Vol. 11: 157–166, 2010
doi: 10.3354/esr00274

ENDANGERED SPECIES RESEARCH
Endang Species Res

Published online April 16

Contribution to the Theme Section 'Responses of animals to habitat alteration'

OPEN ACCESS

Using occupancy as a state variable for monitoring the Critically Endangered Alaotran gentle lemur *Hapalemur alaotrensis*

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ABSTRACT: Although monitoring is an essential tool for biodiversity conservation, monitoring programmes are often poorly designed and thus unlikely to produce results that are meaningful for management. Monitoring is especially challenging when dealing with rare and elusive species in areas where conservation resources are particularly limited. In such cases, monitoring techniques aimed at estimating occupancy represent an attractive alternative to traditional methods concerned with estimating population size, as the collection of detection/non-detection data is in general less costly and easier to implement. In this study, we evaluated the use of occupancy as a state variable for the monitoring of the Alaotran gentle lemur *Hapalemur alaotrensis*, a Critically Endangered primate exclusively inhabiting the dense marshes around Lake Alaotra in Madagascar. We used a likelihood-based modelling approach that explicitly accounts for detectability. This showed that the probability of detection of *H. alaotrensis* was extremely low and depended on site characteristics that can vary in space and time, confirming the need to account for imperfect detection when monitoring this species. We used our models to explore factors affecting the probability of occupancy and detection to identify management implications, and also developed recommendations for the ongoing monitoring of this species. The method applied in this study provides an efficient tool for the monitoring of an elusive species and has the potential to provide a flexible sampling framework for local community-based monitoring initiatives.

KEY WORDS: Occupancy · Detectability · Monitoring · Alaotran gentle lemur · *Hapalemur alaotrensis* · Alaotra · Madagascar

INTRODUCTION

Monitoring is a crucial element in the decision-making process for biodiversity conservation (Possingham et al. 2001). It provides feedback between policy and implementation, allowing managers to make informed state-dependent decisions and practise adaptive management (Walters 1986). Learning about a system through monitoring aids in the development of models for prediction of system responses to potential future interventions (Nichols 2001). Monitoring provides evidence, and therefore promotes confidence among donors who seek to assess the impact of their funding (Sutherland et al. 2004) and is thus essential for ensuring the continuity of conservation initiatives. Unfortunately, despite their importance, monitoring programmes are often poorly designed and hence unlikely to provide informative results (Legg & Nagy 2006, Field et al. 2007). Frequently this occurs as programmes are developed without sufficient focus on how their design relates to their goals (Yoccoz et al. 2001).

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For monitoring to be useful, it needs to be sustainable in the long term and therefore cost effective and straightforward to implement. Traditionally, when dealing with single species, the most commonly used state variable has been abundance or population size. However, occupancy, defined as the proportion of area, patches or sampling units occupied by a species, is becoming increasingly popular, as it is often sufficient for monitoring objectives and requires less effort and expertise in the field (MacKenzie et al. 2006); this can result in increased sample sizes compared to population size methods. Techniques have been developed to deal with the problems derived from imperfect detection in occupancy studies. In most scenarios, individuals and species remain undetected despite being present in surveyed areas; disregarding this key issue leads to biased estimations and incorrect inferences about system state and trends. To be reliable, monitoring programmes must account for detectability, a question addressed by techniques such as distance sampling (Buckland et al. 2001) and capture-recapture (Seber 1982). Although until recently ignored by many in the analysis of presence/absence data, detectability is now receiving more attention in this context (MacKenzie et al. 2002, Tyre et al. 2003, Wintle et al. 2004). Detectability is not simply a trait of the species, but is related to other factors such as habitat characteristics, observer skills, survey design or meteorological conditions. Understanding how these different aspects affect the probability of detection of the target species is critical for the design of efficient monitoring strategies (e.g. Field et al. 2005). Estimates of detectability provide the basis for determining the number of repeated visits required to a site to have a given level of confidence of detecting the species if it uses that site, or conversely, to reliably infer absences in the case of unused sites, a valuable piece of information when deciding on management interventions.

Here, we evaluate an occupancy modelling technique that explicitly accounts for detectability (MacKenzie et al. 2002) as a tool for monitoring a species that is highly difficult to detect in a region where resources for field research are particularly limited. Our species of interest was the Alaotran gentle lemur *Hapalemur alaotrensis*, which is found only in the wetlands surrounding Lake Alaotra, Madagascar. The Alaotran watershed was declared a Ramsar site in 2003, and part of the marsh was recently awarded the status of Nouvelle Aire Protégée ('New Protected Area'). Nevertheless, this Critically Endangered lemur (IUCN 2009) remains threatened by poaching and habitat loss due to encroaching rice paddies and marsh burning. An efficient and informative monitoring scheme is needed to design and evaluate conservation initiatives to secure the future of the species. However, the difficulties in monitoring this species have resulted in a lack of sound estimates of population status and trends to date. The wetland is difficult to survey, as it can only be accessed via canals cut by fishermen, resulting in limited transects for monitoring, while visibility within the wetland is typically restricted to the first few metres, rendering the species very difficult to detect. The probability of detection of *H. alaotrensis* depends on a number of factors that vary across sites and years, necessitating the use of a method that accounts for detectability in order to make reliable estimates. We used repeat transects of existing canals through the wetland to survey the lemur population in marshes managed by 4 village communities during the dry season. We used a likelihood-based modelling approach to estimate both *H. alaotrensis* occupancy and detection parameters simultaneously and to investigate factors potentially affecting these probabilities. Finally, we propose recommendations for the ongoing monitoring of this species, given the financial and logistical constraints faced in the region.

MATERIALS AND METHODS

Study site and species. The Alaotran gentle lemur *Hapalemur alaotrensis* is a small primate that exclusively inhabits the papyrus *Cyperus madagascariensis* and reed *Phragmites communis* beds around Lake Alaotra, Madagascar's largest lake (Mutschler & Feistner 1995). The climate in this region is characterised by pronounced seasonality, with a wet season with elevated temperatures between December and April and a dry season with moderate temperatures between May and November. With over 20 000 ha of open water in the dry season, the lake is rather shallow, varying between 1 and 4 m in depth (Ramanampamonjy et al. 2003). It is surrounded by a vast wetland area consisting of marshes and rice fields and constitutes an important biodiversity area (Pidgeon 1996). The human population in the Alaotra watershed has rapidly increased in the last few decades, from 109 000 in 1960 (Pidgeon 1996) to approximately 550 000 in 2003 (PRD 2003), with most people dependent on rice cultivation and fishing for their livelihoods. The increase in human demands has resulted in severe loss, degradation and fragmentation of the Alaotran marshes. This, together with pressures from hunting and fishing, are threatening many local species, among them *H. alaotrensis* (Mutschler et al. 2001). According to available estimates, *H. alaotrensis* numbers have decreased from >10 000 ind. in 1994 (Mutschler & Feistner 1995) to <3000 in 2002 (Ralainasolo 2004), with habitat destruction and poaching appearing to be the major causes of this dramatic decline. *H. alaotrensis* is highly territorial, and family groups consistently defend their home range against incursions by other conspecific groups (Nievergelt et al. 1998). Groups occupy home ranges of 0.6 to 8 ha (Mutschler & Tan 2003), with an average territory size of around 2 ha (Mutschler et al. 1994). Social groups are small, ranging from 2 to 9 ind. with an average of around 4 ind. (Nievergelt et al. 2002). *H. alaotrensis* exhibits cathemeral activity with peaks at the beginning and end of the daylight cycle (Mutschler et al. 1998).

Data collection. The sampling protocol involved repeatedly visiting a series of transects by canoe and recording the GPS positions of *Hapalemur alaotrensis* by direct observation. Due to the very dense nature of the vegetation, surveys were carried out using natural borders of the marsh and existing channels opened by local fishermen. The study concentrated on the area of marsh delimited by the villages of Anororo, Andreba, Ambodivoara and Andilana, where the southern and largest population of *H. alaotrensis* occurs (Fig. 1). Surveys were conducted in a 7 wk timeframe during the dry season (between 21 April and 4 June 2008), a period in which sites were assumed to be closed to changes in occupancy. Although animals did enter and leave the sampling sites, which were the part of their territory visible from the transect (i.e. a few metres into the vegetation), these movements were assumed to be random so that the occupancy estimator, now interpreted as the proportion of sites 'used', remained unbiased (MacKenzie et al. 2006). The total length of transects was 51 km, and transects were surveyed between 3 and 12 times with a mean of 6 repetitions. This gave a total surveyed length of 321 km. Surveys were carried out at an even speed (≈1 to 3 km h^{-1}) by 2 teams each including 1 fisherman who acted as a local expert, 1 researcher and usually a local villager to act as paddler. Whenever possible, 2 survey sessions were carried out each day (morning and evening), with each transect visited only once per session. All surveys were carried out within the same time bands (05:30 to 09:00 h and 15:00 to 18:00 h), which correspond to times of peak activity of *H. alaotrensis*. To avoid systematic bias in our survey data through observer differences in lemur detectability and daily patterns in lemur behaviour, field teams were rotated around sampling sites and repeat visits to sites were conducted at different times of day.

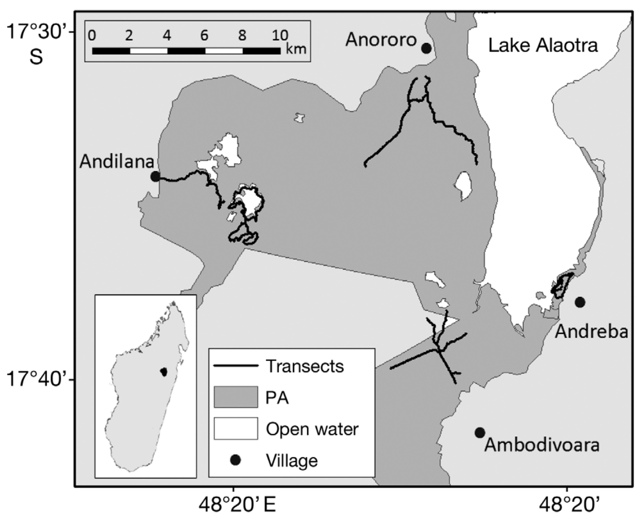

Fig. 1. Study area and transects used for the surveys. The 'New Protected Area' (PA) is shaded dark grey. Inset: location of the study area in Madagascar

Based on our knowledge of the system and on the information obtained from local experts, the main factors potentially affecting occupancy and detectability were identified (Fig. 2). Data on habitat type, human presence, the nearest village and transect characteristics were collected for use as covariates in the model (Table 1). Qualitative information on habitat type was collected along transects at intervals of 30 m (which provide around 5 samples per territory) including the main structural species (papyrus *Cyperus madagascariensis*, reeds *Phragmites communis*, grasses or other floating vegetation), species composition and an overall impression of habitat density and patchiness. These data were then used to assign sites to 4 habitat type categories in a similar classification to the one followed by Mutschler et al. (2001), with an additional class ('Class 0') consisting of vegetated areas that are highly unlikely to harbour lemurs: (0) patches of floating invasive plants; very large patches of grass; extremely low density papyrus stands; (1) very dense, uniform grass and papyrus up to 1 m with little undergrowth; no creepers; (2) dense, uniformly sized papyrus up to 3 m in height; not very diverse undergrowth often composed of fern although not exclusively; no or very few creepers; (3) papyrus or reed over 3 m high covered with dense creepers; dense diverse undergrowth up to about 1 m high.

Human presence was represented by the number of fishermen and reed-cutters encountered along transects. This was recorded for each survey as an indicator of the level of disturbance that animals are subject to in each of the surveyed areas. The information was used to identify infrequently used transects (average recorded traffic <1 canoe h^{-1} of fieldwork) as opposed to those with moderate or high traffic (average recorded traffic >1 canoe h^{-1}). The identity of the nearest village was included in the analysis as a covariate, as it is believed that lemurs are hunted regularly in certain villages but not in others. Finally, transects were characterised as either channel or lake transects, as it was hypothesised that this could have an effect on occupancy or detectability.

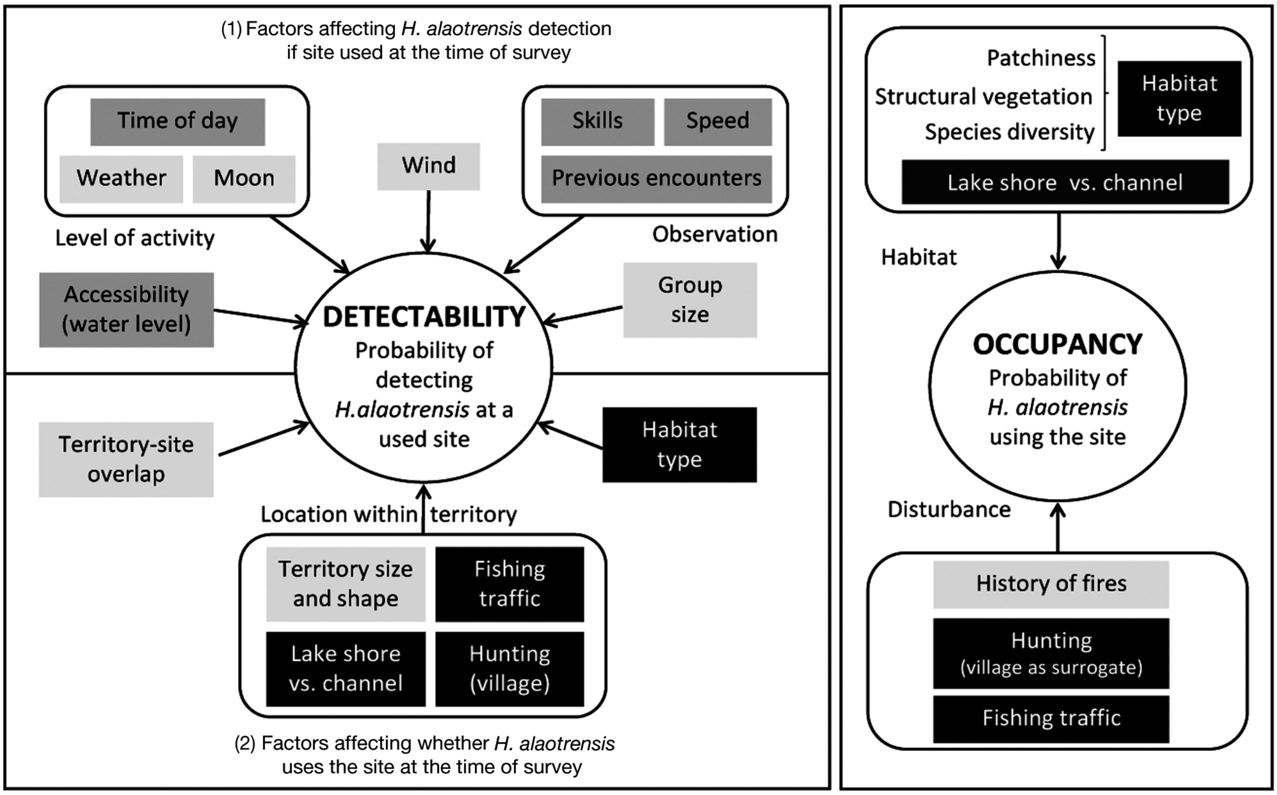

Fig. 2. *Hapalemur alaotrensis*. Selected factors identified as potentially affecting detectability and occupancy of *H. alaotrensis*, including those specifically addressed in the sampling design (dark gray), those incorporated as covariates into the model (black) and those that remained as a potential source of heterogeneity (light gray). Given that in 1 dimension the sampling site was significantly smaller than a typical territory of *H. alaotrensis*, which extends into the dense vegetation, the detectability was composed of (1) the probability of the species being detected conditional to it being present at the sampling site at the time of survey and (2) the probability of the species being present at the sampling site at the time of survey. Factors related to occupancy can be grouped into those related to habitat quality and those referring to different forms of disturbance directly inflicted on the animals

Table 1. Covariates incorporated into the models, including the type of parameter used for their representation

Name	Type	Description
Lake (L)	Binary	Indicates whether the site is near a channel or lake
Village (V)	3 dummy variables (binary) to represent 4 villages	Indicates which is the closest village to the site as a proxy of the different pressures exercised over the species, especially through hunting
Habitat (H)	3 dummy variables (binary) to represent 4 habitat categories	Indicates the habitat category found at the site
Traffic (T)	Binary	Indicates whether the transect has low traffic (<1 canoe encountered h^{-1} of survey) or medium/high traffic (>1 canoe h^{-1})

Analysis of detection/non-detection data. Occupancy of *Hapalemur alaotrensis* was modelled with a method that explicitly accounts for detectability (MacKenzie et al. 2002) and estimated using the maximum-likelihood approach. Transects were divided into a series of sites, and a detection history was built for each of these sites, assigning a '1' for surveys when the species was detected and a '0' otherwise. Sites were defined as sections of transect of a length of the edge of a hypothetically square average-sized lemur territory (i.e. 150 m). Choosing this scale allowed us to make some rough inferences about lemur abundance and ensured that the habitat information associated with each site was collected at a meaningful scale. For transects along channels, separate sites were defined for each of the sides, since territories of *H. alaotrensis* tend to be separated by these borders (Nievergelt et al. 1998). Based on the detection history, a probability model was formulated in terms of parameters ψ_i and p_i, where ψ_i is the probability of site i being used by the species and p_i is the probability of detecting the species at site *i*, conditional upon it being present. Once computed, all site probabilities were combined to build a likelihood function of the occupancy and detectability parameters, given the recorded data. The likelihood function was then maximised to estimate the parameter values for which the observed data appeared to be most likely.

First we evaluated the simplest model, where both detection and occupancy probabilities were assumed to be constant. We then incorporated covariates into the model through a logit link function which, in effect, transformed this model into an extension of the logistic regression model accounting for imperfect detection. We evaluated all potential models without interactions (256 in total) and used the Akaike Information Criterion (AIC) to rank and identify the most parsimonious models (Burnham & Anderson 2002), generating a set of candidate models by selecting those at a distance of less than 4 Akaike units from the best model. We assessed the fit of our models with a goodness-of-fit test based on bootstrapping and Pearson's chi-squared statistic as proposed by MacKenzie & Bailey (2004). This method tests whether the observed frequency of detection histories has a reasonable chance of occurring if the model assessed is assumed to be correct. To assess the degree to which the fit is adequate, an overdispersion parameter $\hat{c}$ was estimated. As recommended, the goodness-of-fit test and overdispersion calculation were performed for the most saturated model (Burnham & Anderson 2002).

For each of the chosen models in the subset, we calculated the Akaike weight. Overall estimates of occupancy and detectability were obtained averaging the individual site estimates, and corresponding standard errors were computed from the variance-covariance matrix of the logistic regression coefficients using the delta method. Given that top-ranked models had similar weights, we applied a model-averaging technique (Burnham & Anderson 2002) to obtain overall estimates based on the results of multiple models:

$$\hat{\theta}_A = \sum_{j=1}^{m} w_j \hat{\theta}_j \qquad SE(\hat{\theta}_A) = \sum_{j=1}^{m} w_j \sqrt{\mathrm{var}(\hat{\theta}_j | M_j) + (\hat{\theta}_j - \hat{\theta}_A)} \quad (1)$$

where w_j is the Akaike weight for model *j*, *m* is the number of models in the set, $\hat{\theta}_j$ is the overall estimate of detectability or occupancy for model *j*, and $\hat{\theta}_A$ is the overall estimate of detectability or occupancy for the averaged model; $\mathrm{var}(\hat{\theta}_j/M_j)$ is the variance of the estimate obtained from model M_j.

We generated detectability curves for the best ranked model, as these provide useful information regarding the number of visits required to a site to infer absence with a given certainty. The probability of detecting the species at an occupied site at least once after *K* repeated surveys was calculated as $p^* = 1-(1-p)^K$, and its approximate standard error was obtained from the standard error of *p* through the delta method.

To provide input for the design of potential future sampling protocols, we calculated the number of required sites and repetitions to achieve a given precision in the estimators using the estimates obtained with the averaged model and assuming a model with constant probabilities. Based on the corresponding expression of the asymptotic variance of the occupancy estimator (Mac- Kenzie & Royle 2005), the optimal number of repetitions was calculated as the one that minimises the total effort TS:

$$\mathrm{TS} = s \cdot K = \frac{K \cdot \psi}{\mathrm{var}(\hat{\psi})}\left[(1-\psi) + \frac{(1-p^*)}{p^* - K \cdot p \cdot (1-p)^{K-1}}\right] \quad (2)$$

where *s* is the number of sites surveyed, *K* the number of repeated surveys per site, ψ the probability of occupancy, *p* the probability of detection given the site is occupied and p^*: probability of detection at least once after *K* surveys, given that the site is occupied. Once *K* was fixed, the number of sites to be visited was obtained by substitution in the same equation.

We performed a sensitivity analysis to evaluate with respect to the way in which transects were divided into sites. We set 4 different starting offsets (0, 33 and 50 m and half the site size) when defining sites, both for the original site length of 150 m and then with a site length of 300 m. The latter distance roughly corresponds to 1 side of a large (hypothetically square) *Hapalemur alaotrensis* territory. Models were re-run using these different sampling layouts, and the support for the different covariates was reassessed.

The scripts for generation of the detection histories and analysis of the different models were written in Scilab (www.scilab.org). The optimisation of the likelihood function was done numerically with the Scilab function *optim*. Estimate standard errors and confidence intervals were obtained with the software PRESENCE 2.2 (Hines 2006).

RESULTS

In more than 120 survey hours, 71 lemur group encounters were recorded, including repeated sightings of some groups. Based on these data and defining sampling sites as 150 m long transect sections, the naive occupancy estimate was 8.84 %. With the simplest model (i.e. fixed occupancy and detectability probabilities) the corresponding estimates for detectability and occupancy were 8.1 and 21.6 %, respectively (Table 2). As expected, the detectability was low, meaning that in most of the surveys animals were not detected in sites that they did actually use. Correspondingly, the estimated occupancy was much greater than the naive estimate obtained without accounting for detectability.

Table 2. Occupancy and detectability estimates obtained for models with an Akaike difference smaller than 4 units, for the averaged model (AV) and for the fixed model (FX). $\hat{\psi}$: estimate of occupancy, $\hat{p}$: estimate of detectability, H: habitat category, L: lake vs. channel, V: village, T: traffic, AIC: Akaike Information Criterion, ΔAIC: Akaike difference, N: Number of parameters in the model, w_j: Akaike weight

ID	Model	AIC	ΔAIC	N	w_j (%)	$\hat{\psi}$ (± SE)	$\hat{p}$ (± SE)
01	p(T)ψ(H+L+V)	438.3	0.0	10	22.4	0.203 (0.034)	0.064 (0.011)
02	p(T)ψ(H+L+V+T)	439.3	1.0	11	13.4	0.184 (0.034)	0.068 (0.013)
03	p(T+L)ψ(H+L+V)	439.4	1.1	11	13.2	0.194 (0.031)	0.071 (0.014)
04	p(H+T)ψ(L+V)	439.5	1.2	10	12.2	0.255 (0.049)	0.048 (0.009)
05	p(H+T)ψ(L+V+T)	440.0	1.7	11	9.3	0.221 (0.045)	0.052 (0.010)
06	p(T+L)ψ(H+L+V+T)	440.7	2.4	12	6.8	0.178 (0.031)	0.074 (0.016)
07	p(T)ψ(L+V+T)	441.1	2.8	8	5.4	0.186 (0.032)	0.067 (0.012)
08	p(H+T+L)ψ(L+V)	441.2	2.9	11	5.3	0.242 (0.047)	0.053 (0.012)
09	p(T)ψ(L+V)	441.5	3.2	7	4.6	0.214 (0.040)	0.061 (0.011)
10	p(T+L+V)ψ(H+L+V)	441.8	3.5	14	3.8	0.209 (0.037)	0.094 (0.030)
11	p(H+T+L)ψ(T+L+V)	442.0	3.7	12	3.5	0.216 (0.046)	0.054 (0.013)
AV	Averaged model					0.208 (0.043)	0.063 (0.015)
FX	p(·)ψ(·)	512.0		2		0.216 (0.048)	0.081 (0.018)

A comparison of models incorporating covariates for occupancy and/or detectability indicated little support for the fixed model, i.e. the fixed model was a much less likely explanation for the observed data than most of the models that included covariates. The goodness-of-fit test (p = 0.22, $\hat{c}$ = 1.14) indicated no evidence of lack of fit for the saturated model, which means that more parsimonious models should also provide an adequate description of the data (Burnham & Anderson 2002).

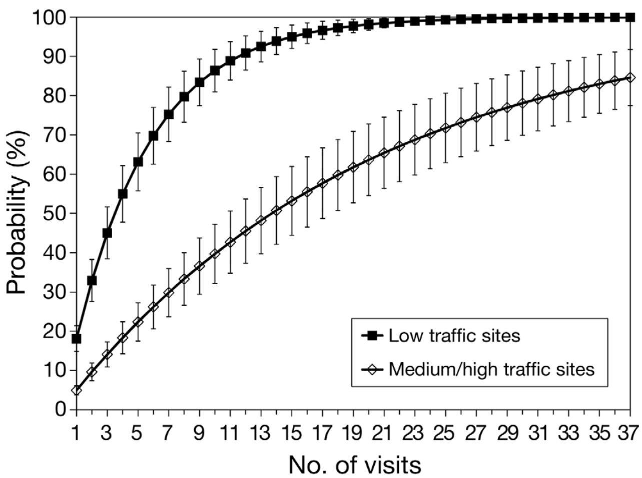

Fig. 3. Probability of detecting *Hapalemur alaotrensis* (±1 SE) at a site that is in use after a given number of visits for different detectability levels (p = 18.1% for low traffic sites, p = 4.9% for medium/high traffic sites). It is necessary to carry out several visits to a site in order to be relatively confident of detecting presence even if the site is being used by the species. Note that because a site only represents part of the territory it may not be occupied at the time of the survey even if it is being used

When summing up the contributions of each covariate (i.e. sum of Akaike weights for all models in the set containing the covariate in question) both 'village' and 'lake' had strong support (≥99%) as factors influencing occupancy, while 'traffic' had strong support (>97%) as a covariate for detectability. The top-ranked model indicated that high human traffic reduces the probability of detecting *Hapalemur alaotrensis*, while low habitat categories, lake edge and certain villages reduce the probability of the species using a site. According to this model, the probability of detecting the species appears to be considerably higher for sites in areas with low traffic (18.1%) than in sites with medium or high traffic (4.9%), which implies that a different number of visits is required to detect the species with a given certainty depending on the traffic experienced by a site (Fig. 3). The model also indicated that the probability of a site being occupied changes substantially depending on its characteristics. *H. alaotrensis* seem to use sites along channels more than sites by lakes. As expected, they appear to prefer higher habitat categories. There was a large effect of village; sites in 2 of the villages (Ambodivoara and Anororo) appear to be used by the species much less than those in the other villages (Andreba and Andilana), even if the habitat is favourable.

In the analysis, no model emerged clearly as a superior explanation for the observed data. The Akaike weight corresponding to the top-ranked model was 22.4%. To obtain a more robust estimation of occupancy and detectability, model averaging was used, taking all models with an AIC difference smaller than 4 units. Occupancy estimates for this set of models ranged from 17.8 to 25.5% and detectability from 4.8 to 9.4%. Weighting these estimates with the corresponding Akaike weights for each model, the final estimates of occupancy (20.8%) and detectability (6.3%) from the averaged model were obtained for the surveyed area.

Based on the estimates from the averaged model and assuming constant probabilities, 25 repetitions per site are needed to minimise the total survey effort (defined as the number of sites to be surveyed multiplied by the number of repeated surveys; Fig. 4A). The optimal number of sites to survey increases from 10 to 100 as the target standard error decreases from 0.15 to 0.05 (Fig. 4B). Using the detection probability estimated for

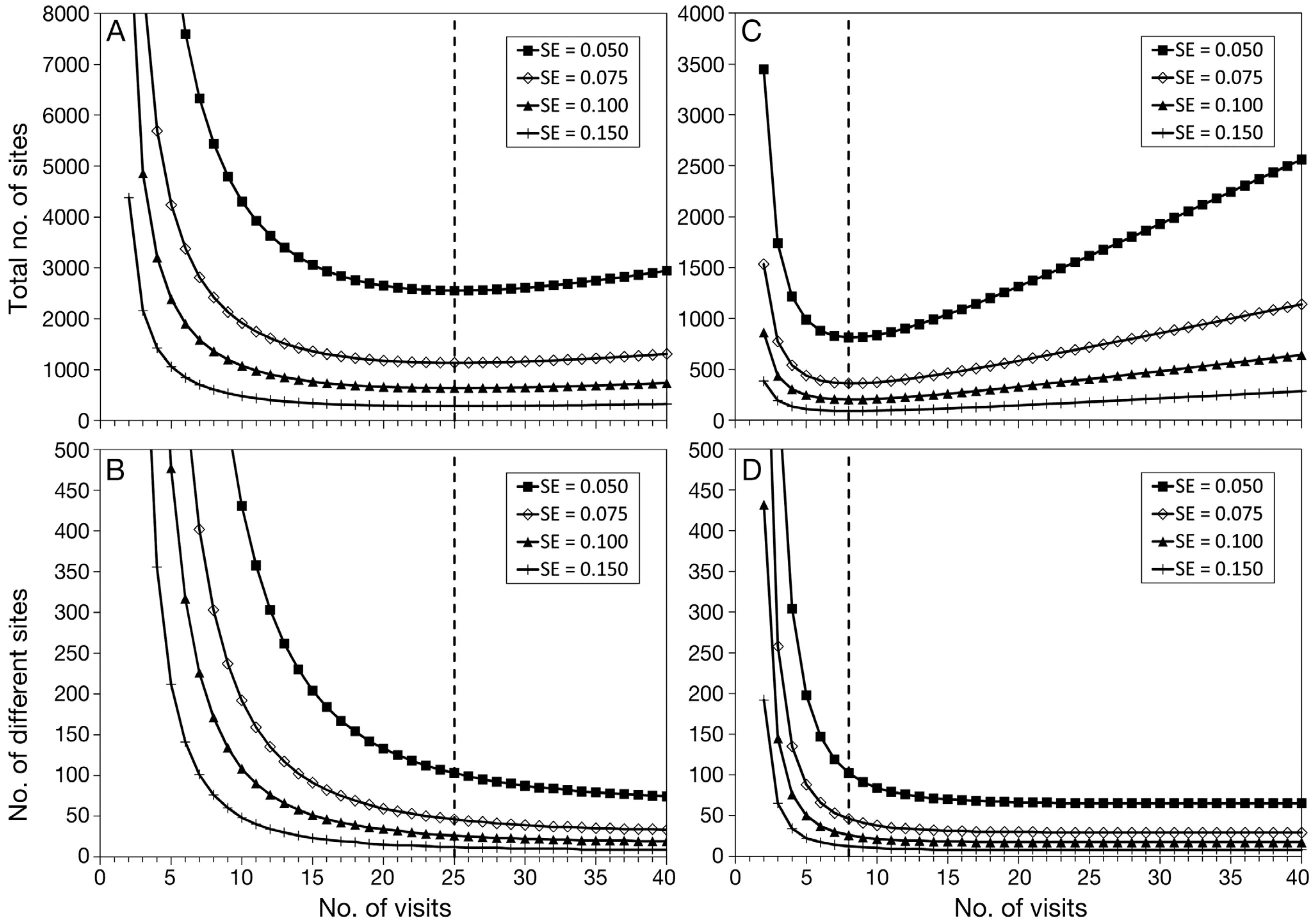

Fig. 4. Total number of sites (A,C) and number of different sites (B,D) to be visited to achieve a given precision in the occupancy estimate as a function of the number of repetitions carried out. Vertical dashed lines mark the optimal number of repetitions. Curves were generated based on the fixed model and on the asymptotic properties of the maximum likelihood estimates. Different curves correspond to different target standard errors in the occupancy estimate. The minima in the curves in (A) and (C) indicate the optimal number of repetitions, i.e. the number of repetitions that minimise the total effort required. Curves in (A) and (B) were generated based on the estimates obtained from the averaged model (detectability, $p = 6\%$ and occupancy, $\psi = 20\%$) and in (C) and (D) using the detectability estimated for low traffic transects ($p = 18\%$ and $\psi = 20\%$). The average number of repetitions in this study was 6 and the number of sites was ca. 300

Table 3. Support for the different covariates as occupancy or detectability explanatory variables for different sampling layouts calculated as the summed Akaike weights of all the models in the full set containing each covariate (H: habitat category, L: lake vs. channel, V: village, T: traffic). The layout used in the main model has size 150 and a 0 offset (first row)

Sampling		Detectability (%)				Occupancy (%)			
Size	Offset	H	T	V	L	H	T	V	L
150	0	33.7	97.7	14.3	36.8	56.4	40.7	99.9	98.9
150	33	34.9	99.6	23.7	35.8	71.4	40.6	99.9	98.5
150	50	46.3	97.2	10.6	30.3	45.9	30.4	100.0	99.0
150	75	44.3	99.0	9.3	71.7	17.0	28.7	99.3	50.0
300	0	29.7	89.8	60.2	33.2	74.4	41.6	99.9	96.7
300	33	70.7	90.0	33.6	33.8	95.9	84.2	100.0	95.4
300	50	52.2	97.7	12.3	31.5	68.6	32.6	100.0	97.3
300	150	53.6	97.7	14.3	36.8	18.8	33.7	97.1	81.4

low-traffic channels, the optimal number of repetitions is 8 (Fig. 4C), and the numbers of sites to be visited corresponding to the hypothetical target standard errors of 0.15 to 0.05 are 12 to 100 (Fig. 4D). These figures provide guidance for the design of future surveys. The length of survey that can be covered each day must also be taken into account. Different survey arrangements are possible to achieve a given level of precision. For example, if an estimate with a standard error of 0.075 were required, this could be achieved with 10 repetitions of 30 km of transects. Assuming that each survey covers 6 km and 2 surveys are carried out each day (morning and evening), this would require 25 survey days. The same precision could also be achieved with 60 km visited 7 times over 35 survey days. The most appropriate set-up would be defined based on the objectives of the programme, resources and other logistical constraints (MacKenzie & Royle 2005).

The sensitivity analysis (Table 3) showed consistency across different sampling layouts regarding the strong support for 'village' and 'lake' as factors influencing occupancy, and 'traffic' as a factor influencing detectability. The contribution of other factors showed great variation, indicating that these results were sensitive to the specific definition of sites.

DISCUSSION

Efficient and effective monitoring is essential for the science-based management of natural systems (Possingham et al. 2001). Here we applied an occupancy modelling method that accounts for imperfect detection to the monitoring of *Hapalemur alaotrensis*, a species of conservation concern in an area where resources are significantly limited. We found that the detectability of *H. alaotrensis* is very low (<10 %) and depends on site characteristics that vary in space and time, thus confirming the need to account for detectability in the monitoring of the species.

Our results indicated that detectability of *Hapalemur alaotrensis* is related to the level of traffic of fishermen and reed-cutters passing the site, a finding that was supported by all higher ranked models. The probability of detection was almost 4 times greater in sites that supported low levels of traffic (≈18 %) than in other sites (≈5 %). Water level is also believed to have an impact on detectability, but we were unable to test this in our study. As water levels vary from year to year, this factor needs to be taken into account in multi-annual studies.

The evaluation of factors affecting occupancy revealed strong support for models that incorporated 'village' as an explanatory variable. This could be explained by variation in poaching levels between villages. According to recent research, the level of hunting remains relatively high in Ambodivoara and Anororo (Andrianandrasana et al. 2005). Our model corroborates these findings. The other factor very strongly supported in the models was that *Hapalemur alaotrensis* seem to avoid using lake edges as part of their territories. However, this does not mean that the whole marsh around lakes is void, as they may still have a territory just a few metres into the vegetation. *H. alaotrensis* may use lake edges rarely to avoid being exposed to the windier weather conditions there, which they appear to dislike, according to local experts (R. Rasolonjatovo pers. comm.). An alternative explanation is that *H. alaotrensis* may not need to defend the edges of territories abutting open water as actively as those adjacent to a channel, because a neighbouring lemur group would be absent. There are reports in the literature of groups trespassing or defending territories on the opposite side of a channel (Nievergelt et al. 1998), a phenomenon witnessed during the course of this study, with animals crossing from side to side to explore another group's territory or chase away intruders.

Habitat covariates allow us to explore relationships between the presence of a species and habitat characteristics and to develop predictive models of habitat preference (see Elith et al. 2006). In our study, a positive relationship between occupancy and habitat category was captured by all 3 top-ranked models. *Hapalemur alaotrensis* prefer diverse and dense mature stands of marsh to areas of poorer vegetation such as very fragmented stands of marsh or uniform areas of young growth. The relatively weak support for this variable was probably due to data limitations rather than to its limited importance. Habitat categories were assigned on a qualitative basis based only on information collected from transects, thus capturing only the characteristics of the first few metres of vegetation. Incorporating habitat information derived from remote sensing data could make the habitat-occupancy relationship more evident. However, other issues may complicate the identification of a clear relationship, such as good habitat being empty due to poaching or having not yet been recolonised after recent fires, while some *H. alaotrensis* individuals may be stranded in unsuitable habitat patches if the surrounding vegetation has been recently burned.

The sensitivity of the results to the definition of sites was investigated by analysing the same dataset with different sampling layouts (size and offset). While showing consistency of the main explanatory variables, the support for some of the model covariates varied from one sampling layout to the other. *Hapalemur alaotrensis* is a highly territorial species, and in this study, the definition of sites was arbitrary. The varying degree of overlap between territories and sites presents a source of heterogeneity in detectability that could not be captured in the model and potentially affects the robustness of the estimation. In studies with small sample sizes, the contribution of each observation may have a significant impact on the estimates. Sensitivity analyses of this type provide a useful means to validate the robustness of results.

The main limitation in this study was the lack of a probabilistic sampling scheme, which restricts the basis for generalising the results beyond the surveyed area. Sampling was limited to existing channels and marginal vegetation. This was seen as the only option, principally because opening new channels contributes to the spread of invasive plants and provides local villagers with improved access to the marsh, with a potential increase in hunting, reed cutting and fires. Minimising the physical impact to the surveyed area was seen as essential. We must therefore accept that these surveys inform us about the population around the channel/lake but provide limited information about the population elsewhere; consequently, we need to be cautious with the inferences drawn. Further limitations come from the potential spatial correlation between consecutive sampling sites. This can happen as a result of 2 sites lying within the same group's territory due to the lack of site-territory alignment. To avoid this situation, the post hoc sampling should ideally have left enough distance between sites to ensure complete independence (e.g. 1 full territory size). Given that the number of detections of *Hapalemur alaotrensis* was very low, we decided not to do this, as the resultant large reduction in the number of samples would have caused a problematic increase of variance in the estimator and thus decreased our capacity to draw inferences from the results. Detection histories did not show many patterns of consecutive detections, suggesting that the potential spatial correlation effect was not a major issue.

Apart from providing useful insights into the status of the population with respect to site characteristics, the model results constitute very valuable information for the design of an efficient monitoring programme. For instance, the fact that *Hapalemur alaotrensis* seems to avoid using the vegetation by the border of lakes suggests that monitoring should focus on channels. Survey design and data analysis should also take into account the level of human traffic. Where sites with high human traffic are to be monitored (e.g. if the focus of the survey is on the status of the population in these areas), more effort should be assigned to these sites to compensate for the low detectability there. The differences in occupancy around different villages identified by the models also need to be considered. In particular, the selection of sampling sites should take this into consideration in light of the programme objectives, e.g. whether the interest is in the overall population or in monitoring sites subject to poaching. Determining the number of sites to be surveyed and repetitions to be carried out in future monitoring efforts involves broad considerations, including the effect size that will trigger management interventions and the availability of financial and human resources. This study provides the tools for deciding on these 2 design parameters given the accepted level of precision and programme constraints. The chosen design must also take into account the assumption that sites are closed, i.e. surveys need to be carried out separately enough in time to ensure independence but closely enough to ensure that the system is closed to changes in occupancy during the sampling season.

Our study contributes to a growing body of evidence on the utility of occupancy as a state variable for monitoring elusive species in situations where resources are particularly limited, so long as models explicitly incorporate detectability (MacKenzie et al. 2006). Although requiring a relatively high level of technical capacity for data analysis, the data collection is inexpensive and relatively easy to implement. Hence this technique has the potential to be used in locally-based monitoring initiatives, which, if properly designed, may be both cost effective and reliable, and thus more likely to be sustainable. In the case of *Hapalemur alaotrensis*, the surveyed channels and marginal vegetation are transited daily by local villagers during the times that the animals are active. This could represent an opportunity for setting up an efficient and informative monitoring programme. In effect, transects are being 'surveyed' repeatedly throughout the year. If information on presence of *H. alaotrensis* could be collected in a systematic way, it would serve as very valuable input for the monitoring of the species. Selecting a few suitable local fishermen who would officially participate in the data collection phase of the monitoring programme could reduce the costs of surveys and increase the sample size while contributing to the engagement of the local community in conservation. A review of locally-based monitoring approaches recognised that, if well designed, these schemes have the potential to provide inexpensive and reliable alternatives to professional monitoring (Danielsen et al. 2005). Since 2001, Durrell Wildlife Conservation Trust has been carrying out a participatory monitoring programme in Alaotra, which includes *H. alaotrensis* as an indicator of marsh health (Andrianandrasana et al. 2005). Building on this initiative by incorporating the monitoring method discussed here has the potential to efficiently provide reliable population estimates, as well as representing an opportunity for engagement of local communities in the conservation of this key species.

Acknowledgements. We thank the Ministry of Environment, Water and Forests of Madagascar for granting the research permit to conduct this study; the Leverhulme Trust and a Royal Society Wolfson Research Merit award to E.J.M.G. for financial support; R. Lewis, J. Ratsimbazafy, H. Andrianandrasana and other Durrell Wildlife Conservation Trust personnel in Madagascar, especially B. J. Rasolonjatovo in Ambatondrazaka; and our expert local guides, R. Rasolonjatovo and A. Rakotonierana, for all their hard work and enthusiasm.

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Editorial responsibility: Anna Nekaris, Oxford, UK

Submitted: August 10, 2009; Accepted: February 17, 2010
Proofs received from author(s): March 29, 2010