Making the most of sparse data to estimate density of a rare and threatened species: a case study with the fosa, a little-studied Malagasy carnivore

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Abstract

Sparse detections in camera trap surveys commonly hinder density estimation for threatened species. By combining detections across multiple surveys, or using informative priors in Bayesian model fitting, researchers can improve parameter estimation from sparse capture–recapture data. Using a spatial mark–resight model that incorporates site-level heterogeneity in the spatial scale parameter via a hierarchical process and prior information, we estimated the density of a threatened carnivore (fosa, *Cryptoprocta ferox*) from multiple sparse datasets collected during extensive camera trapping surveys in northeastern Madagascar (2008–2015). Our objectives were to estimate density for six sites, examine the response of fosa density and movement to habitat degradation, monitor annual density trends across 7 years at two sites, and estimate fosa abundance in the Makira–Masoala protected area complex. We obtained a mean of 16.1 (SE = 0.52; range = 2–49) fosa detections and three observers identified a mean of 3.62 (SE = 0.09; range = 1–8) marked individuals per survey. Fosa daily baseline encounter rate was very low (λ_0 = 0.004; 0.003–0.006) and density/movement estimates were similar across forest types. Density estimates at resurveyed sites suggested annual variability in density, with estimates trending lower during the final surveys [e.g. D = 0.39 (0.14–1.11) versus 0.08 (0.05–0.31) individuals per km^2]. We estimated fosa abundance across the Makira–Masoala region to be 1061 (95% HPDI: 596–1780) adult individuals. On the basis of our estimate and the size of the region, we believe Makira–Masoala harbors a significant portion of the global fosa population. The conservation and management of rare species is commonly limited due to lack of population estimates. By combining detections across surveys, we overcame estimation issues and obtained valuable information on a threatened carnivore, allowing us to better assess its status and prioritize conservation actions. We advocate for practical use of sparse datasets for such data-deficient species.

Introduction

Monitoring populations across space and through time is an important objective for conservationists and wildlife managers. The use of spatial capture–recapture and mark–resight models with camera trap data has allowed researchers to estimate density of a number of wide-ranging carnivore species (Rich *et al.*, 2014; Sollmann *et al.*, 2014; Kane, Morin & Kelly, 2015; Hearn *et al.*, 2016). However, even intensive surveys of rare species often result in low individual-level detectability and recapture/resight rates, making it difficult to estimate density (Foster & Harmsen, 2012; Sollmann *et al.*, 2014). Although these issues are not limited to carnivores

(see Queheillalt *et al.*, 2002), small-sample sizes often characterize carnivore datasets and can bias estimates (Gerber, Ivan & Burnham, 2014), decrease precision (Linkie *et al.*, 2008), or even make density estimation impossible (Alexander *et al.*, 2015; Hearn *et al.*, 2016). For these reasons, it is not uncommon that sparse datasets of rare species are simply not analyzed, providing no information for the assessment of rare species' conservation status and thus wasting valuable resources used to collect such data.

One avenue to make use of sparse capture–recapture datasets of rare species is to share parameter information across simultaneous surveys or even past surveys within a modeling framework. This can be done by jointly modeling shared

detection parameters, which increases the effective sample size (e.g. number of individuals detected; Gerber *et al.*, 2014; Royle & Converse, 2014), thus increasing the likelihood of parameter convergence and decreasing small-sample bias; whereas density is still estimated for each survey separately. This approach makes the most sense when surveying the same species under a standardized design. Alternatively, or in addition to a joint survey model, one could incorporate results of past surveys as prior information within a Bayesian model-fitting framework (Gopalaswamy *et al.*, 2012; Chandler & Royle, 2013). Using either or both approaches relies on philosophical considerations that are inherent in all decisions related to model specification and fitting.

Madagascar's endemic carnivore family (Eupleridae) is highly threatened and understudied (Brooke *et al.*, 2014). The largest extant Malagasy carnivore, the fosa (*Cryptoprocta ferox*), is a generalist predator (Hawkins & Racey, 2008) and can substantially influence prey behavior and limit prey populations through predation (Karpanty & Wright, 2007; Irwin, Raharison & Wright, 2009). Listed as Vulnerable (Hawkins, 2016), fosa share traits with apex predators (Wallach *et al.*, 2015), including low densities (Hawkins & Racey, 2005; Gerber, Karpanty & Randrianantenaina, 2012). Based on estimates obtained from camera trapping in southeastern Madagascar, Gerber *et al.* (2012) predicted that the only protected areas in Madagascar large enough to hold fosa populations exceeding 300 individuals were the Zahamena–Mantadia–Vohidrazana (ZMV) and Makira–Masoala rainforest complexes in the northeast. This prediction has yet to be validated in either protected area.

We used the fosa as a case study for estimating the density of apex predators with sparse detections across multiple surveys. Detections from individual surveys were often too sparse to fit models reliably (i.e. lack of parameter convergence, concern of small-sample bias). Thus, we used a modeling framework aimed at maximizing the utility of the fosa data from all surveys to estimate survey-specific population parameters and make reasonable ecological inferences. This modeling framework incorporates prior knowledge on detection variation to decrease small-sample bias, improve parameter convergence and accommodate common concerns relevant for any population estimation. The results provide the best available information on density and population trends of this imperiled species in a previously unstudied area projected to be of great conservation importance (Gerber *et al.*, 2012). Previous occupancy studies in this region have resulted in a better understanding of space-use at the species-level (Farris *et al.*, 2015, 2017), but such results do not provide information on fosa population size, nor how this may vary across time and space. As a result, targeted and effective management decisions based on reliable estimates of population size are lacking.

Our objectives were to: (1) estimate survey-specific fosa density for six study sites, (2) examine how fosa density and movement were influenced by habitat degradation, (3) monitor annual trends in fosa density at two resurveyed sites and (4) provide a fosa population size estimate for the Makira–Masoala protected area complex as a whole. Because the fosa is a naturally unmarked species and can only be

identified to individual by subtle marks (e.g. scars), we also examined the effect of observer identification on fosa density estimates (Kelly *et al.*, 2008; Oliveira-Santos *et al.*, 2010). Finally, we discuss important considerations of our modeling approach in estimating density with sparse data.

Materials and methods

Camera trapping surveys

The Makira–Masoala protected area complex in northeastern Madagascar is the largest contiguous area of protected forest in Madagascar (5197 km^2 as of 2013, excluding community-managed buffers; Fig. 1). Gerber *et al.* (2012) estimated fosa density in southeastern Madagascar and, applying that estimate to the extent of protected areas, determined that Makira–Masoala and the ZMV protected area complex to the south, should each hold a fosa population exceeding 300 adult individuals. This makes both regions particularly important for fosa conservation.

We were careful to select sites that covered the range of variation observed across the rainforest landscape – from highly fragmented, to degraded and selectively logged, to contiguous, primary rainforest – subject to a variety of factors (i.e. habitat, bushmeat hunting and exotic species presence), as our goal was to examine native carnivore ecology across the wide range of conditions in the region (Farris, 2014). We ranked and labeled our six study sites from least to most degraded using a principal components analysis of landscape-level and station-level habitat data, resulting in one intact (S01), three intermediately degraded (hereafter, intermediate; S02–S04) and two degraded sites (S05 and S06; see Farris, 2014; and Table S1, Supporting Information). Because we heavily surveyed intermediate/degraded sites compared to the wide expanse of contiguous forest still present in the region, our density estimates are more likely to be conservative and underestimate the number of fosa in the region.

Between 2008 and 2015 we conducted 14 camera trap surveys at six sites across the region to monitor native carnivore populations (Table 1). Each survey lasted *c.* 2 months and consisted of 18–25 camera stations spaced 400–600 m apart. Camera station spacing was based on the home range of a sympatric individually identifiable carnivore, the striped civet *Fossa fossana* (Kerridge *et al.*, 2004). We used the striped civet's home range for spacing due to it being the only individually identifiable carnivore in Makira–Masoala. Each camera station had two camera traps of different camera trap brands [DeerCam DC300 (Cuddeback, De Pere, WI, USA), Reconyx (PC85 and HC500), Moultrie (D50 and D55), Cuddeback IR and HCO Scoutguard SG565FV]. Camera traps operated 24 h day^{-1} and were positioned 10–30 cm above the ground on opposite sides of wildlife (0.0–0.5 m) or human-made (>0.5 m) trails. We define a 'photographic event' as a camera triggered by movement and body heat resulting in pictures of the target animal and 'photographic capture' as the number of distinctly different individuals detected within a 30-min period (Di Bitetti, Paviolo & De Angelo, 2006). We calculated fosa trap success (TS) as
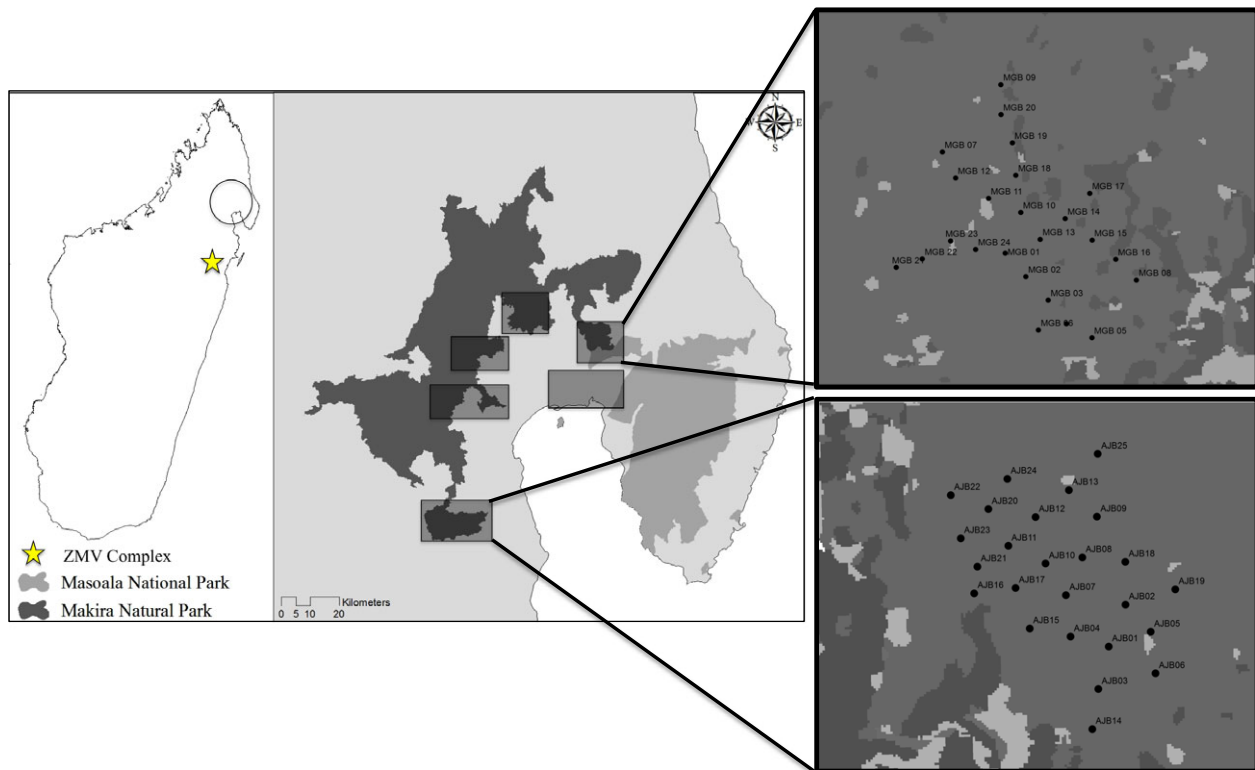
Figure 1 The Masoala and Makira protected areas in northeastern Madagascar are the largest contiguous forests in Madagascar (5197 km^2, excluding community-managed buffers). Insets are representative of the arrangement of camera traps during camera trapping surveys. We photographically surveyed six sites in the regions outlined by the boxes between 2008 and 2015. Due to sensitivity of the data collected in several of these areas on hunting by local people, we are unable to provide the exact locations of survey grids. We also include the location of the Zahamena–Mantadia–Vohidrazana (ZMV) protected area complex to the south (star) as the other region in Madagascar that is predicted to hold more than 300 adult fosa (Gerber *et al.*, 2012). [Colour figure can be viewed at zslpublications.onlinelibrary.wiley.com]

the total number of photographic captures divided by the total number of trap nights (TN) for that survey, multiplied by 100. TN are the number of 24-h periods that a station had at least one camera trap functional.

Fosa identification

Three observers independently examined photographic captures of adult fosa for naturally occurring marks (e.g. ear nicks, tail kinks, scars, etc.) and classified them as marked, unmarked and unusable (Fig. S1, Supporting Information). Surveys were assumed to be temporally and geographically independent. Observer 1 classified photographic captures from all surveys while Observers 2 and 3 classified photographic captures from 10 and 5 surveys, respectively (Table 1). Photographic captures that were unusable were not included in density analyses. Capture histories were made from each observer's classifications and then analyzed using the modified spatial mark–resight model detailed below.

Density estimation

We used a modified spatial mark–resight model (Chandler & Royle, 2013; Sollmann *et al.*, 2013; Royle *et al.*, 2014) to

estimate fosa density (*D*) from an unknown number of marked individuals (Appendix S1, Supporting Information). We assumed individual *i* in survey *q* had an activity center (s_{iq}) uniformly distributed across state space S_q. We determined the area of state space [$A(S_q)$] by buffering each survey's camera trapping grid by 6 km, which is three times the estimated spatial scale parameter (σ; related to animal movement) for fosa in southeastern Madagascar (Gerber *et al.*, 2012). To determine the number of undetected fosa, we augmented the marked and unmarked data with all zero capture histories up to 80 individuals per survey, representing an arbitrarily large population size that is larger than the expected superpopulation *N* (Royle & Dorazio, 2012). The superpopulation is the number of fosa associated with our survey area that, while not necessarily having activity centers within the sampling grid, have some probability of being detected during the sampling period (Kendall, Nichols & Hines, 1997).

We assumed each marked individual *i* was a random sample from the superpopulation N_q (Sollmann *et al.*, 2013; Royle *et al.*, 2014) and had a Poisson observation process (y_{ijq} ~ Poisson($\lambda_{ij} \times K_{jq} \times zm_{iq}$)), where $y_{ijq} \geq 1$ if the individual *i* was detected at least once at camera station *j* during survey *q* and $y_{ijq} = 0$ if the individual was not detected, K_{jq}

Table 1 Details of the 14 photographic surveys of six sites across the Makira–Masoala landscape in northeastern Madagascar (2008–2015) and the number of marked individuals of fosa *Cryptoprocta ferox* and total number of marked photographic captures identified by each observer

Site (survey dates)	Forest type	Season	No. of camera stations	No. of trap nights	Fosa captures[a]	Fosa TS[b]	Observer 1 Individuals (total marked detections)[c]	Observer 2 Individuals (total marked detections)	Observer 3 Individuals (total marked detections)
S01 (September–November 2008)	Intact	Cold	20	1315	40	3.30	5 (8)	6 (14)	5 (6)
S01 (September–November 2010)	Intact	Hot	25	1230	25	2.03	4 (5)	5 (6)	–
S01 (August–October 2011)	Intact	Cold	24	1383	19	1.37	1 (1)	0 (0)	2 (2)
S01 (July–October 2012)	Intact	Cold	24	1536	26	1.69	2 (5)	2 (3)	–
S01 (September–October 2013)	Intact	Cold	24	1198	42	3.51	6 (21)	–	–
S01 (September–November 2015)	Intact	Cold	24	1316	30	2.28	5 (17)	–	–
S02 (August–October 2009)	Intermediate	Cold	19	1067	13	1.22	1 (2)	1 (3)	–
S03 (June–August 2011)	Intermediate	Cold	23	1462	15	1.03	3 (6)	1 (2)	–
S04 (March–May 2011)	Intermediate	Hot	24	1509	105	6.96	6 (19)	3 (7)	5 (10)
S04 (June–July 2012)	Intermediate	Cold	24	1015	21	2.07	2 (2)	3 (4)	–
S04 (November 2013–January 2014)	Intermediate	Hot	24	1188	43	3.62	8 (19)	–	–
S04 (November–December 2015)	Intermediate	Hot	24	636	20	3.14	5 (10)	–	–
S05 (November 2009–January 2010)	Degraded	Hot	18	881	6	0.68	2 (3)	1 (1)	1 (1)
S06 (December 2010–February 2011)	Degraded	Hot	24	1570	30	1.91	3 (7)	2 (8)	2 (3)
Total			341	17 204	435	2.55	53 (125)	24 (48)	15 (22)

[a]Fosa captures is the number of fosa photographic captures for each survey.
[b]Fosa TS is the number of fosa photographic captures during an individual survey divided by the number of trap nights for that survey and multiplied by 100.
[c]Individuals (total marked detections) is the number of marked individuals identified by each observer for that survey, and the number of times marked individuals were detected.

denotes the number of sampling occasions for camera station j available to detect fosa during survey q and zm is an augmented matrix of marked individuals that were either present and detected, or present but not detected during survey q. The expected frequency of encounters (λ_{ij}) was equal to $\lambda_0 \exp\left(-\frac{d_{ijq}}{2\sigma_q^2}\right)$, where λ_0 was the baseline encounter rate, σ was the spatial scale and $d_{ijq} = ||s_{iq} - x_{jq}||^2$, which is the squared Euclidean distance between individual i's activity center (s_{iq}) and the number of times they are detected at camera stations j during survey q (x_{jq}). The matrix K allows for varying survey effort within each survey by specifying the number of sampling occasions at each camera trap. Unmarked fosa also had a Poisson observation process ($yu_{ijq} \sim \text{Poisson}(\lambda_{ij} \times K_{jq} \times z_{iq})$) where z_{iq} was an augmented count of unmarked individuals that were either present and detected, or not detected during survey q. The latent parameter models for marked and unmarked fosa were $zm_{iq} \sim \text{Bernoulli}(\psi_q^M)$ and $z_{iq} \sim \text{Bernoulli}(\psi_q^U)$, where ψ_q^M and ψ_q^U were the proportions of the augmented capture histories that were marked and unmarked individuals, respectively, that were present but had not been detected. The count of unmarked individuals (nU_{jkq}) was the sum of yu_{ijq} over all individuals i. Survey-specific fosa population N_q was the sum of zm_{iq} and z_{iq}, whereas D_q was estimated as $N_q/A(S_q)$.

We jointly modeled the baseline encounter rate (λ_0) as constant across all surveys (Prior: $\lambda_0 \sim \text{Uniform}(0, 5)$); we did so based on previous camera studies of fosa showing that detection is often very low (i.e. challenging to estimate) and consistent across climatic seasons and variation in habitat (Gerber *et al.*, 2012; Farris *et al.*, 2015). In addition, investigations of survey-specific λ_0 indicated little variation and poor parameter convergence. The spatial scale parameter (σ) was also jointly modeled across all surveys, but was not considered constant. Instead, we estimated a survey-specific parameter (σ_q), which was constrained within a higher order population-level distribution defined by a mean and variance that pertains to all surveys (i.e. random effect; log ($\sigma_q) \sim \text{Normal}(\mu, \tau)$. This population-level distribution allows the incorporation of survey-specific heterogeneity, while also improving parameter estimability, compared to separate survey-specific analyses. Prior probabilities for the hyperparameters (μ, τ) were set according to previously estimated values for the spatial scalar (Gerber *et al.*, 2012): mean $\mu \sim \text{Normal}(6.98 \text{ m}, 0.24 \text{ m})$ and variance log ($\tau) \sim \text{Normal}(0, 2)$. We used the scale prior on the augmented latent capture histories for marked (ψ_q^M) and unmarked (ψ_q^U) individuals ($\psi_q^M, \psi_q^U \sim \text{Beta}(0.000001,1)$) because the uniform prior showed signs of improper posterior distributions for survey estimates, as is common for sparse datasets (Link, 2013; Gerber & Parmenter, 2015).

We implemented models for each observer within the software R version 3.2.2 (R Core Team, 2014) and rjags (Plummer, 2014), in which Markov chain Monte Carlo is used to simulate from the full conditional distributions of unknown parameters. We ran three chains with 2000 adaptation iterations and an additional 20 000 iterations each, discarding 10 000 iterations as burn-in. We determined chain convergence by calculating the Gelman–Rubin statistic R-hat (Gelman *et al.*, 2004) using the R package coda (Plummer *et al.*, 2006) with values <1.1 indicating chain convergence. To determine if there was an observer effect, we compared parameter estimates from the five surveys where all three observers identified fosa, in addition to comparing estimates from 11 surveys for Observers 1 and 2, and six surveys for Observers 1 and 3. We report the posterior mode (i.e. the most probable value; Chandler & Royle, 2013; Sollmann *et al.*, 2013) and 95% highest posterior density intervals, due to our sample sizes and expectation of asymmetric posteriors (Chen, Shao & Ibrahim, 2000).

Factors that influence fosa density and annual trends

We determined whether fosa density and movement estimates among forest types (e.g. degraded status) were different by examining posterior distribution overlap. If posterior distributions overlapped, they were considered to be similar. We examined the posterior distribution overlaps between mean density estimates from surveys at intact (n = six surveys at one site), intermediate (n = six surveys at three sites) and degraded (n = two surveys at two sites) forest sites (Table 1). To monitor fosa density trends at two resurveyed sites (intact forest site S01 and intermediate forest site S04), we examined the posterior distribution overlap for the initial (2008 and 2011, respectively) and final (2015) surveys.

Landscape population estimation

To estimate the landscape-wide fosa population, we estimated mean fosa density by averaging site-level density posterior distributions. Resurveyed sites (S01 and S04) were averaged across years to avoid over-representation in the landscape estimate. After we determined the mean fosa density for all surveys, we applied the estimate to the current protected area forest extent to estimate fosa abundance across the protected forest region. Given that we surveyed and estimated fosa density across a wide range of habitat types (Farris, 2014) and fosa density estimates reflected some of these variations in habitat type, we suggest this extrapolation across the entire landscape is reasonable. Indeed, we feel that our landscape population estimate is likely to be conservative and underestimate the true number of fosa in the region due to our heavily surveying intermediate/degraded sites compared to the wide expanse of contiguous forest still present in the region.

Results

We obtained 435 fosa photographic captures over 17 204 TNs across 14 surveys at six sites (2008–2015). Fosa landscape TS was 2.55/100 TNs (Table 1). The mean proportion of photographic captures that each observer included in analyses was 0.49 (SE = 0.03). Mean number of usable marked and unmarked fosa detections per survey was 8.29 (SE = 0.28) and 7.76 (SE = 0.56), respectively. Mean number of marked individuals identified per survey was 3.62

(SE = 0.09). Despite variations in the number of marked fosa each observer identified, we found little evidence of a difference in density estimates based on posterior distribution overlap among observers (Fig. S2, Supporting Information), but do note the uncertainty in estimates could mask true differences. As a result, we present Observer 1's density estimates.

Fosa baseline daily encounter rate was low ($\lambda_0 = 0.004$; 0.003–0.006; Table 2). Survey-specific fosa density varied from 0.06 (0.02–0.33) individuals per km² at S05 in 2009 to 0.39 (0.14–1.11) individuals per km² at S01 in 2008 (Table 2). Fosa density was similar at degraded ($D = 0.16$; 0.05–0.43 individuals per km²), intermediate ($D = 0.23$; 0.12–0.37 individuals per km²) and intact ($D = 0.26$; 0.15–0.44 individuals per km²) forest sites. Fosa movement was also similar at intact ($\sigma = 1379.3$ m; 957.6–2023.9 m), intermediate ($\sigma = 1326.2$ m; 950.1–1910.2 m) and degraded ($\sigma = 1273.7$ m; 711.5–2019.1 m) forest sites.

Annual trends varied by site. Fosa density from S01's initial survey in 2008 was $D = 0.39$ (0.14–1.11) individuals per km²; by the final S01 survey in 2015, density was $D = 0.08$ (0.05–0.31) individuals per km². Density from S04's initial survey in 2011 was $D = 0.24$ (0.06–0.60) individuals per km²; by the final S04 survey in 2015, density was $D = 0.16$ (0.04–0.52) individuals per km².

Landscape fosa density estimate was 0.20 (0.12–0.34) individuals per km² (Table 2). Extrapolating these estimate to the 2013 forested extent of the Makira–Masoala protected area complex resulted in an estimate of $N = 1061$ (596–1780) adult individuals. Comparatively, the IUCN estimate from Gerber *et al.* (2012) estimates the global fosa population to be 8626 adult individuals (Hawkins, 2016).

Discussion

Small-sample sizes can hinder the ability of researchers to estimate population size and density for the rare, threatened, and/or understudied species, that is those most in need of a conservation status assessment (Queheillalt *et al.*, 2002; Foster & Harmsen, 2012; Gerber *et al.*, 2014). We were motivated to make use of a sparse dataset, as fosa are an apex predator for which very few density estimates are available, in addition to the number of factors (e.g. bushmeat hunting and habitat loss) potentially leading to population declines of this understudied and threatened carnivore. No study has estimated fosa density in Madagascar's largest protected area, a potentially important conservation area for this, and many other, endemic species. Despite an effort of 17 204 TNs over 14 camera trapping surveys, we only detected a mean of 3.62 (SE = 0.09; range = 1–8) unique individuals per survey. The mean proportion of marked individuals detected was 0.15 (SE = 0.04; range = 0.07–0.23). These low detections – particularly of marked individuals – are comparable to camera trapping surveys of much larger carnivores (Linkie *et al.*, 2010), and can hinder parameter estimation if researchers attempt to estimate density for each survey alone (e.g. Lynam *et al.*, 2009).

Using our approach to share information via jointly modeling the detection process across surveys, and using an informed prior, we were able to estimate fosa density across all surveys. Without this approach, there was concern that small-sample bias, extreme parameter uncertainty, and difficult parameter convergence for survey-specific analyses, would result in poor inference regarding fosa density. Instead, we found that point estimates did differ among the

Table 2 Mode and highest point density intervals of fosa density (D), spatial scale (σ) and baseline encounter rate (λ_0) for 14 photographic surveys in the Makira–Masoala protected area complex, northeastern Madagascar (2008–2015)

Parameter	λ_0			σ (m)			D (individual per km²)		
Site code-year	Mode	2.50%	97.50%	Mode	2.50%	97.50%	Mode	2.50%	97.50%
All	0.004	0.003	0.006	–	–	–	–	–	–
S01–08	–	–	–	824.31	484.26	1633.70	0.39	0.14	1.11
S01–10	–	–	–	1321.61	760.48	2280.95	0.23	0.06	0.69
S01–11	–	–	–	1044.50	385.20	2065.75	0.11	0.02	0.60
S01–12	–	–	–	746.88	340.79	2316.73	0.14	0.02	0.77
S01–13	–	–	–	1644.11	1025.89	4161.36	0.11	0.06	0.45
S01–15	–	–	–	1452.03	865.86	3326.61	0.08	0.05	0.31
S02–09	–	–	–	1213.58	412.34	2442.69	0.07	0.02	0.53
S03–11	–	–	–	1328.87	692.97	2563.39	0.10	0.03	0.41
S04–11	–	–	–	1347.94	842.49	2678.93	0.24	0.06	0.60
S04–12	–	–	–	1039.76	345.12	1936.92	0.08	0.02	0.49
S04–13	–	–	–	1308.76	834.45	2363.87	0.25	0.08	0.60
S04–15	–	–	–	1229.79	647.30	2220.74	0.16	0.04	0.52
S05–09	–	–	–	1239.44	429.06	2120.37	0.06	0.02	0.33
S06–10	–	–	–	1300.06	678.80	2401.04	0.19	0.06	0.67
Intact	–	–	–	1379.30	957.59	2023.87	0.23	0.11	0.43
Intermediate	–	–	–	1326.23	950.14	1910.19	0.23	0.12	0.37
Degraded	–	–	–	1273.72	711.54	2019.05	0.16	0.05	0.43
Landscape	–	–	–	–	–	–	0.20	0.11	0.34

different forest types, with intact and intermediate forests having higher density estimates than degraded forests. However, we do note that because of high parameter uncertainty, we cannot say with confidence that mean fosa density or movement varied across a habitat degradation gradient. Nonetheless, local site use probabilities at the same sites (Farris *et al.*, 2015) potentially suggest that fosa are tolerant of some habitat degradation.

We found a potential decline in fosa density at our intact, resurveyed site S01, as the posterior distributions for the density estimates from 2008 and 2015 were mostly different (i.e. not overlapping). However, because fosa density at this site varied from year to year, the population might be experiencing natural fluctuations. While it is possible that fosa are immigrating and emigrating to and from the site, we consider it more likely that hunting in the area is taking its toll on the local population (Farris *et al.*, 2015). Continued surveys of this site would solidify whether the possible decline we noted from 2008 to 2015 is a continuing trend. It is interesting to note that despite the initial survey density estimate decreasing from 0.39 (0.14–1.11) in 2008 to 0.08 (0.05–0.31) individuals per km^2 in 2015, Farris *et al.* (2017) did not find evidence for declines in fosa probability of local site use via occupancy analysis between 2008 and 2013, despite four of the six native carnivores at this site showing declines of up to 60%. Because fosa home ranges are larger than the other carnivores and one fosa could occupy a substantial proportion of a camera-trap grid, local site use probabilities would not detect declines in abundance, and this emphasizes the importance of density versus occupancy/site use when monitoring population trends, particularly for wide-ranging carnivores that might range beyond the camera trapping grid (Alexander *et al.*, 2015).

Finally, fosa abundance in the Makira–Masoala complex was estimated to be 1061 (596–1780) adult individuals. Gerber *et al.* (2012) suggested that there were 1855 adult fosa living within protected areas in eastern Madagascar, with the Makira–Masoala and the ZMV rainforest complexes protecting the bulk of the eastern fosa population. Our estimate agrees with this prediction; however, while we believe that our sites are representative of the larger protected forest extent – and indeed might lead to conservative region-wide population estimates due to our overrepresentation of degraded forest – we only surveyed six sites. Future surveys at different sites within the Makira–Masoala complex would shed more light on spatial heterogeneity and the true number of fosa protected in this important conservation region. It should be recognized, however, that without novel developments to improve detection of this rare and elusive carnivore, single-survey studies can expect challenging estimation and high parameter uncertainty.

Model framework, assumptions and sharing information across surveys

Our modeling approach sought to maximize the information from hard-won, yet sparse, datasets to garner ecological inference for rare and understudied species. Our approach requires

several considerations, but we were still able to incorporate many common concerns in population estimation by accounting for: (1) spatial heterogeneity in detection, (2) an unknown effective sampling area, (3) marked and unmarked individuals, (4) observer identification consistency, (5) survey-level heterogeneity in movement, (6) unequal sampling effort and (7) estimating parameters despite very low detection probability. Researchers with sparse datasets should consider when, and if, sharing information across concurrent or previous surveys is reasonable and justifiable, and conceptualize a model that incorporates important sources of variability. Decisions regarding how and when to model parameter variation are typically considered in a model selection process, which is difficult for sparse datasets and unclear with hierarchical Bayesian models with spatial dependency.

For this study, we were able to incorporate heterogeneity in σ across surveys using a random effect. While assuming a single baseline encounter rate (λ_0) for all surveys may not be preferred, and could potentially lead to biased estimates, it was necessary for model convergence. Obtaining reasonable density estimates of this threatened and ecologically important carnivore motivated this simplifying assumption, which is likely to be a common theme in carnivore capture–recapture studies. Identifying individual fosa is challenging due to their naturally unmarked status, and necessitated comparing multiple observers to assess reliability of identification. As our marks were natural and included markings that would not be sex-specific (i.e. kinked tails), and similar markings have been used in other studies using similar modeling approaches (Rich *et al.*, 2014), we assumed we met the assumption of random distribution of marked and unmarked individuals necessary for mark–resight models. We do note that, due to the sparseness of fosa detections, we could not incorporate heterogeneity in the baseline encounter rate (λ_0) among the surveys, and we assumed the informed prior from southeastern Madagascar was similar to fosa movement in the northeast. We think our choices and assumptions were reasonable in our modeling approach.

Future research and conservation implications

On the basis of recent research (Gerber *et al.*, 2012; Farris *et al.*, 2015), we suggest that fosa populations might be somewhat tolerant of habitat degradation and cautiously recommend that fosa conservation efforts in the region give greater priority to reducing locally high rates of bushmeat hunting and consumption (Golden, 2009; Golden *et al.*, 2011) than protecting intact forest habitat (Gerber *et al.*, 2012; Farris *et al.*, 2015). In addition, our region-wide population estimate (1061 individuals) and the extent of protected forest in the region indicate that Makira–Masoala is an important stronghold for this endemic carnivore. The current global biodiversity crisis (Dirzo *et al.*, 2014; Newbold *et al.*, 2014) demands accurate assessments of wild populations to inform conservation and management; demands that could be met by sharing information on detections across surveys and using informed priors to estimate parameters. Thus, we

suggest such methods as a way forward in parameter estimation from sparse datasets, but caution researchers to carefully consider model assumptions before adopting this approach.

Acknowledgments

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Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Figure S1. Representative photographs of the different photographic classes: (a) marked and identifiable, (b) unmarked and (c) unusable.

Figure S2. A visual comparison of MCMC iterations (left) and posterior distributions (right) of baseline encounter rate (a; λ_0), spatial scale (b; σ; m) and density (c and d; D; individuals per km^2) among observers at two sites (S01 and S04; see c and d).

Table S1. Station-level[a] and landscape-level[b] habitat features (SE) for six forest sites in the Makira and Masoala protected areas, northeastern Madagascar (2008–2015).

Appendix S1. Notation for a hierarchical spatial mark-resight model used to estimate fosa (*Cryptoprocta ferox*) density and related parameters..