérationnelle du développement durable. Une telle situation suscite particulièrement des questionnements importants dans un pays tel que Madagascar, qualifié de *hotspot* de la biodiversité mondiale, concernant le rôle et les responsabilités publiques dans la protection du patrimoine naturel, dans l'intérêt des générations actuelles et futures. Notre démarche prospective nous a conduits à nous intéresser aux contributions du concept juridique d'« État gardien » en droit de l'environnement, pour alimenter ces réflexions. Nous avons donc tenté un premier survol de la littérature sur le concept d'État gardien afin de comprendre dans un premier temps les origines, les objectifs et la portée de ce concept. Puis, à travers l'examen de quelques textes de lois nous avons cherché à identifier les éléments de base du concept dans le droit de l'environnement malgache et ses implications possibles pour le secteur minier, notamment en termes d'obligations fiduciaires attribuées à l'État dans la protection de la biodiversité.

LE CONCEPT D'ÉTAT GARDIEN EN DROIT DE L'ENVIRONNEMENT

Le concept d'État gardien n'est pas nouveau ; ses origines sont anciennes, même si le vocabulaire utilisé pour le décrire a varié selon les époques et les systèmes juridiques. De nos jours par exemple, on y rattache d'autres qualificatifs comme fiduciaire, mandataire, garant, *public trust*, *stewardship* ou *patriae*.

Concept hybride, ses origines sont situées à l'intersection entre le droit romain de l'antiquité et le droit anglo-saxon contemporain. Il puise en effet dans les notions de *patrimonium* et de *res communis*, *res publicae*, *res univertatis* du droit romain antique, qui décrivent à différents degrés des choses (biens ou ressources) non-appropriables ou dont la propriété est reconnue à l'ensemble de la communauté, et dans la théorie du *public trust* en droit de *common law*, qui évoque un patrimoine (le *trust* ou la fiducie) qui est géré par une personne (le *trustee* ou fiduciaire) pour le bénéfice d'une autre personne (le bénéficiaire) (Jones 1992).

La doctrine du *public trust* ou fiducie publique appliquée au droit de l'environnement et des ressources naturelles a d'abord été développée par le juriste américain Joseph Sax en 1970 et a depuis fait l'objet de débats fournis dans la littérature juridique. D'une manière générale, Sax (1970) identifie trois éléments constitutifs d'une fiducie publique : (i) l'existence d'un bien public commun, (ii) la responsabilité d'assurer la protection de ce bien pour les générations actuelles et futures et (iii) la gestion publique dont le caractère désintéressé, transcendant des intérêts individuels, est à privilégier. À partir de là, on peut déduire la relation qui est à la base du concept d'État gardien ou fiduciaire : il réfère à un régime de protection et de gestion publique dans l'intérêt public et dont la finalité est l'équité intra et intergénérationnelle (Brown-Weiss 1984, Baslar 1998). Il attribue à l'État la mission et la responsabilité de préserver le patrimoine naturel, afin qu'il puisse être transmis en héritage aux générations futures (Moench 2001). Les bénéficiaires, qui sont les générations actuelles et futures, ont le droit d'attendre de l'État qu'il prenne toutes les mesures nécessaires pour protéger le patrimoine et pour en assurer la gestion prudente et diligente (Wood 2014).

Une fois le concept défini, on peut aussi dégager certains principes qui fondent le concept et les effets qui s'y rattachent. Il est intéressant de noter que les prérogatives octroyées par le concept se déclinent d'abord en devoirs en regard des objectifs d'intérêt public : le devoir de l'État de « prendre toute mesure nécessaire à la conservation du bien » (Vincent 2008), le devoir d'impartialité et de loyauté envers les bénéficiaires, le devoir de diligence, de précaution et de prévention, le devoir d'intégration des considérations environnementales à l'ensemble des politiques publiques, le devoir de préserver le droit à un environnement sain et les droits fondamentaux des bénéficiaires de la ressource, la responsabilité pour inaction en cas de dommages environnementaux, le devoir de prévoir des mécanismes de plaintes, de reddition de comptes, de transparence, etc. sont autant d'obligations qui sont soulignées dans la littérature (Fort 2012). Ces obligations permettent de souligner l'importance de renforcer les compétences réglementaires de l'État dans la définition, la planification et la mise en œuvre des règles devant permettre de parvenir aux objectifs de protection. Il est également intéressant de comprendre les implications de ces responsabilités étatiques, comme le droit des bénéficiaires à demander réparation au fiduciaire pour les détériorations du bien, le droit à l'information, à la participation.

Le concept d'un État gardien de l'environnement et des ressources naturelles présenterait, semble-t-il, l'intérêt de renouveler la réflexion sur le rôle de l'État, la légitimité de ses interventions au regard de sa mission d'intérêt public et de sa souveraineté sur ses ressources naturelles, ainsi que sur sa responsabilité dans la mise en œuvre de l'objectif d'équité du développement durable. Il se distingue de la conception traditionnelle de l'État centralisateur dans la mesure où il propose de baliser le pouvoir discrétionnaire de l'État par une gestion consensuelle et la mise en place de mécanismes d'imputabilité, permettant la surveillance et le contrôle par le public de l'usage des ressources. Par ailleurs, la répartition des pouvoirs de l'État vers des instances publiques plus restreintes, plus territoriales (États fédérés, provinces, municipalités) est une autre idée proposée dans la littérature pour encadrer l'autorité publique (Girard 2012).

L'idée véhiculée par le concept, selon laquelle la nature constitue un patrimoine commun à préserver au nom d'intérêts collectifs, est aussi présente dans certains droits nationaux, régionaux et en droit international. Par exemple, à l'échelle internationale, la Convention pour la protection du patrimoine mondial, culturel et naturel de l'UNESCO et la Convention des Nations Unies sur le droit de la mer réaffirment le principe d'un « patrimoine commun de l'humanité » à l'égard de certaines ressources sensibles, écosystèmes fragiles ou d'une valeur inestimable pour les générations actuelles et futures. À l'échelle régionale, le droit communautaire européen considère que les oiseaux migrateurs constituent un « patrimoine commun » sous la garde de l'Union Européenne et qu'il en résulte une obligation de résultat en matière de protection de la ressource (Directive concernant la conservation des oiseaux sauvages, préambule, 3e et 8e considérants). Enfin, à l'échelle provinciale, la Loi québécoise sur l'eau par exemple, affirme que les ressources en eau sont le « patrimoine commun de la nation québécoise », qu'elles revêtent un « caractère collectif », et que l'État québécois en est le gardien et doit ainsi s'assurer que les utilisations de la ressource par les personnes privées n'affectent pas la ressource et les usages collectifs.

Compte tenu de l'ampleur des atteintes que peuvent porter les activités du secteur minier au patrimoine naturel de pays riches en biodiversité comme Madagascar, il est pertinent de questionner l'ancrage ou l'application du concept d'État-gardien dans l'encadrement de ce secteur spécifique.

L'HYPOTHÈSE D'UN ÉTAT GARDIEN ET LE SECTEUR MINIER À MADAGASCAR : SUR QUELLE BASE ET QUELS ENJEUX?

UNE NOTION DE PATRIMOINE COMMUN À GARDER DANS LE DROIT DE L'ENVIRONNEMENT MALGACHE. La biodiversité malgache est l'une des plus riches au monde, avec des écosystèmes, une flore et une faune à très grande endémicité : 85% de la flore, 39% des oiseaux, 91% des reptiles, 99% des amphibiens et 100% des lémuriens sont endémiques à la Grande île (Goodman et Benstead 2005). Les écosystèmes forestiers sont les plus riches mais aussi les plus menacés par les activités humaines et certains d'affirmer que la perte d'un hectare de forêt à Madagascar a un effet irréversible sur la biodiversité mondiale (Hufty et Muttenzer 2002). Une partie de cette richesse naturelle est aujourd'hui considérée comme faisant partie du patrimoine mondial de l'UNESCO, dont deux sites naturels d'une grande importance figurant sur la Liste du patrimoine mondial et huit autres sites figurant sur la Liste indicative (UNESCO 2017). À l'échelle internationale, Madagascar est partie à un certain nombre d'instruments internationaux dédiés à la protection de la biodiversité et qui la consacrent comme un patrimoine naturel commun à préserver. C'est le cas, par exemple, du Protocole relatif aux zones protégées ainsi qu'à la faune et à la flore sauvages dans la région de l'Afrique orientale. La création et le maintien d'aires protégées constituent un des moyens privilégiés pour promouvoir la protection de la biodiversité. Lors du cinquième Congrès mondial des parcs de l'UICN en 2003, Madagascar s'est engagé à tripler la surface de ses aires protégées avec pour objectif d'atteindre six millions d'hectares en 2012, soit environ 10 % du territoire national, un objectif qui a depuis été atteint (Gouvernement de Madagascar 2016).

Dans le droit interne, l'idée de la biodiversité malgache comme un patrimoine naturel à préserver pour les générations actuelles et futures (par exemple, pour les communautés locales dépendantes de ces ressources, dont les droits d'usage sont conservés, ou encore pour les membres de la communauté scientifique nationale et internationale) se retrouve aussi dans plusieurs textes stratégiques et juridiques, dont la plus importante est sans doute la Charte de l'environnement malgache qui parle d'un « patrimoine Malagasy de biodiversité », déclare que « [l]'environnement constitue une préoccupation prioritaire de l'État » et que « [l]a protection et le respect de l'environnement sont d'intérêt général » (Charte de l'environnement malgache, art 6, 3 et 4). On peut lire dans la Politique nationale de l'environnement (PNE) que ce « patrimoine revêt un intérêt particulier pour la communauté scientifique », qu'« en raison de son caractère unique dans le monde, le patrimoine environnemental malgache est considéré comme patrimoine de l'Humanité » dont la sauvegarde doit être faite « pour le bien être de la population malgache et celui des générations futures » (Charte de l'environnement malgache, titre II, chapitre 1, section 2).

UN PATRIMOINE NATUREL AFFECTÉ PAR LE DÉVELOPPEMENT MINIER. Or, ce patrimoine national et mondial est aujourd'hui plus que jamais touché par un secteur minier en pleine expansion; ces deux espaces (exploitation minière et conservation) venant à se superposer. Plus particulièrement, les aires de conservation sont directement affectées, comme c'est le cas de la forêt de Mikea dans le Sud-Ouest de l'île, d'une très grande importance socioéconomique et culturelle pour les communautés locales, laquelle pourrait-être en partie déboisée par la construction de routes destinées à acheminer l'ilménite extrait par le projet *Toliara Sands* vers le port de Toliara (Rakotondrainibe 2015). À l'Ouest, la construction d'infrastructures routières et portuaires nécessaires au projet d'extraction de fer de la compagnie chinoise *Madagascar Wuhan Iron and Steel Corporation* ont fait également naître des inquiétudes pour le Parc national de la baie de Baly à Soalala (Valis 2012). Parmi d'autres exemples, l'exploration de terres rares par *Tantalus Rare Earths* sur la presqu'île d'Ampasindava s'étendrait sur 20 km^2 de forêts intactes, à proximité de la nouvelle aire protégée d'Ampasindava-Galoko-Kalobinono, elle-même entourée par environ six autres compagnies minières (Gouvernement de Madagascar 2015). Ensuite, plusieurs milliers d'hectares de forêts dont des forêts humides intactes de la région Alaotra-Mangoro abritant une multitude d'espèces endémiques ou parmi les plus menacées de l'île, sont aussi affectés par la mine de nickel et le pipeline du projet Ambatovy (Projet Ambatovy 2006). Enfin, le projet d'exploration de sables bitumineux à Tsimiroro et Bemolanga par *Madagascar Oil* pourrait présenter des risques pour la biodiversité, avec trois aires protégées à proximité : Ambohijanahary, le Tsingy de Beanka et le fameux Tsingy de Bemaraha, inscrit au Patrimoine mondial de l'UNESCO depuis 1990 (Les Amis de la Terre France 2012, Waeber et al. 2015).

QU'EN EST-IL DU DEVOIR DE PROTECTION ET DU RÔLE DE L'ÉTAT MALGACHE ? La multiplication de telles situations soulève un certain nombre de questions sur la façon dont ce conflit d'intérêt est abordé dans la réglementation des impacts du secteur minier et fait surgir des enjeux concernant les discours avancés et la capacité de l'État à percevoir d'abord puis à investir le rôle de gardien. En effet, si le droit positif malgache affirme haut et fort qu'il y a un patrimoine environnemental à protéger, un objectif qui est maintes fois rappelé par les instruments légaux et réglementaires encadrant le secteur minier comme les Codes miniers de 1999 et de 2005 (titre 5, chapitre 2) et la Charte de l'environnement malagasy actualisée de 2015 (préambule et article 3, 1er objectif), le droit n'est pas aussi clair sur le rôle que l'État doit jouer et les moyens à sa disposition pour mettre en œuvre cet objectif. Plusieurs autres dispositions législatives alimentent cette confusion. Par exemple, dans un premier temps, la Loi constitutionnelle n° 2007-001 du 27 avril 2007 déclare dans son article 37 que « l'État garantit la liberté d'entreprise dans la limite du respect de l'intérêt général, de l'ordre public, des bonnes mœurs et de l'environnement », ce qui semble accorder à l'État un certain rôle de garde-fou en faveur de l'environnement. Mais, dans un deuxième temps, selon l'article 7 de la Charte de l'environnement de 1990, la protection de l'environnement concerne un large éventail d'acteurs comme l'État, bien entendu, mais aussi les opérateurs économiques. De plus, la Politique nationale de l'environnement insiste sur la nécessité pour l'État de se désengager et de « céder sa place aux opérateurs privés » comme « des associations d'usagers, les ONG et des entreprises privées appelées à préserver et mettre en valeur les ressources du pays »; son rôle doit se limiter à « développer les incitations nécessaires, (…) suivre et évaluer les actions sur le terrain » (Charte de l'environnement malgache de 1990, titre II, chapitre III, ii). Dans cette optique, le Plan d'action environnementale a intégré explicitement les principes de l'ajustement structurel, de la décentralisation et de libéralisation dans la mise en œuvre de la Politique nationale de l'environnement (Charte de l'environnement malgache de 1990, titre III, chapitre 1, §§ 3.2, 3.3 et 3.5).

Quelques-unes des implications de ce régime en termes d'impacts sociaux et environnementaux des projets miniers peuvent être alors soulignées. Tout d'abord, une des stratégies choisies pour tenter de concilier ces extrêmes semble résider dans un glissement de la prise en charge de la protection de l'environnement qui s'est opéré de la sphère publique vers la sphère privée, cette dernière étant présentée comme la mieux placée pour prendre en charge les coûts des dégradations environnementales que le discours dominant associe à la pression démographie et aux pratiques agricoles des communautés locales (Sarrasin 2005). Ce transfert de compétences est consacré, par exemple, par la Loi n° 2001/05 portant Code de gestion des aires protégées qui convient dans ses articles 4 et 31 que la gestion des aires protégées peut être confiée à un organisme autonome, public ou privé. C'est ainsi que parmi les mesures d'atténuation de leurs impacts environnementaux, des projets miniers comme le Projet Ambatovy ou le projet de *QIT Madagascar Minerals* ont mis en place des programmes pour la conservation de la biodiversité malgache, à travers la création d'aires protégées dont le financement et la gestion sont confiés aux compagnies minières. Ce qui n'est pas sans conséquence sur les communautés locales puisqu'on peut s'attendre à ce que la gestion par les acteurs privés soit, à priori, différente de celle de l'État dont la mission d'intérêt public suppose la prise en compte et la protection des droits d'usage traditionnels sur la ressource, cela même si dans la pratique les deux types de gestion peuvent comporter des lacunes. Dans le cas de l'aire protégée sous la gestion du projet Ambatovy, le Collectif pour la défense des terres malgaches rapporte que des cultivateurs de cresson provenant des communautés avoisinantes avaient besoin d'accéder à la rivière comprise dans les limites de l'aire protégée pour leurs activités, qu'ils exerçaient depuis des dizaines d'années. Certains d'entre eux auraient été arrêtés pour avoir introduit une espèce végétale exogène (le cresson) dans l'aire protégée, puis relâchés sous réserve de cesser leurs activités (Rakotondrainibe 2015). Pour ce qui est de l'aire protégée gérée par la compagnie *QIT Madagascar Minerals* dans le Sud-Est de l'île, la situation peut sembler paradoxale si l'on considère que parmi les zones visées par le projet d'extraction d'ilménite, les sites de Petriky et Sainte Luce ont vu la création d'aires protégées confiées à la gestion de l'entreprise. Dans ce cas, cette gestion a été marquée par la restriction de l'accès à ces zones par les communautés locales (Randriamiarantsoa 2015). La question de l'accès à la terre et aux ressources naturelles qui semble relier les enjeux de la conservation et du développement minier à Madagascar a été soulevée et est toujours d'actualité (Seagle 2013).

Par ailleurs, un rapport des Amis de la Terre après une enquête sur le terrain en 2012 souligne la faiblesse des capacités scientifiques, matérielles, financières et humaines des institutions publiques dans l'appréciation et l'évaluation des impacts environnementaux, ainsi que dans le contrôle et le suivi des pratiques des compagnies, qui ne permet pas d'assurer la préservation du patrimoine naturel commun. Comme l'explique le rapport : « [e]n dépit d'un cadre législatif et réglementaire apparemment contraignant en matière environnementale, les pouvoirs publics ont de grandes difficultés à faire respecter les obligations qu'ils ont eux-mêmes édictées » (Les Amis de la Terre France 2012). Ainsi, si la loi malgache exige que le promoteur obtienne un permis environnemental avant le permis d'exploration ou d'exploitation, plusieurs permis d'exploitation auraient été délivrés durant la crise de 2009 et au cours de la période de transition qui a suivi jusqu'en 2014, pendant laquelle les capacités de l'État malgache étaient les plus affaiblies (Les Amis de la Terre France 2012). Cette période a vu la suspension de l'aide internationale et la mise en place d'un gouvernement de transition dont la légitimité, les fonctions et les responsabilités mêmes n'étaient pas clairement établies. Dans ce contexte d'affaiblissement des capacités institutionnelles, les générations futures mais surtout actuelles, bénéficiaires présumés de la préservation du patrimoine, deviennent les grands perdants : selon le rapport des Amis de la Terre, privées de leur droits traditionnels sur les ressources en plus des atteintes à leur droit à un environnement sain, mal informées, « osant rarement se plaindre par peur des représailles, et ne bénéficiant pas de la protection des autorités, les populations se retrouvent donc face à face avec les multinationales, qui cherchent régulièrement à faire taire, ou à contrôler, les oppositions potentielles émanant de la société civile » (Les Amis de la Terre France 2012).

En bref, il semble que le droit soit nuancé sur le rôle de gardien que devrait jouer l'État malgache dans la préservation de son patrimoine naturel. Les textes juridiques font ressortir un rôle partagé et ne lui reconnaissent qu'un rôle limité de promotion et de coordination, ce qui n'est pas sans équivoque sur le partage des responsabilités et l'imputabilité des différents acteurs impliqués, au regard des bénéficiaires de ce patrimoine. Toutefois, ce contexte renforce l'idée d'explorer l'application de la théorie de la fiducie publique. En effet, selon Catherine Ribot : « la théorie de la fiducie publique ne soutiendrait l'avancée du droit protecteur des ressources naturelles que lorsque l'État est privé des instruments traditionnellement reconnus pour justifier ses interventions en matière d'intérêt général » (Ribot 2012), ce qui semble bien être le cas à Madagascar, suite aux réformes successives de libéralisation dans le secteur des ressources naturelles. L'intégration du concept dans le droit malgache pourrait alors contribuer à renforcer les mécanismes de protection des ressources naturelles.

LIMITES AU CONCEPT ET À L'IDÉE D'UNE APPLICATION À MADAGASCAR

Une première limite, parmi les plus soulevées par la littérature, concerne la confusion des critères et méthodes de qualification du patrimoine commun et son État gardien, une confusion qui peut se manifester à travers la grande variété des termes utilisés, les textes de droit parlant par exemple de « patrimoine commun de l'humanité », « patrimoine commun des êtres humains », de « patrimoine commun de la nation » (Paquerot 2012). Il en résulte un régime juridique tout aussi confus, mal défini, entre appropriation et non appropriation, consensualisme et réglementation. L'effectivité du concept pose également problème : il est intégré dans le droit positif mais souvent sous la forme de déclarations qu'il n'est pas aisé de transcrire en règles strictes et dont les effets juridiques demeurent relatifs (Paquerot 2012). Par ailleurs, comme le souligne Jacqueline Morand-Deviller (2012), l'ordre économique mondial pèse de tout son poids dans la balance et il arrive souvent que des ressources déclarées « patrimoine commun » car non rentables ou encore inexploitables changent de statut dès que les progrès de la science les rendent exploitables. L'autre faiblesse la plus fréquemment soulignée dans la littérature se rapporte à la détermination de la personnalité juridique des bénéficiaires du patrimoine (l'humanité, la nation, le peuple ou les générations futures), qui pose la question du droit d'action devant les tribunaux en cas de dommages environnementaux (Fort 2012).

Si le concept comporte plusieurs faiblesses, il a tout de même le mérite de susciter un renouvellement du débat sur la question de la conservation environnementale et du rôle que l'État peut ou doit jouer. Il permet aussi de questionner les rapports juridiques d'appropriation des ressources naturelles, d'intégrer les enjeux liés au caractère limité de ces ressources et d'appréhender le partage des responsabilités dans la gestion durable des ressources (Fort 2012). Ainsi, lorsqu'envisagé dans le contexte de Madagascar, il permet de raviver le débat sur les questions de capacités (indissociables de celles des responsabilités), surtout politiques, institutionnelles et normatives, et de légitimité de l'action publique dans la gouvernance du secteur minier. Il offre par ailleurs une avenue de réflexion concernant un changement de paradigme dans l'encadrement du développement minier dans le pays. C'est aussi un concept qui a l'avantage d'être évolutif, flexible et dynamique, qui peut donc être adapté aux différents contextes, aux besoins et circonstances changeants de la protection du patrimoine naturel (Slade 2009). À ce propos, Jacqueline Morand-Deviller souligne que le concept se veut mobilisateur face à la généralisation de la « logique productiviste », qu'il « permet de mettre en évidence les valeurs éthiques propres à l'ordre écologique qui ne sont pas les mêmes que celles de l'ordre économique » et « peut inspirer le choix des institutions et des méthodes propres à répondre à la fonction particulière des biens ». En quelque sorte, il s'agirait selon elle de mettre de l'avant « une nouvelle manière de gérer les biens du patrimoine commun et de rappeler aux gardiens de ces biens les devoirs qui leur incombent » (Morand-Deviller 2012).

CONCLUSION

S'agissant du patrimoine commun naturel, certains juristes n'hésitent pas à suggérer un courant de « post-post-modernisme » du droit, qui permettrait un renouvellement conceptuel des missions et responsabilités de l'État, lequel dépasserait le rôle de simple régulateur qu'on lui a attribué dans un monde global administré par une main invisible, pour endosser un rôle de gardien des ressources naturelles mais aussi des droits et des intérêts de la population qui dépendent de ces ressources (Morand-Deviller 2012). Autrefois très critiquée, son intervention est de plus en plus considérée comme incontournable et centrale dans la poursuite du bien commun, de l'équité et de l'intérêt général (Arnaud 1998, Arnaud et Farinas Dulce 1998, Halley 2012), notamment en matière de protection de la biodiversité. Les responsabilités associées à cette intervention dans le concept d'État gardien permettent de soulever des questions cruciales comme celle de la capacité des États à prendre en charge ces responsabilités, et souligne ainsi les transformations institutionnelles et normatives à opérer. En tant que tel, il nous semble que le secteur minier ouvre un champ de réflexion intéressant et des questionnements importants pour l'application de ce concept, pour des recherches futures.

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MCD SPECIAL SECTION

WHALES

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EDITORIAL

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Humpback whales are present in all oceans. Although their population was decimated during the 20th century by industrial whaling, their numbers are now slowly increasing. This has been observed for both the North Atlantic and the North Pacific humpback whale populations. More investigations are needed to confirm this positive trend regarding South hemisphere stocks. Observations will also be useful to better estimate the effects of human activities, such as climate change, fisheries, oil prospection, and marine traffic on their population. The high mobility of this species, both during their migration and during breeding seasons, means that people from all countries have to work together towards a common objective: collect more data to create more knowledge to better protect them.

This is especially required in the South Western Indian Ocean, where islands belonging to many different countries are dispersed on their migration pathways. For the past 10 years, we have been working in collaboration with the Association Cetamada on this population in order to describe their distribution, their interactions, their behaviors, and their habitats. We wanted to share our methods and our results with other researchers in this geographic area, from which came the idea of creating an international conference.

We were very surprised that no scientific conferences were specifically dedicated to humpback whales. Many conferences are general to all marine mammal species or specific to methods and observation techniques. We therefore started to think about creating a place where researchers could come to exchange specifically about this species. Two main reasons were behind this idea. Firstly, humpback whales are probably baleen whales, which are the most observed whales across the globe. This means that datasets are increasing in size and quality, and could be shared to provide new results. Secondly, research on this species can be carried out using large multi-disciplinary approaches, including animal biology, marine ecology, ethology, genetics, applied mathematics and engineering.

Bringing together experts from different areas but all working on humpback whales and their marine ecosystems was the strong motivation behind the Humpback Whale World Congress that we created and organized with the Association Cetamada. The first session was held on Sainte Marie Island (Madagascar) from June 29 to July 3, 2015. More than 70 professionals and students from 16 countries gathered at this Congress. Renowned keynote speakers came from across the world, and 10 oral sessions were planned to give the chance to speakers to show their original methods and their recent results, making this conference a great success.

This special issue of the Journal Madagascar & Development is a compilation of the best presentations of this congress.

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Humpback whale, *Megaptera novaeangliae*, song during the breeding season in the Gulf of Tribugá, Colombian Pacific

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ABSTRACT

A key feature of humpback whale behavior, documented primarily on the breeding grounds, is the repertoire of the males' song. Song is made up of single units combined together into phrases, which are repeated to make up themes. A song consists of several themes sung in succession. This study qualitatively investigates the presence and structure of song recorded in the Gulf of Tribugá in the Colombian Pacific. Data were collected between June and September 2013, from which approximately 4 hours and 30 minutes of song were analyzed from five individual whales. Three distinct themes, always sung in the same order (theme 1-theme 2-theme 3) were identified. Theme 1 was the most predominant theme overall, and was present in each song session that was analyzed. The structure of each theme is described with accompanying spectrograms, and specific acoustic parameters further illustrate theme progression and characterize differences between whales. This study serves as the first published descriptive analysis of the song of stock G in this area, and suggestions are made for future directions of investigation. Research on humpback song is used as a part of the overall efforts of Macuáticos Colombia Foundation to educate the communities of the Gulf of Tribugá about the importance of conservation, and to advocate for stricter guidelines for safe whale-watching practices.

RÉSUMÉ

Les baleines à bosse ont été observées dans le monde entier et elles migrent chaque année entre leurs zones de nourrissage dans les latitudes élevées et les aires de reproduction aux latitudes basses. Le chant des baleines à bosse est l'un des comportements lié à l'accouplement qui a été documenté sur les aires de reproduction. Ce chant est composé d'unités simples combinées dans des phrases et qui sont répétées pour composer des thèmes. Les chants sont composés de plusieurs thèmes et sont principalement émis par les mâles. L'étude actuelle a porté sur la présence et la structure du chant des baleines à bosse du G-stock enregistré dans le golfe de Tribugá dans le Pacifique colombien. Les données ont été recueillies entre juin et septembre 2013 à l'aide d'un hydrophone SQ26-08 au cours d'excursions en bateau qui se sont déroulées 3 fois par semaine. La structure du chant a été codée en utilisant Raven Pro 1.4. Environ 4 heures et 30 minutes de chant ont été analysées et les chercheurs ont identifié trois thèmes distincts qui ont toujours été entendus dans le même ordre. Le thème 1 dominait dans tous les enregistrements et était composé de répétitions de légères variations de l'expression 'ABABABAA'. Le thème 2 était composé de répétitions des unités 'F' et 'Bl', avec des variations de la phrase de multiples unités répétées dans une rangée. Le thème 3 était composé de phrases répétées d'une unité longue 'upsweep' tonale 'LU', suivie par une unité courte 'upsweep' tonale 'SU', parfois avec une unité 'downsweep' dans le motif. L'unité 'S' a été entendue pendant les transitions du thème 3 au thème 1. Le thème 1 a été entendu beaucoup plus fréquemment que les autres thèmes et le thème 3 était le moins fréquemment enregistré. La structure changeante de chaque thème a été décrite avec des spectrogrammes d'accompagnement et les paramètres acoustiques ont été utilisés pour différencier les unités. Cette étude est la première analyse descriptive du chant du stock G dans ce domaine et des suggestions sont proposées pour les orientations futures de l'étude. Les enregistrements sonores ont été utilisés pour soutenir les efforts déployés par la Fondation Macuáticos Colombie pour sensibiliser éduquer les communautés du golfe de Tribugá sur l'importance de la conservation et pour renforcer les directives portant sur les pratiques sécurisées d'observation des baleines et de la pêche.

INTRODUCTION

Humpback whales are a cosmopolitan species that annually migrate between high-latitude feeding areas and low-latitude breeding areas. Behaviors exhibited by humpback whales in breeding areas help researchers better understand group social dynamics and conspecific communication (Winn and Winn 1978, Darling 2001). One such behavior is the singing of reproductive male humpback whales (Winn and Winn 1978). Humpback whale song

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has been documented in many breeding areas (Payne et al. 1983, Payne and Payne 1985, Cerchio et al. 2001, Darling and Sousa-Lima 2005, Eriksen et al. 2005, Murray et al. 2012, Oviedo et al. 2008). Additionally, song has been recorded during migration (Norris et al. 1999, Noad et al. 2000) and on a few feeding grounds (Clark and Clapham 2004, Stimpert et al. 2012, Garland et al. 2013).

Humpback whale song was initially described by Payne and McVay (1971) as being hierarchical in structure, in that a song will consist of a series of sound clusters that are termed units, phrases, and themes that repeat to form the succeeding cluster. A unit is defined as the shortest continuous sound to the human ear (Payne and McVay 1971). Cerchio et al. (2001) found that units can have fundamental frequencies ranging from 30 Hz to over 10,000 Hz. A phrase is an organized pattern of 2-20 or more units (Cerchio et al. 2001), which repeats with slight variation to form a theme (Payne and McVay 1971). A song is a series of discrete ordered themes, which can range in length from 8 to 16 minutes. However, some recordings demonstrate that songs can last for over 35 minutes (Payne and Payne 1985). A series of several songs repeated without pause is termed a song session. Song sessions can endure for several hours (Payne and McVay 1971).

Individual whales have been recorded altering their song throughout the breeding season (Payne and McVay 1971) and across different seasons (Guinee et al. 1983) by adding new units and reordering previously sung units (Winn and Winn 1978). This behavior is not restricted to individual whales, but rather these changes are often represented within the whole population (Winn & Winn 1978, Guinee et al. 1983, Payne et al. 1983, Payne and Payne 1985). Many similarities have even been noted between distinct populations (Winn et al. 1981, Cerchio et al. 2001, Darling and Sousa-Lima 2005, Garland et al. 2013). Due to the nature of migration, these distinct populations are able to transmit song across large distances (Noad et al. 2000, Clark and Clapham 2004, Darling and Sousa-Lima 2005). Cultural transmission is thought to be one of the possible explanations for these large-scale changes and similarities within and between populations (Guinee et al. 1983, Payne et al. 1983, Garland et al. 2011).

With such a large-scale transmission, the song structure from each distinct population needs to be documented in order to characterize longitudinal and geographic progression of song. The authors identified the Gulf of Tribugá as a breeding ground where no recordings of humpback whale song had previously been reported. It was the aim of this study to describe the structure of the southeastern Pacific (stock G) song from the Gulf of Tribugá in the Colombian Pacific.

METHODOLOGY

STUDY SITE. The current study was conducted in coastal waters of the Gulf of Tribugá, located in the northern Colombian Pacific within the state of Chocó. The gulf limits are El Valle, municipality of Bahía Solano (W077° 25′, N 06°06′) to the north, and Cape Corrientes, municipality of Nuquí (W077° 16′, N05° 43′) to the south (Díaz 2002). Boat trips originated from the small fishing village of Coquí (W077° 21′, N05° 36′), located in the southwestern section of Tribugá's Gulf. The Gulf of Tribugá is located within the Inter-tropical Convergence Zone influence. As a consequence, weather is characterized by low winds and high pluviosity (Eslava 1993). Considering the interaction of superficial marine currents and freshwater from the continent, coastal waters tend to be turbid. Sea surface temperature is relatively warm (22–28°C) and of medium-low salinities (Cantera 1993, Díaz 1998). Tides are characterized by a macro-tidal regime of up to 5 meters (Jaramillo and Bayona 2000, Díaz 2002). The Gulf of Tribugá is characterized by a considerably narrow and inclined continental shelf, and as such, the 300 m isobath is located only a few kilometers from the coast (Galvis and Mojica 1993).

DATA COLLECTION. Acoustic data were collected between 7 June and 13 September 2013 within coastal waters of the Gulf of Tribugá in the Colombian Pacific. Within this time period, recordings were made on 28 days, totaling 49 recording sessions. Date, GPS coordinates, photographs (if applicable), and environmental measurements (e.g., weather, salinity, and sea state) were collected in situ (Table S1.1). Boat surveys using an eight-meter fiberglass boat with an outboard motor alternated north and south from Coquí to limit the chance of re-sightings (see Payne et al. 1983). The research team conducted these surveys three times per week for approximately 8 hours per day, weather and fuel permitting. These trips were a part of data collection efforts by Macuáticos Colombia Foundation that included photo-identification and behavioral studies in addition to acoustic data collection. A single SQ26-08 hydrophone with a 0.02 to 50 kHz frequency range and 100 m maximum operating depth was connected to a 24-bit Zoom H1 digital recorder with 96 kHz sampling rate, 40 kHz recording capacity, and automatic gain settings turned off for more accurate reporting of measurements (Au and Hastings 2008). The hydrophone was deployed to the full extent of the 10 m cord whenever singers were detected, either visually or audibly. Recordings began only when song was clear and consisted of no more than two whales, and if possible, continued for the duration of the song. Given the reduced visibility encountered in the Gulf of Tribugá, the possibility of identifying individual whales underwater was limited. However, the authors registered 144 individual whales via fluke photographs in 2010 and 2013, and there was only one known re-sighting of those individuals. Moreover, the current estimation of 4000 individual whales in stock G (Clapham and Mead 1999) produces a very small likelihood of recording the same whale twice. Therefore, authors assumed that recordings made in a different area on a different day contained different individuals (see also Guinee et al. 1983, Payne et al. 1983). This assumption is adequate for the descriptive nature of this study.

DATA ANALYSIS. All recordings were screened for quality to determine which songs could be analyzed. Songs met the inclusion criteria if they contained one predominant singer and if they had sufficient signal-to-noise ratios (SNR) greater than 10dB, and on average 24.95dB ± 10.31dB, such that all units were easily visible above ambient noise. Only recordings with these SNR values were transcribed, ensuring that all frequency parameters of each unit were visible and no units were missed in the analysis (Cholewiak et al. 2013). Not all recordings met the inclusion criteria due to the frequent and interspersed interruption of ambient noise. Ambient noise was defined as containing some environmental (e.g., wind, waves) or anthropogenic (e.g., water craft) features, as well as song from other humpback whales in the distance. The song sessions of five different whales met the inclusion criteria and were included in the final analysis (Table 1). Raven Pro 1.4 bioacoustics software (Bioacoustics Research Program, Cornell Lab of Ornithology) was used to create time by frequency spectrograms (4096 FFT, Hann window, 50% overlap, window size 4045 for precise frequency measurements, hop size 31.5 ms) of high quality recordings to qualitatively describe the song structure (Figure 1). Spectrograms were transcribed for the individual units, phrases, and themes that constituted each song. Three independent observers [CEP, MEZ, DR] transcribed a subset of each theme from spectrograms, including both unit and phrase structure, both aurally and visually, to develop a reliable scheme for transcription. Authors [CEP, MEZ, DR] analyzed one entire recording together, to become familiar with the song structure (J. Darling, pers. comm. 2014). Subsequently, each observer analyzed a second recording independently for unit, phrase, and theme structure. Authors agreed upon this structure 90% of the time. Predominant discrepancies in transcription related to the exact start and end times for each theme. However, all discrepancies were addressed and collaboratively transcribed by the authors as a group. Acoustic parameters were measured for individual units using Raven Pro sound analysis software, and included duration (seconds), highest, lowest, and fundamental frequency (hertz). For reliability, each author analyzed a subset (25%) of the total data. High reliability on acoustic parameter transcription (85% agreement) was required before authors began transcribing independently. For analysis, acoustic parameters were measured for the first, middle, and last minute of each complete song within a recording. To ensure consistency and reliability in the transcription of phrases, rules suggested by Cholewiak et al. (2013) were applied. Specifically, subphrases, defined as distinct repetitions of units in a repeating pattern that together make up a phrase (Payne et al. 1983, Cholewiak et al. 2013) were maintained within phrases, and phrases were labeled to separate complete patterns of units (Cholewiak et al. 2013). For descriptive analyses, phrases were unambiguously associated with a particular theme type, as determined through inter-observer agreement between three of the authors [CEP, MEZ, DR]. Transitional phrases, which occurred when the structures of the previous and consecutive themes combined (Payne and Payne 1985), were analyzed separately from the three main themes.

RESULTS

Approximately 285 minutes of song were recorded during the 2013 season, of which 219 minutes (77% of the data) were analyzed. Three distinct themes (Figure 1) were found in each song, and these were composed of 11 units (Figure 2, Table S1 (modeled after the approach of Au et al. 2006)). In total, approximately 158.5 minutes of theme 1, 42.5 minutes of theme 2, and 18 minutes of theme 3 were recorded. The longest song session consisted of seven complete songs. Additionally, these themes were consistently heard in the same order throughout all five recordings. Individuals did not deviate from this theme order or skip themes. It cannot be determined if theme 1 was the first theme of each song, since recordings often began in the middle of a song.

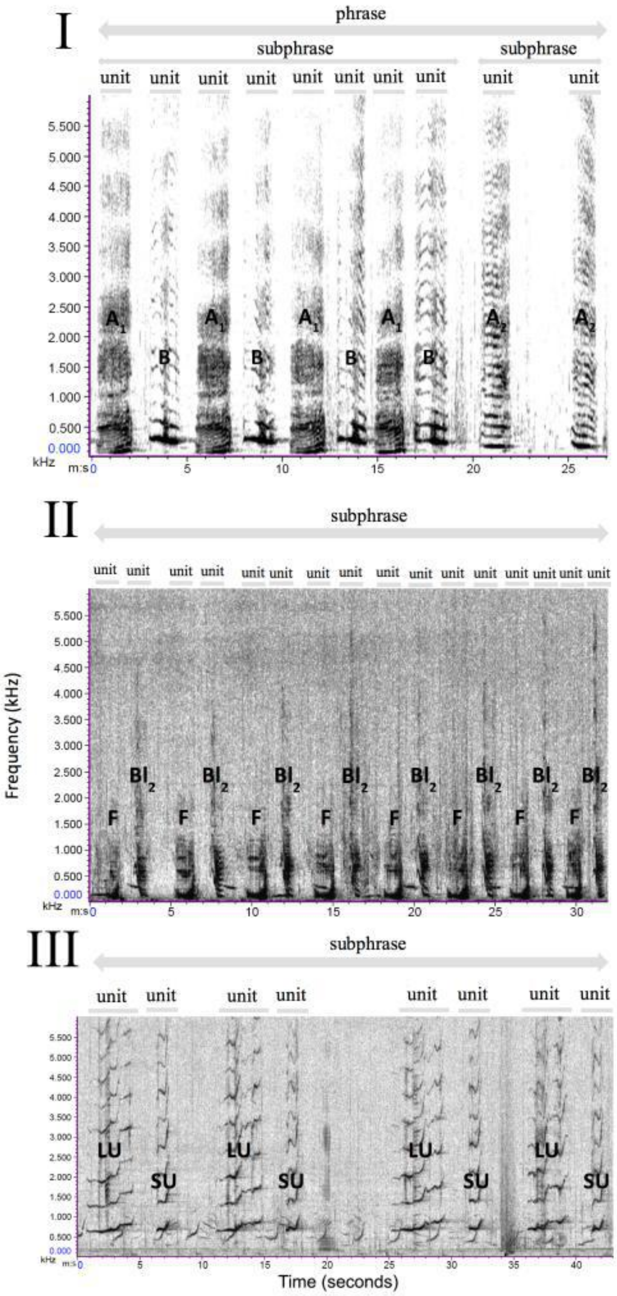

Figure 1. I. Spectrogram of theme 1 illustrating the phrase structure from whale 4. Subphrase 1A includes four repetitions of two units (A1 and B), and subphrase 1B is a single A2 unit repeated twice. II. Spectrogram of theme 2 illustrating subphrase 2A, the most common subphrase structure, from whale 4. These two units (F and BI2) are repeated eight times within this subphrase. III. Spectrogram of theme 3 illustrating subphrase 3A, the most common subphrase structure, from whale 3. This rendition of the subphrase consists of 4 repetitions of two units (LU and SU). High frequencies extended beyond the cut off. However, all themes (I, II, and III) have the same cut off for the purposes for this figure. Spectrograms created in Raven 1.4 Hann window with an FFT of 4096 and an overlap of 50%. Time (seconds) is along the x-axis and frequency (kHz) is along the y-axis.

Table 1. Quantitative summary of the analyzed recordings for the Colombia 2013 songs.

Date (2013)	2 VIII	9 VIII	9 VIII	12 VIII	12 VIII	9 IX	9 IX	13 IX	Totals
Whale #	1	2	2	3	3	4	4	5	
Duration of Recording	00:34:41	01:02:08	00:40:55	00:06:57	00:32:04	00:12:43	00:37:07	00:58:06	04:44:41
Total Number of Songs	3	7		2		NA	2	4	
Total Number of Themes	9	22		2	8	1	7	13	
Theme Order	1-2-3	1-2-3	1-2-3	1-2-3	1-2-3	1	1-2-3	1-2-3	
Total Duration of Theme 1	00:18:32	00:32:23	00:17:38	00:05:33	00:18:31	00:12:14	00:22:37	00:30:59	02:38:27
Total Duration of Theme 2	00:05:34	00:08:01	00:10:05	00:00:00	00:00:57	00:00:00	00:06:47	00:11:15	00:42:39
Total Duration of Theme 3	00:03:28	00:03:19	00:02:33	00:00:08	00:01:24	00:00:00	00:02:01	00:05:06	00:17:59

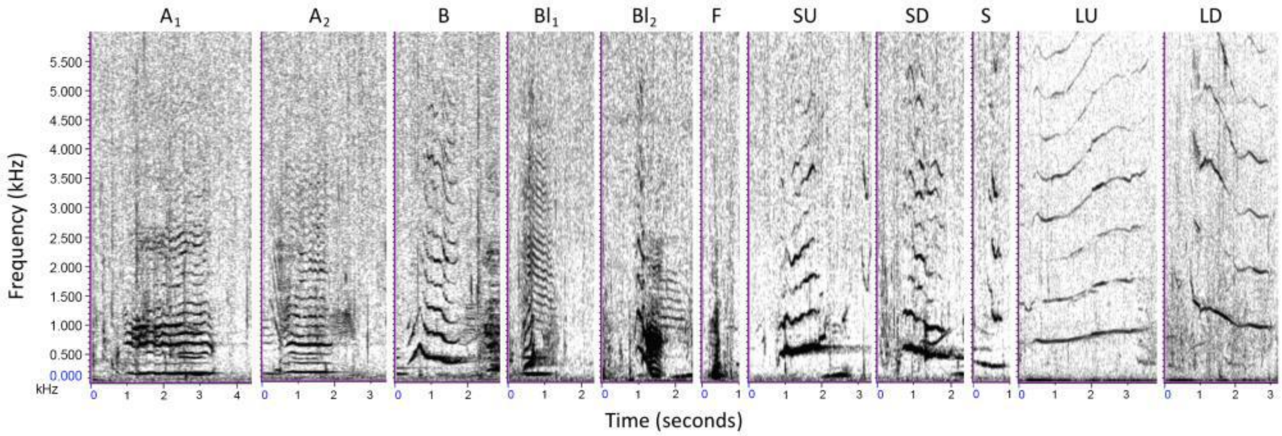

Figure 2. Spectrographic depictions of each unit type from the 2013-breeding season. Spectrograms created in Raven 1.4 Hann window with an FFT of 4096 and 50% overlap. All units have the same frequency cut off for the purposes for this figure.

THEME DESCRIPTION. Theme 1 was made up of three units (A1, B, and A2) that formed slight variations of the phrase A1BA1BA1BA1B A2A2 (Figure 1.I). Within this phrase, there were two subphrases (Figure 3.I). Subphrase 1A consisted of the unit A1 and unit B. The pattern A1B was usually repeated on average 6.14 ± 2.33 times in a phrase, but it was produced as few as 4 and as many as 17 times. There was no consistent pattern to the differing number of A1B repetitions within a recording or across the breeding season. These variations were consistent with the current understanding of subphrase structure (Cholewiak et al. 2013). Subphrase 1B consisted only of the unit A2, repeated a variable number of times (Figure 3.I). Unit A2 was labeled separately from unit A1 due to acoustic distinctions. Unit A1 had a greater frequency range and higher average frequency than A2; however, A2 had a higher average fundamental frequency (Table S1). Subphrase 1B is considered a "similar motif" according to the description of song structure proposed by Winn and Winn (1978), as unit A2 was the only unit in the subphrase (Figure 3.I). This subphrase most commonly manifested as a double repetition (A2A2, mean ± SD, 7 ± 3.87) within a theme rendition. However, subphrase 1B was occasionally expressed as a single A2 (2 ±1.73) or a triple repetition (A2A2A2, 1 ± 0). Although the subphrase 1A was always followed by subphrase 1B predictably, the five whales varied in their use of the second subphrase. All five whales used A2A2 in subphrase 1B. Whale 1 and whale 5 varied between A2 and A2A2 in subphrase 1B, whale 2 used only A2A2 in subphrase 1B, whale 3 used either A2A2 or A2A2A2 in subphrase 1B, and whale 4 varied between A2, A2A2, and A2A2A2 in subphrase 1B.

Both frequency and duration parameters further differentiated the individual units identified within theme 1. On average, unit B had a greater average high (4319.1 Hz) and a greater average low frequency (207.5 Hz) compared to both A1 (3479.9 Hz, 117.4 Hz) and A2 (4103.0 Hz, 102.0 Hz). This was also evident in the aural classification of units (Table S1). Additionally, unit A2 did not reach the low frequencies that both A1 and B did. Unit A1 had a greater average duration than either A2 or B, but also the greatest range of duration (Table S1).

Theme 2 was comprised of phrases that included three units (Bl1, Bl2, and F). Each phrase was broken into two subphrases, but was primarily composed of subphrase 2A (Figure 1.II, Figure 3.II). Subphrase 2A consisted of a variable number of F and Bl (either Bl1 or Bl2) repetitions (Figure 3.II). The Bl unit was characterized as either Bl1 or Bl2 based on acoustic parameters and spectrogram appearance (Figure 3.II, Table S1). Clear harmonics were not present in the Bl2 unit. Unit Bl2 had a higher average fundamental frequency (486.6 Hz) and average high frequency (2872.7 Hz) than unit Bl1 (Table S1). With the exception of the S unit (theme 3), unit Bl1 had the shortest average duration of all units in the dataset (0.5 s). These differences are consistent with literature that explains the gradual changing nature of phrases within a theme with respect to both frequency and duration parameters (Cholewiak et al. 2013). All whales utilized both Bl1 and Bl2 units in subphrase 2A in at least one song within their song session. Variations consisted of an average of 4.58 F-Bl2 repetitions (SD=3.50) alternating with an average of 4.9 F-Bl1 repetitions (SD=5.20). Subphrase 2B consisted of a variable number of F units (Figure 3.II) and is also a "similar motif" (Winn and Winn 1978). Not all whales sang this subphrase, but in all instances within the dataset it followed subphrase 2A. Unit F had the lowest average fundamental frequency of all units in the dataset (209.9 Hz).

Whale 1 exhibited variations to the phrase structure of theme 2 that no other whale used, including repetitions of F and 2 Bl2 units (mean ± SD, 2 ± 1.41), repetitions of F and 3 Bl2 units (mean=1), a single phrase of F and 4 Bl2 units, and a single phrase of F and 5 Bl2 units. Whale 2, whale 4, and whale 5 produced an average of 2 ± 0.71 F unit repetitions, while whale 3 was the only whale to repeat the Bl1 unit twice.

Theme 3 was characterized by phrases with five tonal units (LU, SU, LD, SD, S) and two subphrases (Figure 3.III). Each phrase was primarily composed of subphrase 3A, which consisted of a varying number of repetitions of a long, tonal upsweep (LU) unit followed by a short, tonal upsweep (SU) unit (Figure 1.III). Subphrase 3B always consisted of fewer repetitions than 3A, and included alternating long and short downsweep units (LD and SD) and S units (Figure 3.III). The pattern of units within subphrase 3B changed across phrase repetitions, which is supported in the literature (Cholewiak et al. 2013). Subphrase 3A persisted throughout every rendition of theme 3 in all five whales. However, whale 1 and whale 5 were the only individuals to incorporate subphrase 3B (Figure 3.III). Long units, upsweep or downsweep, ranged in duration between 1.8–4.3 seconds, and short units ranged between 0.5-1.5 seconds (Table S1). LU units had a greater average and range of duration compared to LD units. On average, SD units (1.0 s) were slighter shorter than LD units (2.6 s), but were similar in average duration to SU units (1.2 s). All upsweep units were lower in measured frequency parameters in comparison to downsweep units (Table S1). The S unit had the shortest average duration of all units in the dataset (0.3 s) with the highest average frequency (15776.3 Hz).

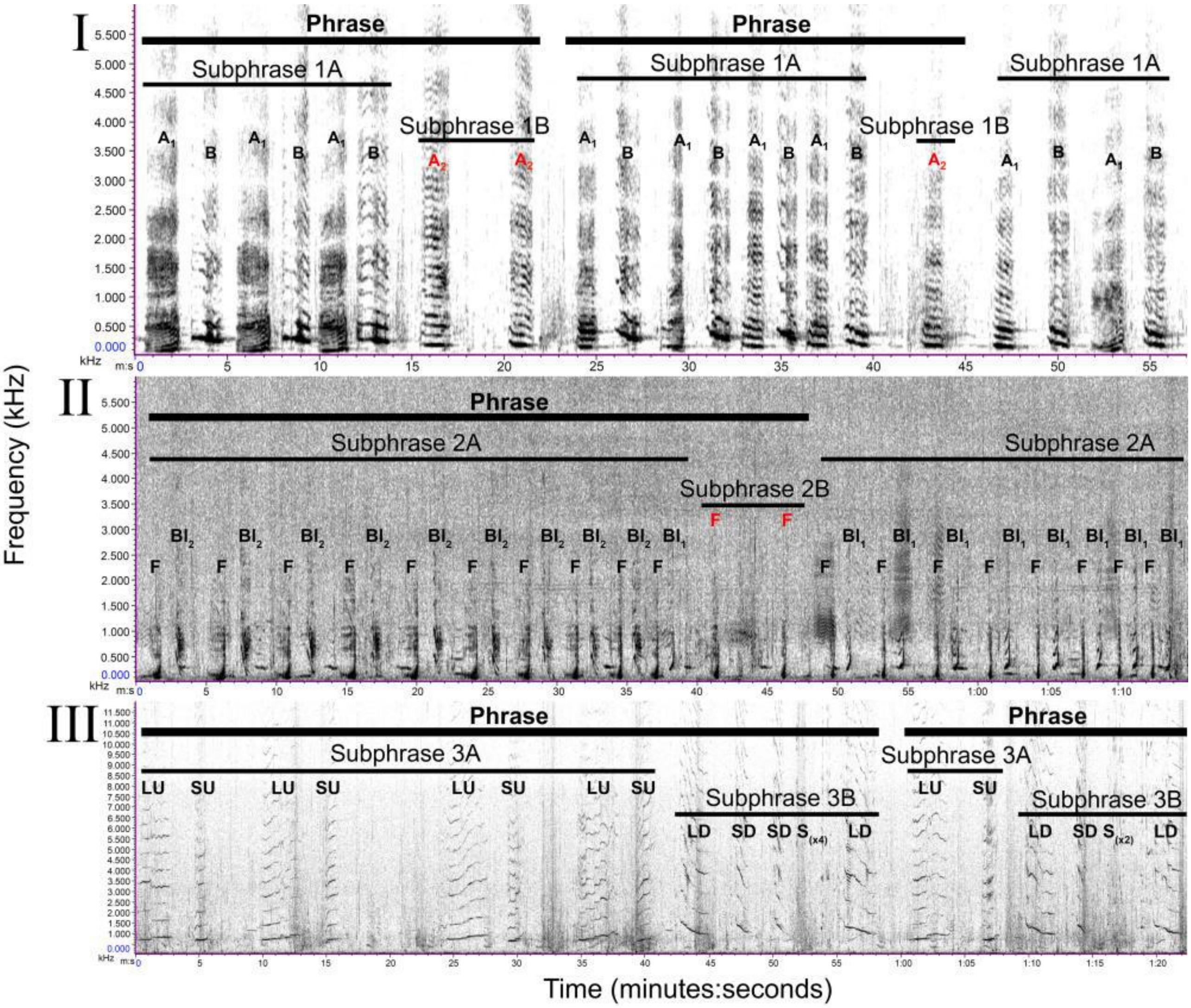

Figure 3.I. Spectrographic depiction of whale 4's variation on theme 1, illustrating the use of A2A2 vs. A2. This spectrogram shows 2 complete phrase renditions, and the beginning (of subphrase 1A) of a third phrase. II. Spectrographic example of theme 2's phrase structure from whale 4. Subphrase 2A consists of 10 repetitions of units F and BI, nine of which use BI2 and one uses BI1. Subphrase 2B consists of 2 F units repeated. Whale 4 is one of three whales that use subphrase 2B. The next rendition of subphrase 2A marks the start of a new phrase, this time with 8 repetitions of F and BI1. III. Spectrographic example of theme 3's phrase structure from whale 1. This theme rendition begins with 4 repetitions of LU and SU units (subphrase 3A). Subphrase 3B consists of LD, SD, and S units. The second subphrase 3A marks the start of the second phrase. Spectrograms created in Raven 1.4 Hann window with an FFT of 4096 and an overlap of 50%. Time (minutes:seconds) is along the x-axis and frequency (kHz) is along the y-axis.

Two transitional phrases were identified in the dataset: phrase 1-2 (Figure 4.I) and phrase 3-1 (Figure 4.II). No consistent transition was found between themes 2 and 3. These phrases were simple, and included a combination of units from two phrase types, one from each of the themes they separated. All five whales produced phrase 3-1, and phrase 1-2 was identified from all recordings with the exception of whale 1. These transitional phrases were consistent throughout the song sessions of each whale.

DURATION ANALYSES. The duration of each theme per individual whale was analyzed due to its importance and discussion in early song studies (Payne et al. 1983). It is evident that the three main themes were not used equally (Figure 5). Across all recordings, the average duration of theme 1 (424 s) accounted for the greatest proportion of the song when compared to themes 2 (120 s) and 3 (53 s) (Figure SM1.2A). More specifically, the number of renditions (i.e., each time a specific theme was heard within a single whale's song session) was analyzed. Theme 1, 2, and 3 comprised 39%, 30%, and 31% of total theme renditions, respectively (Figure SM1.2B). In summary, while theme 1 was longer in duration when compared to the two other themes, the use of each theme over the season was fairly similar.

The duration of each theme was also compared across individual whales. For each whale, theme 1 constituted the greatest average duration across song sessions, and theme 3 constituted the smallest average duration, with the exception of whale 3 (Figure 5). Whale 3 was the only individual to consistently spend more time singing theme 3 than theme 2 (Figure 5, Figure 6). When duration values were measured for each consecutive theme rendition within a whale's song session, theme 1 was consistently the longest theme, with the exception of whale 5's first song (Figure 6). There was a trend for the durations of theme 1 for whales 2, 3, and 5 to evolve in a bell-shaped distribution over the course of the song session (Figure 6). This pattern was also true in theme 2 for whales 1 and 4 (Figure 6).

Song duration followed a reliable pattern in each recording. The shortest complete song recorded was 7 minutes and 21 sec-

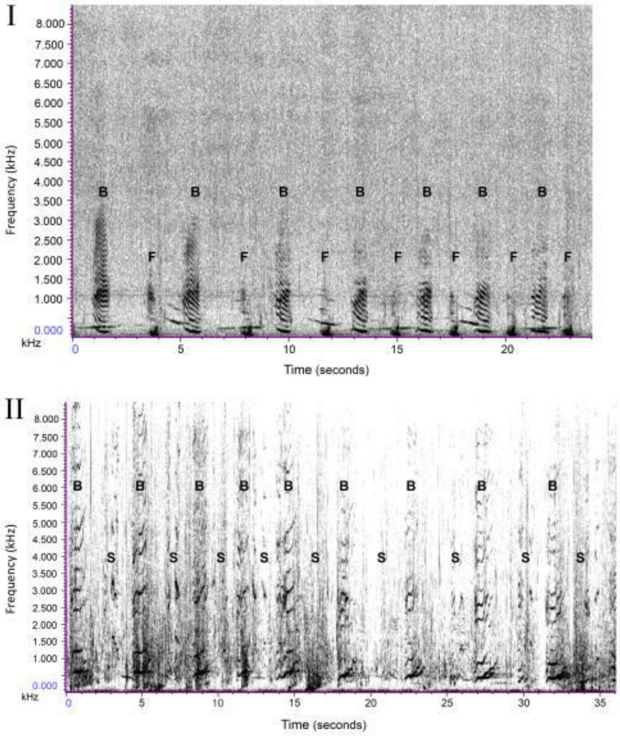

Figure 4. Spectrograms of transitional phrases. I. Phrase 1-2 (from whale 4) is the common transition between themes 1 and 2, and consists of alternating B units (theme 1) and F units (theme 2). II. Phrase 3-1 (from whale 1) persists between themes 3 and 1, and consists of alternating B units (theme 1) and S units (theme 3). Spectrograms created in Raven 1.4 Hann window with an FFT of 4096 and an overlap of 50%. Time (seconds) is along the x-axis and frequency (kHz) is along the y-axis.

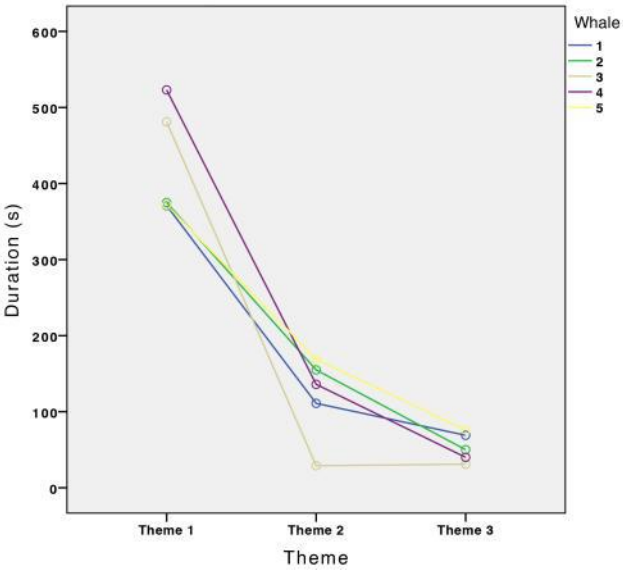

Figure 5. The average duration (in seconds) that each individual whale spent singing each theme. Each whale is denoted by a different color.

onds, and the longest was 12 minutes and 57 seconds. However, within an individual whale's song session, the duration of each song increased with successive renditions. In song sessions consisting of more than 3 songs, the duration of the last song recorded was always slightly shorter than the previous song. The number of songs in a song session ranged from less than 1 complete song to 7 songs. However, recordings occasionally had to be stopped between songs due to limitations in the field (e.g., weather, fuel complications), which made comparisons regarding song session length from the current data set impossible.

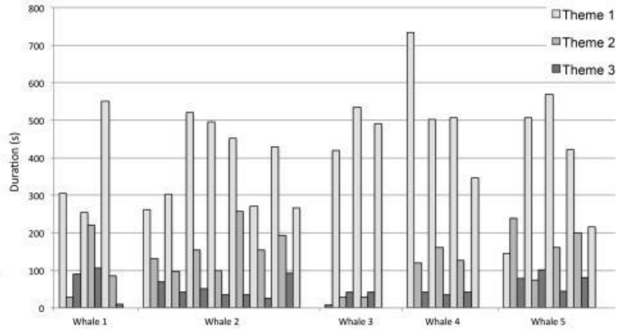

Figure 6. Distribution of themes across song sessions for each whale. Theme 1 (in light grey) is consistently the longest theme overall, and is generally the longest theme in each song session.

DISCUSSION

Research efforts on species preservation and habitat diversity in the Gulf of Tribugá remain limited, and significant information gaps persist in the study of the behavioral ecology of humpback whales in this area. Most importantly, the study of humpback whale song along the Pacific coast of Colombia is novel. In this report, the authors have put forth the first description of stock G's song in the Gulf of Tribugá during the breeding season of 2013. This paper illustrates that the song is highly organized (e.g., Winn and Winn 1978, Payne et al. 1983) and shared by individuals of the specific population (e.g., Winn and Winn 1978, Winn et al. 1981, Guinee et al. 1983, Payne and Payne 1985, Garland et al. 2015). It follows the same ordered and consistent theme repetition described in other populations (Payne and McVay 1971, Winn and Winn 1978, Payne et al. 1983, Payne and Payne 1985, Jenkins et al. 1995, Darling and Sousa-Lima 2005).

Initial duration analyses like the one detailed in this report are critical to the long-term understanding of song, as this parameter is a result of the hierarchical structure of song (Payne et al. 1983). Furthermore, Payne et al. (1983) suggested that differences in song duration might be due to the omission of certain themes within a song. However, the current study provides documentation that the five whales recorded never omitted a theme. The range of song duration reported here falls within the normal durations reported in early studies (Payne and McVay 1971, Payne and Payne 1985). Song duration can also be affected by the duration and number of phrase repetitions, which influence the length of each theme (Payne et al. 1983). Accordingly, duration was variable across themes in the current study, as has been reported in other populations (Payne et al. 1983, Darling and Sousa-Lima 2005, Darling et al. 2014,). Theme 1 was the dominant, or most frequently sung, theme in the 2013 recordings, consistent with previous descriptions of certain themes or phrases as consistently more frequent in production than others (Mercado et al. 2003, Darling and Sousa-Lima 2005, Murray et al. 2012).

Duration of phrases, and therefore themes, may eventually change over time. In 2013, theme 1 was the longest in duration, potentially due to the simplicity of unit types that constituted each phrase. For example, one phrase of theme 3 consisted of 5 different units, while in theme 1 there were only 3 units used within a phrase. Payne et al. (1983) suggest that the evolution of duration in phrases, and therefore themes, is something that needs to be analyzed over a multi-season comparison, which is beyond the limits of the current study. Subsequent analyses will determine if the same phrases continue to account for the greatest proportion of the song across years, as was the case for two phrase types in a study conducted in Hawaii (Mercado et al. 2003). The current initial description will allow for these necessary multi-year comparisons for stock G.

Transitional phrases in Colombian song are composed of a combination of units present in the previous and subsequent themes, thus acting as a transition between the two (Payne et al. 1983). Although Payne and colleagues (1983) stated that transitional phrases may vary in their complexity, both transitional phrases transcribed in the current analysis were fairly simple in that they did not vary in complexity across individuals or within song sessions. However, their structure will likely change in subsequent years as the stability of the song changes (Payne et al. 1983). Phrases 1-2 and 3-1 were used consistently throughout each song session, which is consistent with what has been cited as transitional in other studies (e.g., Murray et al. 2012). Interestingly, a transitional phrase was never noted between themes 2 and 3. This consistent absence of a transition between specific themes has also been noted elsewhere in the literature (Cholewiak et al. 2013). The presence or absence of transitions may also be related to the stability of the song (Payne et al. 1983), and may indicate that song during the 2013-breeding season in Colombia was undergoing structural changes. Further work studying consecutive breeding seasons in Colombia will address the consistency and complexity of these transitional phrases.

The hierarchical structure of the song of stock G was composed of units, which were grouped together into distinct phrases, which were repeated to form a theme. Three different themes were transcribed from 2013 data. The vagueness of phrase, and therefore subphrase, structure across the literature has been discussed in terms of comparability of song descriptions (Cholewiak et al. 2013). The authors chose to delineate subphrases within each phrase to describe the song of stock G in detail to aide future geographic and longitudinal comparisons (Winn and Winn 1978, Payne et al. 1983, Cholewiak et al. 2013 (motifs)). Two subphrases were noted within each theme, consistent with early descriptions from Hawaii (Payne et al. 1983). The strong similarities in hierarchical structure of stock G's song to the song of multiple stocks on other breeding grounds provide the foundation for further comparative analyses.

Many studies within the song literature compare the song of different populations (Cerchio et al. 2001, Darling and Sousa-Lima 2005, Murray et al. 2012, Garland et al. 2011, 2015). Future studies should seek to expand the current report on Colombia's stock G song via collaborative global comparisons with whale stocks in other locations. These collaborative efforts will help the scientific community to better understand the underlying mechanism of cultural transmission of song across ocean basins (Garland et al. 2011).

While the data presented here come from a single breeding season and five individual whales, the re-sighting history and physical description of the study site provided in the methods suggest that each song session analyzed was from a distinct individual, which is critical to the analysis of song structure (Cerchio et al. 2001, Murray et al. 2012). Continued longitudinal analyses will elucidate the changing nature of the song, which may have been limited during the 2013 season of data collection by occasional weather or fuel-related interruptions to recordings. Weather is an unavoidable and unpredictable issue within the Colombian Pacific, but continuing grants in future years will alleviate fuel limitations.

LOCAL CONSERVATION IMPLICATIONS. Song is heard extensively in breeding areas, and this migratory species faces a complex set of environmental and anthropogenic pressures within limited breeding areas. Fishing and whale watching ecotourism are major sources of livelihood for the local communities in the Gulf of Tribugá. While local residents and visitors see humpback whales frequently, many have never heard humpback whale song. Since the initiation of this study in 2013, song recordings have been used as a tool to educate the communities about the importance of conservation and to increase awareness of the whales' presence in the Gulf. Groups of students and environmental guides from the local communities were invited on boat trips to hear the whales in situ and learn about the research process. Continued efforts to educate the community and ecotourism industry will endeavor to promote behavioral changes that improve the safety of the public's interactions with humpback whales during their breeding season.

CONCLUSION

The data presented in this study provide an important initial description of song structure in the Gulf of Tribugá, and are part of an ongoing study to characterize the shared song type of stock G used during a given season and across consecutive years. Understanding the song of a single stock over time will allow for specific descriptions of individual changes over time, as photo-identification records are matched to known singers. Correspondingly, the long-term results of this ongoing work will contribute to our understanding of song. Future work to acoustically assess the relationship of Colombian song to song on other breeding grounds will add to the ongoing discussion of the similarities in song within an ocean basin and the dissimilarities across discrete locations.

ACKNOWLEDGEMENTS

Our greatest gratitude is extended to the local communities in The Gulf of Tribugá. We are very grateful to Dr. Jim Darling for assistance with methodology and the structure needed to transcribe the data early on, to Dr. Eduardo Mercado III for invaluable feedback and input on the analysis and interpretation, and Dr. Ellen Garland for help with statistical questions and input on future endeavors. We would also like to acknowledge the valuable input we received from three anonymous reviewers. Cetacean Society International, Idea Wild, Rufford Small Grants for Nature Conservancy, the Society for Marine Mammology, and indiegogo.com provided grants and funding for this project. We would like to thank Andrés Cañas, Maria Camila Medina, Andrea Caicedo González, Nadya Ramírez, and Alejandra Neira for assisting with data collection, and Luz Helena Rodriguez for assisting with grant applications. Finally, the authors would like to dedicate this publication in memory of the late Dr. Stan A. Kuczaj II.

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SUPPLEMENTARY MATERIAL

Available online only

Table S1. Auditory descriptions, duration (seconds), and frequency (hertz) parameters of individual units analyzed from the Colombia 2013 songs.

Table S2. Additional information from data collection protocol and environmental parameters (when available) to compliment methodology.

Figure S1. A. The relative theme representations for the Colombia 2013 songs. The dominant theme (theme 1) was sung for >70% of the song, and the minor themes (themes 2 and 3) were sung for 20% of the song or less. B. The proportion of total theme renditions (64) throughout the Colombia 2013 songs. Themes 1, 2, and 3 had 25, 19, and 20 renditions respectively.

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ARTICLE

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Where does the air go? Anatomy and functions of the respiratory tract in the humpback whale (*Megaptera novaeangliae*)

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ABSTRACT

Air is a limited resource under water. Pressure changes during diving and ascent further affect buoyancy and sound production/transmission by changing air volumes, densities, and shapes of air spaces and vibration pathways. This paper will focus on how humpback whales use air, and the respiratory tract adaptations that help overcome these challenges. These highly modified respiratory tract tissues function to shunt air to increase oxygenation for extending breath-hold time, conserve and recycle air, maintain hearing at depth, generate sound for communication and navigation, transmit vibrations to water, mitigate noise, support air spaces from collapsing, regulate chamber volumes, produce bubbles as visual signals, control air release as a tool to trap prey, modify center of gravity, regulate buoyancy, and reduce energy expenditure during locomotion. The humpback whale is able to utilize air in an aquatic environment in ways that allow it to support a wide range of unique behaviors.

RÉSUMÉ

L'air est une ressource limitée sous l'eau. Les changements de pression au cours de la plongée et de la remontée affectent la flottabilité et la production / transmission des sons en changeant les volumes d'air, les densités et les formes des espaces aériens et des voies de vibration. Cet article se penche sur la façon dont les baleines à bosse utilisent l'air ainsi que les adaptations des voies respiratoires qui participent au processus. Les tissus des voies respiratoires sont hautement modifiés et fonctionnent de manière à shunter l'air pour augmenter l'oxygénation afin de prolonger le temps d'apnée, de conserver et de recycler l'air, de maintenir l'audition en profondeur, de générer des sons pour la communication et la navigation, de transmettre des vibrations à l'eau, d'atténuer le bruit, d'empêcher les espaces devant contenir l'air de s'effondrer, de réguler les volumes des chambres, de produire des bulles servant de signaux visuels, de réguler la libération de l'air qui servira d'outil pour piéger des proies, de modifier le centre de gravité, de réguler la flottabilité, et enfin de réduire les dépenses d'énergie lors de la locomotion. La baleine à bosse utilise l'air dans un milieu aquatique de manière à assurer une multitude de comportements uniques.

INTRODUCTION

Humpback whales (*Megaptera novaeangliae*) are air-breathing mammals adapted to fully aquatic life. They are able to perform many functions underwater, including swimming, feeding, excreting, communicating, mating, birthing, nursing, and sensing their surroundings (Reidenberg 2007). One function, however, remains restricted to the surface: breathing. However, their simple "blow" is in sharp contrast to the complex respiratory tract hidden within their bodies.

Air (actually it is a mixed gas that is not necessarily atmospheric "air", as the molecular composition will vary depending upon the respiratory phase) is moved throughout the humpback whale's respiratory tract. What happens to that air? It is used for respiration, hearing, communication, navigation, visual displays, feeding, air conservation and recycling, locomotion, and buoyancy control, among other behaviors. The humpback whale respiratory tract consists of lungs, trachea, larynx, nasopharynx, bony nasal cavities, external nasal cavities, and blowholes, with air sac extensions into the pterygoid air sacs or "sinuses" (under the skull, near the ear) and the laryngeal sac (ventral to the larynx). This study explores the various air-containing spaces in the humpback whale, including the tissue folds, valves, and muscles that regulate these spaces, and how these structures are used for so many different functions.

MATERIALS AND METHODS

It is not feasible to observe internal respiratory tract anatomy in live humpback whales, as these methods generally utilize invasive approaches or internal imaging technologies (e.g., computerized axial tomography or CT scanning, magnetic resonance imaging or MRI, ultrasound scans) that are difficult or currently impossible to deploy in a field situation on wild, large-bodied whales. Therefore, this study uses post mortem anatomical findings to reconstruct the properties of the living tissues and derive the functions of the respiratory tract.

Observations were made from postmortem dissections of humpback whales. Twelve specimens were studied: four adults (all females), three juveniles (one female and two males), and five calves (three females, two males). No whales were killed for this

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study. All specimens were obtained after death.

One whale was found beach stranded on the east coast of Madagascar, and was collected and examined by the scientific team of the Cetamada organization. This is the first scientific specimen of a mysticete larynx collected in the Indian Ocean. The remaining eleven whales were from the Atlantic Ocean, and were found beach stranded along the northeast coastline of the United States of America (USA), specifically in the states of New York and Massachusetts. Specimens from these whales were collected and distributed through the Marine Mammal Health and Stranding Response Program (MMHSRP) of the National Marine Fisheries Service (NMFS) under the National Oceanic and Atmospheric Administration (NOAA), USA. Response to and examination of these stranded whales (including collecting tissue samples from the carcass) were authorized under NMFS permit No. 932-1905/MA-009526 in accordance with the Marine Mammal Protection Act. Tissue specimens are maintained under a letter of authorization from NMFS NOAA to possess and receive marine mammal hard and soft parts for comparative anatomy research (issued to the author). Specimen transfers were approved and arranged by the state Regional Stranding Coordinators of the MMHSRP: Riverhead Foundation for Marine Research and Preservation (New York), Atlantic Marine Conservation Society (New York), and the New England Aquarium (Massachusetts).

Visual inspection was made of the external nares (blow holes), including limited exposure of the nasal plugs and lateral plates that surround the nasal openings. The blowhole tissues were removed for further dissection from one male calf.

Laryngeal samples were taken whole whenever possible, including most of the trachea. Specimens varied greatly regarding degree of freshness or decomposition. Each larynx specimen was removed from the whale carcass using standard butchering techniques (knives and retracting hooks), occasionally assisted by use of heavy machinery to move or retract adjacent tissues. Whenever possible, the larynx was removed along with the hyoid bone (the attached bone was often used as a handle to assist in retracting the larynx out from the carcass). The larynx was then put into a holding container (plastic bag or plastic tub) and brought back to our laboratory for preservation by either freezing or immersion in formalin (10% formaldehyde solution).

Laryngeal dissections were carried out to assess the anatomy of the muscles, cartilages and joints, and soft tissues associated with sound production. Most larynges were initially cut along the dorsal midline and each side retracted laterally to reveal the ventral lumen including the laryngeal sac. The bisection was continued into the ventral aspect for some specimens, dividing the larynx in the midsagittal plane into left and right halves. Once photographs were taken, some specimens had the vocal folds (U-fold) removed so they could be prepared for future MRI or CT scanning. The rest of the specimen was then defleshed to assess the cartilaginous skeleton.

Visual assessments of pulmonary anatomy were made whenever possible while on site during the dissections of stranded whales. In many cases, limitations on dissection time prevented a full necropsy. In many dissections, the thoracic cavity was only partially opened, and thus lungs were not fully exposed. Lungs were thus usually examined in situ. No whole lung specimens were recovered for further dissection.

RESULTS

Specimens ranged in size (straight linear length from rostrum tip to notch between flukes) from 538cm to 1550cm. Specimen data are given in Table 1.

The humpback whale respiratory tract consists of lungs, trachea, larynx, nasopharynx, bony nasal cavities, external nasal cavities, and blowholes, with air sac extensions into the pterygoid air sacs or "sinuses" (under the skull, near the ear) and the laryngeal sac (ventral to the larynx). The larynx is interlocked with the nasal cavity, and the digestive pathway passes lateral to this interlock (Figure 1). The lungs are paired, and reside mostly along the dorsal aspect of the thoracic cavity. Interestingly, they are not divided into lobes, even though the primary (mainstem) bronchi do divide into secondary and tertiary bronchi within the lungs.

Tracheal cartilages are irregular in shape and spacing, but are generally of similar thickness. Sometimes they form discrete O-shaped rings, and sometimes they bifurcate or fuse with neighboring rings. Rings closer to the carina tend to be distinct, but rings close to the larynx are usually fused together dorsally and incomplete ventrally. This fusion becomes more pronounced rostrally, where they cannot be distinguished from the cricoid cartilage of the larynx (Figures 2 and 3). The primary (mainstem), secondary, and tertiary bronchi are reinforced by cartilage rings. There is an eparterial bronchus branching into the right lung rostral to the right mainstem bronchus (Figure 4).

The lumen of the tracheo-laryngeal junction contains several parallel and thin soft tissue folds along the ventro-lateral aspect (Figure 4). These folds are gently curved into an S-shape that begins parallel to the trachea (i.e., parallel to the long axis of the trachea but perpendicular to the tracheal cartilage rings) and ends directed towards the lateral edges of the vocal folds (i.e., parallel to the tracheal rings and perpendicular to the long axis of the trachea). There do not appear to be any muscles associated with these S-shaped folds, but they appear to contain tough connective tissue fibers, as they do not decompose as easily as the adjacent mucosal tissues.

A midline thickening is found along the dorsal aspect of the laryngeal lumen (Figures 4 and 5). It appears to be mostly comprised of fatty tissue. We referred to this swelling as a "cushion" due to its soft, compressible texture. The cushion is positioned directly dorsal to the gap between the vocal folds. The cushion's shape is ovoid and elongated in the long axis of the trachea and

Table 1. List of the 12 specimens of humpback whale (*Megaptera novaeangliae*), including age, sex, body length, field ID number, and location of stranding. (Field ID letter codes: NY = Okeanos Ocean Research Foundation, or Riverhead Foundation for Marine Research and Preservation, New York; MH = New England Aquarium, Cape Cod Stranding Network, or International Fund for Animal Welfare, Massachusetts; MAD = Cetamada, East coast of Madagascar)

Age	Sex	Length	Field ID number	Location
Calf	Female	548cm	NY-2411-00	New York, USA
Calf	Female	794cm	NY-881-92	New York, USA
Calf	Male	845cm	MH-96-479-MN	Massachusetts, USA
Calf	Male	not available	MH-98-629-MN	Massachusetts, USA
Calf	Female	850cm	NY-2700-01	New York, USA
Juvenile	Male	960cm	NY-4270-2010	New York, USA
Juvenile	Female	962cm	NY-814-91	New York, USA
Juvenile	Male	not available	AMCS20Mn2017	New York, USA
Adult	Female	1386cm	NY-766-91	New York, USA
Adult	Female	1535cm	NY-2818-2002	New York, USA
Adult	Female	not available	NY-4790-2013	New York, USA
Adult	Female	1550cm	MAD-201601-MNX	Sambava, Mada.

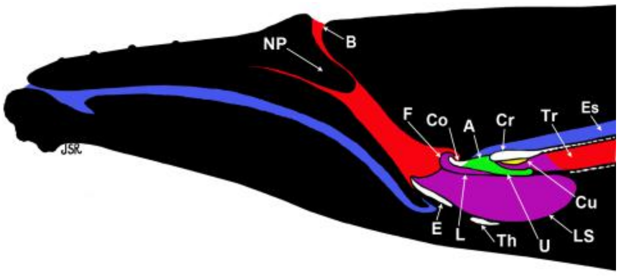

Figure 1. Schematic diagram of a humpback whale head showing the respiratory tract (red), digestive tract (blue), laryngeal lumen (purple), cartilages (white), cushion under the cricoid cartilage (yellow), and U-shaped vocal fold supported by the arytenoid cartilage of the right side (green). (A = arytenoid cartilage, B = blowhole, Co = corniculate cartilage, Cr = cricoid cartilage, Cu = cushion under the cricoid cartilage, E = epiglottic cartilage, Es = esophagus, F = flap of tissue from the corniculate cartilage, L = lip of the vocal fold, LS = laryngeal sac shown partially inflated, NP = nasal plug, Th = thyroid cartilage, Tr = trachea, U = U-shaped vocal fold)

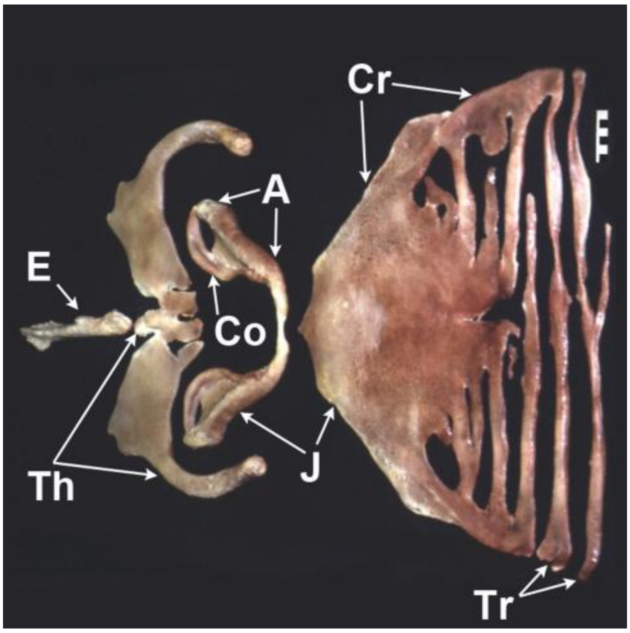

Figure 2. Disarticulated laryngeal cartilages from a juvenile female humpback whale, dorsal aspect. (Rostral is to the left, caudal is to the right, dorsal is exposed, and ventral is hidden. A = arytenoid cartilage, Co = corniculate cartilage, Cr = cricoid cartilage, E = epiglottic cartilage, J = synovial joint between the arytenoid and cricoid cartilages, Th = thyroid cartilage, Tr = trachea. Scale bar: each black or white square = 1 cm)

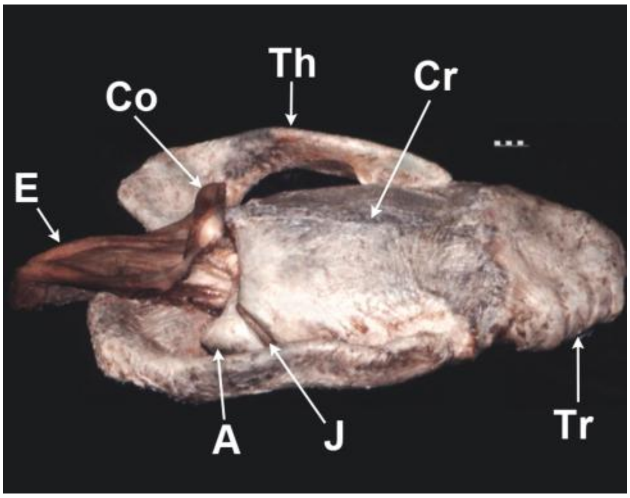

Figure 3. Articulated laryngeal cartilages from an adult female humpback whale, lateral-oblique aspect. (Rostral is to the left, caudal is to the right, dorsal is top, and ventral is bottom of figure. A = arytenoid cartilage, Co = corniculate cartilage, Cr = cricoid cartilage, E = epiglottic cartilage, J = synovial joint between the arytenoid and cricoid cartilages, Th = thyroid cartilage, Tr = trachea. Scale bar: each black or white square = 1 cm)

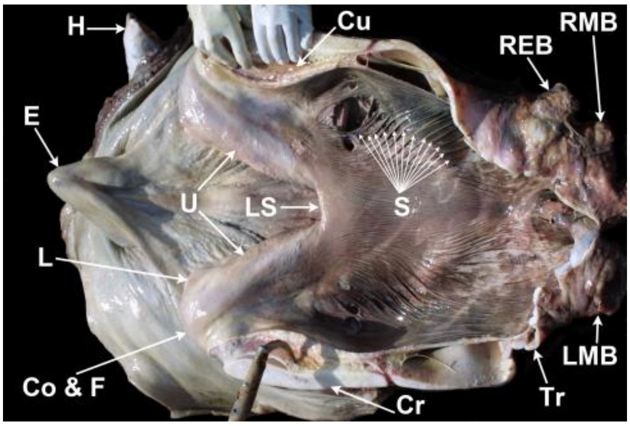

Figure 4. Larynx from an adult female humpback whale, viewed from dorsal aspect. Rostral is to the left, caudal is to the right, cricoid cartilage incised in midline and reflected laterally to expose lumen. (A = arytenoid cartilage, Co & F = corniculate cartilage and flap (they have become soft with decomposition and are draped over edge and disappear ventrally), Cr = cricoid cartilage (retracted on the left by a metal hook, and on the right by two gloved hands), Cu = cushion under the cricoid cartilage, E = epiglottic cartilage, H = hyoid apparatus (probably the thyrohyal portion), L = lip of the vocal fold, LMB = left mainstem (primary) bronchus, LS = laryngeal sac (begins underneath the letters U and LS, but extends in the direction of the arrow under the ligament that joins the two U-shaped vocal folds), REB = right eparterial bronchus (epibronchus), RMB = right mainstem (primary) bronchus, S = S-shaped folds, Tr = trachea, U = U-shaped vocal folds. Note: Although there are some holes in the mucosa due to decomposition, the S-shaped folds remain intact thus indicating they may be comprised of stiffer tissues (more collagen connective tissue fibers?). The many parallel S-shaped folds may direct air from the trachea to the gap between the U-shaped vocal folds)

larynx, being thickest in the midline and tapering laterally, rostrally, and caudally. This ovoid shape is matched to the long gap that runs rostro-caudally between the U-shaped vocal folds in the plane of the glottis (glottic gap). It appears to seal the glottic gap when the vocal folds are raised towards the cushion, or perhaps dampen vocal fold vibrations when making slight contact.

There are three unpaired cartilages (cricoid, thyroid, and epiglottis), and two fused paired cartilages (aryteno-corniculate complex) that comprise the larynx (Figure 2). The cricoid is located dorsally. It is very broad but incomplete ventrally. As previously mentioned, it is fused to the tracheal rings caudally and laterally. The rostro-lateral edges are tapered diagonally away from the midline, and support the synovial joint for the articulation of the arytenoid cartilages (Figure 3).

The midline of the thyroid cartilage is located on the ventral aspect of the larynx, and is positioned closer to the rostral end of the larynx (Figure 2). Its body is relatively small, compared to that found in most other mammals. It does not fold sharply between the two lamina, nor does it have a strong ventral prominence ("Adam's apple"). It does have a notch in the rostral midline that is largely occupied by the epiglottic cartilage (Figure 6). The superior horns (cornua) extend superiorly and curve caudally in an arch that connects to the lateral aspects of the cricoid cartilage (Figure 3).

The epiglottic cartilage is softer than the other cartilages, even in fresh specimens. In decomposed specimens, it appears to decompose faster (perhaps indicating a higher water content and lower degree of perichondrial fibrous tissue), and becomes very flexible (Figure 6). When defleshed, its boundaries are difficult to ascertain, as the edges do not have a thickened covering of fibrous tissues as do the other cartilages. The epiglottic cartilage has many holes throughout its body, giving it a perforated appearance. It is unclear what occupies these holes in life. The overall shape resembles the curved outer walls of a half cylinder (i.e., with a hollow center), with the convex aspect facing rostrally towards the oral cavity, and the concave aspect facing toward the laryngeal aditus. The base is thicker than the apex. The apex is pointed, and directed into the nasopharynx. The rostral aspect (the convex surface) faces the oral cavity, and is covered along the superior aspect by the soft palate. The epiglottis (epiglottic cartilage with its covering flesh) rests posterior to the soft palate, and is positioned in contact with this tissue at rest (Figure 5).

Arytenoid cartilages are paired, and each one is fused to a corniculate cartilage (Figure 2). The aryteno-corniculate complex extends both caudally and rostrally. The caudal extension is comprised of arytenoid cartilage, and supports the tissue of the vocal fold (Figure 1). The distal caudal tip is curved medially and is attached to the other arytenoid cartilage's distal caudal tip by a ligament (likely the homolog of the vocal ligament) (Figure 2). This joining gives the pair of vocal folds the appearance of one continuous U-shaped fold (Figures 4 and 5). The caudal extensions are cylindrical, and give this same shape to the vocal fold tissue that covers them. This tissue has several smaller folds along the dorsal aspect that may indicate some flexibility during vibrations. The tissue covering the medial aspect is smooth and flat, and appears to seal against its pair during adduction. The tissue covering the rostro-ventral region (just before the corniculate portion of the complex) is extended into a thickened lip-like shape (Figures 4 and 5). The "lips" of the opposed pair may part and re-seal, perhaps interrupting airflow to create pulsed sounds. The ventral surface of the vocal folds is continuous with the lateral walls of a ventral diverticulum called the laryngeal sac (vide infra).

The aryteno-corniculate complex extends as the corniculate cartilage rostrally (Figure 2). The corniculate projects superiorly and curves cadually towards the cricoid cartilage. The rostral, convex edge supports a flap of tissue called the corniculate flap (Figures 3 and 5). This tissue projects rostrally as a thin plate. As it is only supported by cartilage caudally, the rostral extension is very flexible. The paired corniculate flaps lie side by side, oriented in the sagittal plane. If the flaps move medially then they contact each other (adduction), and if the flaps are parted laterally then the space between them is enlarged (abduction). They are joined dorsally by a thin tissue that spans the midline. Ventrally, the space between them is continuous with the laryngeal aditus. The two flaps appear to nest into the trough-shaped lumen of the dorso-caudal aspect of the epiglottis.

At the midpoint of the aryteno-corniculate complex, there is a joint surface (on the caudal aspect) that is part of the arytenoid portion of the cartilage complex. Each arytenoid joins the rostro-dorsal edge of the cricoid cartilage at a synovial joint – one on each side of the larynx (Figure 3). The joint is curved, and elongated on a diagonal slope away from the midline. The curved shape enables the cartilage to rock rostrally and caudally, rotating around an axis oriented between left and right. The extension of the joint surface along a diagonal slant allows the cartilage to slide rostro-caudally, while also adducting as it moves rostrally and abducting as it moves caudally. There also appears to be an ability to rock the arytenoid medially and laterally along this diagonal surface, causing the distal (caudal) arytenoid tips to abduct or adduct.

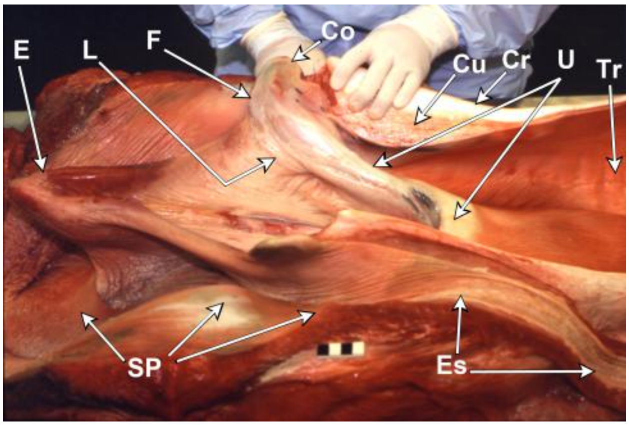

Figure 5. Larynx from a juvenile male humpback whale, viewed from lateral-oblique aspect. Rostral is to the left, caudal is to the right, cricoid cartilage incised in midline and reflected laterally to expose lumen. (Co corniculate cartilage, Cr = cricoid cartilage (retracted on the right by two gloved hands), Cu = cushion under the cricoid cartilage, E = epiglottic cartilage, Es = esophagus, F = flap of corniculate cartilage, L = lip of the vocal fold, SP = soft palate (note epiglottis lifted up so is not in direct contact with area indicated by left arrow, and note additional center and right arrows indicating extension around corniculate cartilage as palatopharyngeal sphincter, that was cut in the dorsal midline, exposing the musculature above the scalebar), Tr = trachea, U = U-shaped vocal folds. Scale bar: each black or white square = 1 cm. Note: the cushion is positioned directly above the vocal folds, and matches the gap between them in length. The cushion may serve as a valve blocking airflow between the laryngeal sac and the trachea, or may dampen vibrations from the U-shaped vocal folds)

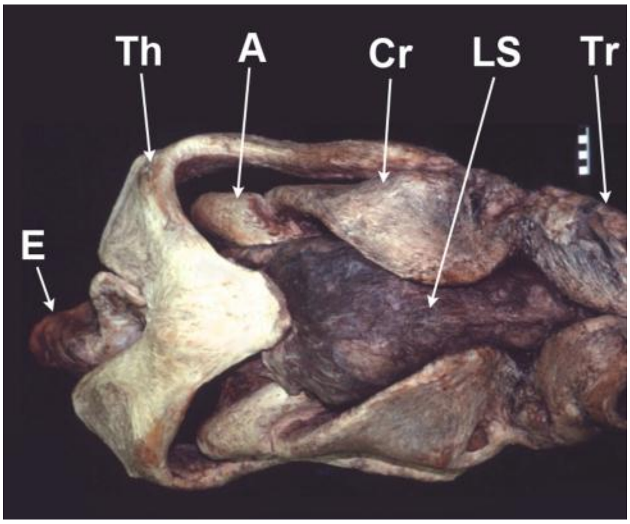

Figure 6. Articulated laryngeal cartilages from an adult female humpback whale (same specimen shown in figure 3), ventral aspect. Rostral is to the left, caudal is to the right, dorsal is hidden, and ventral is exposed. (A = arytenoid cartilage, Cr = cricoid cartilage, E = epiglottic cartilage, LS = laryngeal sac, Th = thyroid cartilage, Tr = trachea. Scale bar: each black or white square = 1 cm. Note: some of the laryngeal sac is hidden underneath the thyroid cartilage in the midline. However, the bulk of the laryngeal sac is positioned in the gap caudal to the thyroid cartilage and between the lateral aspects of the cricoid cartilage)

Each arytenoid has a projection on the lateral aspect called a muscular process (Figure 3). The muscular process supports the posterior and lateral cricoarytenoid muscles. Manual manipulation of the joint reveals that the posterior cricoarytenoid can pull the muscular processes towards the midline, perhaps resulting in rotation of the vocal folds. Further manipulation of the joint reveals that the lateral cricoarytenoid can pull the muscular processes laterally, parting the vocal folds. There is also an interarytenoid muscle between the base of each corniculate extension. Squeezing the arytenoids together in the direction of this muscle's fibers causes adduction of the vocal folds and corniculate flaps. The cricothyroid muscle was not manipulated, but the fiber direction indicates that it can bring the base of the thyroid cartilage closer to the cricoid. It is unclear what this action accomplishes, but it may collapse the laryngeal lumen and laryngeal sac. Manual pressing of the V-shaped thyroid cartilage against the ventral aspect, where there is no other cartilage support (as the cricoid is incomplete ventrally), collapses the laryngeal sac (Figure 6).

The musculature of the thyroarytenoid and/or vocalis appear to be extended circumferentially around the laryngeal sac. This is verified by the presence of the recurrent laryngeal nerve innervating the sac's musculature. The circumferential muscle layer surrounding the laryngeal sac is very thick, and appears to be a forceful means of contracting the sac (independent of thyroid cartilage compression). No intrinsic laryngeal muscles were observed that can expand the sac. Extrinsic muscles were not fully dissected as they were always severed from the sternum and sometimes detached from the hyoid. Remnants of their attachments indicate that when they pull the larynx rostrally (e.g., hyoepiglotticus, thyrohyoid) they can extend the laryngeal sac in the rostrocaudal axis, and when they pull it caudally (e.g., sternothyroid, sternohyoid) they can help compress it.

The laryngeal sac is a ventral diverticulum located below the vocal folds (Figures 1 and 6). The glottic gap is the entrance to the laryngeal sac's lumen (Figure 4). The lateral walls are supported dorsally by the arytenoid cartilage extensions inside the vocal folds. The laryngeal sac extends caudally under the trachea. There are no tracheal cartilages immediately above the laryngeal sac. This may allow the sac to distend into the tracheal lumen from below and narrow the trachea's volume. The deflated laryngeal sac (including its thick musculature) occupies a volume that is approximately equal to that of the trachea and larynx, and appears to be able to swell to an even greater volume. During dissection, it was apparent that the combined volume of the collapsed laryngeal sac and larynx was very close to the volume of one whole (mostly deflated) lung, but likely can double in size and inflate to a volume close to the total of both lungs. The laryngeal sac has a row of pits on either side in the caudal region of the lumen. It is unclear what is inside the pits. The left and right sides of the sac are joined in the midline at a median raphe. This raphe is supported by a ligament that connects caudally in the midline to the ligament between the caudal tips of the vocal folds, and connects rostrally in the midline to the caudal edge of the thyroid cartilage. It appears to be the remainder of the homolog of the fused vocal ligaments. This homology is supported by the presence of the internal laryngeal branch (sensory portion) of the superior laryngeal nerve innervating the mucosal surface of the laryngeal sac on either side. As in other mammals, this sensory branch only innervates the larynx superior/rostral to the level of the glottis.

The rostral aspect of the larynx (unpaired epiglottis and paired corniculate cartilages with their flaps) is inserted into the nasopharynx (Figure 1). The opening into the larynx (laryngeal aditus) is thus aimed at the nasal region. The soft palate is extended laterally around the epiglottic and corniculate cartilages, and connects behind them, forming a circular sphincteric valve (palatopharyngeal sphincter) sealing the entrance to the nasopharynx (Figure 5). The soft palate's mass is much larger anteriorly than it is posteriorly, and contains musculature that can tighten its grip around the epiglottic and corniculate cartilages. This appears to help seal the aditus from incursions of water or food during swallowing or other open-mouthed behaviors. The epiglottis can be removed from behind the soft palate, and inserted into the mouth. Although it is difficult to bend the epiglottis in a fresh specimen, this movement into the oral cavity is easily accomplished when the soft palate (rostral portion of the palatopharyngeal sphincter) is lifted superiorly manually.

Above the nasopharynx are the openings to the paired bony nasal passageways at the bottom of the skull (posterior choanae). These two cylindrical chambers are angled superiorly in a diagonal rostro-dorsal plane. The bony nasal passageways widen as they approach the top of the head, and terminate in two separate blowhole openings. The blowholes are protected from water incursions by a prominent rostral ridge that serves as a splash-guard, deflecting water laterally (Figure 1). The blowholes (nostrils, external nares) are valvular, and can be closed by opposing the lateral surface towards the medial surface. This tissue is stiffened by cartilage plates that are moved by facial muscles. In addition the nostrils can be completely sealed by the nasal plugs. Each plug is a curved tongue-like structure that is inserted into the nasal passageway. It can be retracted during breathing, but at rest it remains covering the passageway, thus sealing it from water (Figure 1). Facial muscles are responsible for retracting the plugs anteriorly to open the blowholes.

DISCUSSION

AIR SHUNTING. During respiration (inhalation and exhalation), the air moves between the blowholes and the lungs, following the most direct pathway. When the whale is submerged, air inspired into the lungs is likely to become oxygen depleted relatively quickly. The whales may be able to extend their breath holding time by shunting air between the lungs and other respiratory spaces. This would allow the whale to turn over the oxygen-depleted "used" air in the lungs, exchanging it for more oxygen-rich "unused" air that was previously trapped in non-respiratory spaces (nasal cavities, respiratory diverticulae, larynx, and trachea). Shunting oxygen-rich air from these spaces to the lungs may allow continued gas exchange to occur, effectively giving the whale additional breaths underwater.

The shunting mechanism appears to involve pushing air back and forth between two flexible-walled spaces that can alternately stretch and recoil. The parallel nasal passageways through the skull are not likely to be involved in such shunting because their walls are not flexible since they are constrained by bone. However, the lungs and the soft-sided laryngeal sac are perfect for this function. As the diaphragm contracts, air is drawn from the nose, past the larynx, through the trachea, and into the lungs. No more air can move in from the nostrils while underwater. Air is also unlikely to move in from the mouth, even if it were held above water, because the oral cavity is usually isolated from the respiratory tract (Reidenberg and Laitman 2007a). This isolation of the two pathways is an essential cetacean adaptation that prevents drowning during underwater open-mouthed behaviors (Reidenberg and Laitman 1987). Instead, additional respiratory-like movements may occur through shunting of air between various chambers. As air is unlikely to move back into the rigid nasal region, shunting probably occurs between the lungs and laryngeal sac. Air is may be diverted from the full lungs (through thoracic intercostal muscle contractions compressing the ribs together and shrinking lung volume) and into an expanding laryngeal sac, located ventral to the larynx. Capturing the air in the sac ensures that it is not lost to the environment (conserved) and therefore can be used again (recycled). Once the laryngeal sac is fully expanded, it can compress via contraction of its circumferential musculature, evacuating its gas back through the larynx and trachea and to the lungs. The volume of the laryngeal sac is at least as large as one lung (Reidenberg and Laitman 2010), and possibly can be expanded to match the volume of both lungs. If so, compression of the sac would expel laryngeal sac air back into both lungs, filling them completely. This shunting most likely occurs when dive depths pressures are relatively shallow and ambient pressure does not force complete collapse of the airways.

Of course, the degree of expansion of any of these spaces is subject to the forces of ambient pressure. The lungs collapse and gas volumes shrink with increasing ambient pressure during a dive (Kooyman and Ponganis 1998). Presumably, there is a depth (and therefore pressure) at which these air spaces will completely collapse, and shunting will no longer be possible. The expandable laryngeal sac may therefore also function as an accessory air reservoir, allowing the whale to compensate for the effects of pressure. It may use these reserves to add volume to the essential air chambers, thereby maintaining a functional volume (e.g., for vocalizations) under conditions in which the more typical respiratory space volumes would have otherwise completely collapsed.

Maintaining essential air spaces at depth is also important for hearing, as the tympanic membrane (ear drum) and ossicles (ear bones) cannot vibrate to transmit sounds unless they are suspended in an air-filled chamber. In this mechanism, sound vibrations are likely received by fat associated with the lower jaw (Yamato et al. 2012). This is the mechanism toothed whales use for sound reception (Koopman et al. 2006). The sound is then transmitted to the fat/tissue interface of the tympanic membrane. Movement of the tympanic membrane (that is extended into a structure often called the "glove finger"), causes vibration of the attached ossicles that, in turn, vibrate the oval window and the fluid within the cochlea (Ketten 2000). Different frequencies (i.e., sound wavelength) and magnitudes (i.e., sound amplitude) are then detected by the specialized hair cell receptors of the cochlea that then transmit the signal to the brain. As air spaces collapse, some of the remaining air is preferentially held in the pterygoid air sac (Reidenberg and Laitman 2008). This air sac is located under the skull and connects with the middle ear space. Air fills this sac through a connection with the pharynx. As the pharynx collapses at depth, what little air remains is likely shunted into the pterygoid sac. As the pterygoid sac then begins to collapse, its remaining air is shunted in turn to the middle ear. Diving depth may thus be limited to ranges where hearing is still functional because the middle ear airspace has not yet collapsed. Alternatively, another hearing mechanism may be used that avoids the necessity of maintaining a middle ear air space. This would enable the whale to dive even deeper, reaching depths where the pterygoid air sac would completely collapse. This alternative mechanism uses vibrations that are conducted along the bone of the skull directly to the ear (Cranford et al. 2010, Cranford and Krysl 2015).

SOUND PRODUCTION AND TRANSMISSION. Humpback whales are well known for their elaborate songs, sung by the adult males predominantly in a range between 40Hz and 4kHz (Au et al. 2001, 2006, Mercado et al. 2003, Herman et al. 2013). Singing behavior occurs in both the northern and southern hemisphere humpback whales and, although all whales in a given population sing the same song at the same time, neighboring populations are influenced through cultural transmission to sing the same song (Clapham 2017). As mammals, whales have inherited a pneumatic sound generating system, similar to what land animals use. This presents a major transmission problem underwater, as sound waves generated in air by vibrations of the vocal folds (vocal "cords") do not transfer to water. Through evolution, humpback whales and other baleen whales (mysticetes) have developed a unique larynx (voice box) with vocal fold homologs that are fused caudally (called "U-shaped fold") that enables them to generate and then transfer sounds to water (Laitman and Reidenberg 1999, Reidenberg and Laitman 1999, 2007b). Air passing from the lungs to the trachea is diverted away from the usual path to the blowholes. Instead, it is directed 90 degrees inferiorly away from the nasal cavities and towards the throat region. The air passes through a gap between the U-shaped vocal folds. The vocal folds are also re-oriented 90 degrees (compared to terrestrial mammals) so that they are parallel to the long axis of the trachea. Interestingly, a similar configuration also occurs in toothed whales (odonotcetes), except that the reorientation of vocal folds parallel to airflow occurs in the opposite direction (Reidenberg and Laitman 1988, 1999). Air passing between these folds should cause the tissues to vibrate, generating sound (Mercado et al. 2010, Adam et al. 2013, Cazau et al. 2013).

Note that while singing is typically done by adult males, the females and juveniles have also been recorded making sounds. These sounds are more social, including mother-calf calls or feeding calls that coordinate the upward lunge through a bubble-net. The same anatomy described for song production is likely used for these calls as well. Further work is needed to elucidate the specific sounds that can be generated by the various parts of the vocal apparatus (vide infra on corniculate flaps).

Unlike terrestrial mammals, whales must transfer sound energy to water. Any sound waves generated in the air spaces of the head are "lost" as they are not transmitted out of the whale and into water. Rather, it is the vibrations within the tissue itself that are likely propagated to water. These vibrations appear to be transferred to the laryngeal sac tissue that is attached immediately ventral to the vocal folds. As the walls of the sac vibrate, they move the overlying blubber and skin of the throat region that is made more flexible by the presence of expandable throat grooves. The laryngeal sac and the overlying blubber and skin then pulse, like a drum-head, transferring these pressure waves directly to the water. As flesh is very close in density to water (it is largely comprised of water), there is relatively little transmission loss. This makes it more efficient than the terrestrial mechanism of transferring vibrations from tissue to air.

The many axes of movement of the vocal folds, and their geometry, likely plays a major role in determining the qualities of the produced sounds. Versatility of vocal fold movements may indicate nimble muscular control, and pulse speed (frequency) and intensity (amplitude) may indicate robust fitness. Thicker and longer folds likely produce lower frequency and louder amplitude sounds. As such, the vocalizations may be a true advertisement of the whale's health, stamina, agility, and size, and therefore may be very important in mate competition/selection and in establishing social hierarchy.

The head-down position of singing whales may also assist in directing the sound waves in a trajectory that allows maximum propagation away from whale. In the head-down position, the laryngeal sac faces outward, rather than inferiorly towards the sea floor. As the laryngeal sac vibrates the overlying blubber and skin, the pulses transferred to the water would be directed horizontally. Additional vibrations may also occur through pulses directed at the air columns of the nasal cavities (like a pipe organ). These pulses may move the nasal plugs and emit sounds dorsally (that would be directed horizontally, in the opposite direction from the laryngeal sac, in a head-down position). Alternatively, the bony walls of the nasal cavities may vibrate and send pulses through the skull to be transmitted circumferentially from the head to the water. These air-containing resonant spaces may contribute to the overall quality of the emitted sound (Mercado et al. 2010).

A second sound production mechanism may occur in the larynx at the site of the corniculate flaps. These flattened tissues are aligned side-by-side, and can be parted by air flowing between them. As air flows past, these tissues likely clap against each other, generating pulsed sounds. It is unclear how these pulses are transmitted outside the head, although it is possible that they are either transmitted inferiorly by the attached vocal folds to the laryngeal sac, or that they are propagated superiorly along the walls of the nasal cavity. Having a dual sound source may explain some of the unusual sounds humpback whales can generate.

There are several other points of constriction along the respiratory tract (vide infra on valves), and vibration of any of these may generate sound. Perhaps some dual or multiple energy peaks of whale sounds are generated in a manner similar to how a bagpipe works. If a fundamental frequency is made at the laryngeal sac (similar to the bagpipe's main "bag"), then overtones may be created by adjusting structures downstream of the compressive forces on the laryngeal sac (similar to fingers on the holes of one pipe, harmonics in the other pipes). In some ways, it is reminiscent of overtone singers (or Mongolian throat singers) who generate laryngeal fundamental frequencies, and then create higher frequency overtones by adjusting airflow through the mobile constrictions made by opposition of the tongue, soft palate, and pharyngeal wall.

While it is generally assumed that sounds are made as air flows egressively (away from the lungs), it is also possible that sounds may be made on the ingressive flow (towards the lungs). In this case, contraction of the laryngeal sac may drive the system by increasing sac pressure thus sending air flowing back to the lungs. Air rushing past any constrictions in the respiratory tract would generate vibrations for sound production.

It is important to note the role of the laryngeal sac in extending the length of a vocalization. In a closed system, the volume of air is limited. With rigid walls, the flow of air can only occur until both sides reach equilibrium. Once flow stops, so does sound production. However, if the air-receiving chamber is flexible, then flow time (and therefore vocalization length) can be extended until the distensible chamber reaches full capacity. Therefore, the laryngeal sac, being a highly distensible chamber, facilitates longer songs because the expansion delays pressurization of the respiratory system.

VALVES. The laryngeal sac also may function as a valve when it is fully inflated, an idea originally proposed for the bowhead whale's larynx (Schoenfuss et al. 2014). As the sac is located directly underneath the cartilage-free region of the trachea, this tissue is very flexible. Expansion of the sac may therefore raise the ventral tracheal wall, thereby creating a valve as it collapses the tracheal lumen. Schoenfuss et al. (2014) proposed that this arrangement forced air to only be shunted between the laryngeal sac and the nasal region. This is difficult to accept, as the bony nasal passageways in the skull do not have flexible walls that can expand to accommodate the air from the sac. Rather, we propose that the inflated laryngeal sac does not completely obstruct the trachea.

Rather than serving as a valve that blocks airflow in the trachea, it is possible that the upward bulge of the inflated laryngeal sac simply divides the trachea in the midline into two lateral chambers. This might enable simultaneous bi-directional flow, and therefore continuous sound production, as air on one side may flow ingressively towards the lungs while on the other side it may flow egressively towards the larynx. This idea is slightly flawed, however, because continuous flow would imply a steady contraction of both sac muscles and intercostal muscles. This cannot happen, because contraction of both structures would simply compress the total volume and raise the pressure, rather than send the air flowing in a particular direction. It could only work if the division extends all the way to the carina and allows one lung to inflate while the other deflates. This implies unilateral thoracic wall contraction. This theory is still not ideal because it is unclear how a single laryngeal sac could accommodate bidirectional flow. Rather, the inflated laryngeal sac's effect on the trachea may simply be a mechanism to compensate for volume loss at depth due to raised ambient pressure. Maintaining lateral air channels, however, would still allow flow to occur between the laryngeal sac and the lungs (although it is unlikely to be simultaneously bi-directional). The rationale for collapsing the trachea in this manner is that it allows airflow even though the total air volume is shrinking due to the higher pressure at depth.

TRACHEAL FOLDS. The trachea's lumen has a series of thin parallel tissue folds along the lateral aspects that direct airflow in an S-shaped pattern. The folds appear to act like sails on a sailboat, or blades on a turbine. As the airflow passes along these folds, they become stiffened and are pushed laterally. In this manner, the folds appear to act as buttresses for the tracheal walls, helping to rigidify them. Since the S-shaped folds are curved (like the cupped blades of a fan), the vector of force from the airflow hitting the folds appears to be directed rostro-laterally, forcing the tracheal wall outwards. The airflow is then reflected off this curved surface in a rostro-medial direction, towards the vocal folds. Therefore, the curving shape of the parallel series of folds helps to simultaneously push the walls laterally while directing air towards the vocal folds. Without such lateral support, the entire trachea would collapse and shut off all airflow at depth, and likely prevent any vocalizations. The unusual anatomy of this part of the trachea therefore indicates that extra support is given to the lateral passageways to hold the passageways open (despite rising ambient pressure forcing volume collapse), and thus enable airflow for vocalizations.

Another possible function of the tracheal folds is to reduce "noise" generated by airflow passing over the textured surface of the tracheal lumen. The small ridges created by the tracheal rings can disrupt laminar airflow and generate turbulence along the edges, in turn generating accidental noise. Since the tracheal folds are oriented perpendicular to the tracheal rings, they could break up this accidental noise and thus contribute to a "cleaner" output of intentional sounds.

LARYNGEAL FOLDS AND FLAPS. The valvular action of the U-shaped vocal folds closes the glottic gap and the inflated laryngeal sac compresses the lumen of the trachea. However, there are two other sites of constriction in the respiratory passageways: opposition of the epiglottis and corniculate flaps, and opposition of the lumenal surface of the dorsal cricoid cartilage with the glottic gap between the vocal folds. Epiglottic-corniculate flap opposition can obstruct flow between the larynx and the nasopharynx or nasal cavities. If the two corniculate flaps are opposed to each other, then the only path for air to leave the larynx is for it to flow rostro-superiorly over the lumenal surface of the epiglottis. This part of the epiglottis is trough-shaped. While it can channel air rostro-superiorly towards the nasal cavities, it can also be blocked by opposition with the corniculate cartilage's flaps. If these opposed pair of flaps are nested into the epiglottic concavity, then the channel will be closed. This would restrict air to flowing only between the larynx/laryngeal sac and the trachea/lungs (via the glottic gap between the vocal folds).

Opposition of the cricoid and glottic gap is accomplished by a thickening of the midline lumenal surface of the cricoid cartilage. This thickened "cushion" fits exactly into the concavity of the glottic gap between the vocal folds. When opposed, air cannot flow between the vocal folds, effectively sealing the laryngeal sac from the larynx, trachea, and lungs. Air in the sac would only be able to flow rostro-superiorly towards the nasal cavities. Likewise, air from the lungs would have to bypass the laryngeal sac and instead also flow towards the nasal cavities. As the cushion is in the midline, and does not obstruct the lateral tracheal channels, air could flow around this connection. It would then flow between the corniculate flaps (assuming they are not nested into the epiglottis) and towards the nasal cavities. Another potential function would be to dampen vocal fold vibrations when making slight contact.

BUBBLE RELEASE. Another interesting function of the respiratory tract is its role in generating a visual signal of released bubbles. Bubbling behaviors (e.g., nets, clouds, curtains) occur in both the northern and southern hemisphere humpback whale populations (Clapham 2017). Generally, air is not released during sound production because that would waste the air and prevent it from being recycled for re-use. The blowholes are closed by nasal plugs in the relaxed state, and energy is only spent to occasionally open them for intermittent breaths (Buono et al. 2015). However, when a visual signal of bubbles is necessary, the nasal plug muscles can be contracted, withdrawing the plugs to allow release of air from the blowholes. This creates a column of bubbles or, if the whale is swimming, can create a curtain or wall of bubbles. Such bubble walls are used to signal other whales, usually as an aggressive display. Alternatively, when nasal air release is combined with an upward spiral swimming motion, it can be used to make a bubble net that can trap and concentrate fish for feeding (Sharpe and Dill 1997). Air may also be emitted from the mouth. This appears to occur when the epiglottis is withdrawn from behind the soft palate and is inserted into the oral cavity, and then the tongue is raised to push air out through the sieve of the baleen plates (Reidenberg and Laitman 2007a). This causes the airstream to break into many tiny bubbles called a bubble cloud. This latter function is useful in generating an aggressive visual display, or can be used as a smoke screen or camouflage that disrupts echolocation signals from predatory toothed whales such as orcas or pseudorcas.

BUOYANCY. Air, being less dense than water, is also useful for regulating buoyancy. It is not surprising, then, that whales may adjust their buoyancy by changing the volume of air in various chambers of respiratory tract. Many diving mammals exhale before descent to ensure the body has negative buoyancy and limited exposure to the high partial pressures of gases that could lead to decompression sickness when submerged (Withers et al. 2016). Reducing the air volume makes the whale heavier, allowing it to sink, and increasing the air volume keeps the whale buoyant, allowing it to rest at the surface. This dynamic adjustment in buoyancy requires releasing or acquiring air. However, whales need to keep air in their respiratory tract for sound production, and therefore do not exhale before diving. They must therefore rely upon dynamic internal adjustment of their center of gravity and through movement create a change in buoyancy relative to ambient pressure. They can accomplish this through minor adjustments in the chambers where the air is stored that shift the center of gravity and enable a more energy efficient dive or ascent (Reidenberg and Laitman 2008). If most of the air is shunted to the lungs, then the head becomes heavier than the thorax, and the whale's head will begin to sink. As the head points down, this initiates the dive behavior. Very little tail thrusting may be necessary to continue this ascent, for as the whale begins diving, the ambient pressure rises. This compresses the volume of air in the lungs, and makes the whale heavier so it should sink passively. The opposite may happen on ascent. If the whale shifts the small volume of air available at depth to the nasal region, then the head becomes lighter than the thorax. This will help point the head towards the surface. A few thrusts of the tail may be necessary to begin the ascent, but as the whale rises, the air volume begins to expand. This makes the whale more buoyant and should help lift it passively towards the surface.

Humpback whales appear to have the ability to confine air into various chambers of the respiratory tract (due to the multiple valve sites). Given that at least one of these chambers has muscular control of its volume (the laryngeal sac), it is reasonable to infer that the volume in that chamber can be independently regulated through such muscular contraction. This means that the whale may be able to adjust its buoyancy independently of, or in addition to, the effects of ambient pressure on the volume of air in that chamber (Gandilhon et al. 2015). Such independent control may give the whale a unique mechanism for adjusting its buoyancy. One major advantage of this independent control is the ability to increase the force propelling the whale to the surface. Such increase in buoyancy reduces the need for great energy expenditure to raise the whale up. This would be very useful in a favorite mode of humpback whale feeding: lunges. The energy spent in acquiring prey shouldn't exceed the energy gained from digesting prey. Using buoyancy gained from independent expansion of respiratory spaces would help make lunge feeding an energy efficient activity. There would be evolutionary selection for such a feeding behavior because it results in a net gain in energy acquired. Breaching may simply be an extension of this behavior. Independent adjustment of buoyancy may enable rapid ascent with relatively little fluke movements, relative to what would normally be necessary to propel a whale's full body above the water's surface against the force of gravity.

CONCLUSION

The respiratory tract of the humpback whale is a dynamic system that appears to serve several functions besides respiration. There are many highly modified chambers, tissue folds, and valves that can maintain or modify air spaces and surrounding tissues, some in conjunction with, and some independently of, extreme changes in pressures during diving and ascent. These highly modified respiratory tract tissues function to shunt air to increase oxygenation for extending breath-hold time, conserve and recycle air, maintain hearing at depth, generate sound for communication and navigation, transmit vibrations to water, mitigate noise, support air spaces from collapsing, regulate chamber volumes, produce bubbles as visual signals, control air release as a tool for trapping prey, modify center of gravity, regulate buoyancy, and reduce energy expenditure during locomotion. The humpback whale is not only arguably the most talented singer among all whales, it is also able to utilize air in an aquatic environment in ways that allow it to support a range of other unique behaviors.

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"Cyclo-pousse dans la brume matinale de l'allée des baobabs // Rickshaw in the smoke covered Allée of the Baobabs"
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