

When carnivores roam: temporal patterns and overlap among Madagascar's native and exotic carnivores

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Abstract

Madagascar's Eupleridae carnivores are perhaps the least studied and most threatened family of Carnivora. Investigating potential direct and indirect competition among these native species and sympatric exotic carnivores is necessary to better direct conservation actions. From 2008 to 2013, we photographically surveyed a diverse rainforest landscape, comparing six native and three exotic carnivores' activity patterns throughout the diel cycle. We used hierarchical Bayesian Poisson analysis to describe the activity patterns of Madagascar's carnivore community, assessed effects of season and site on temporal activity patterns, and estimated coefficients of overlap between carnivore pairings to assess effects of body size and ecological niche on temporal overlap among native and exotic carnivores. We observed changes in temporal activity patterns across seasons particularly during the austral summer (hot-dry season) for four native and two exotic carnivores, including evidence of fossa *Cryptoprocta ferox* altering their temporal activity during their mating season (hot-dry season). We found evidence of high overlap between natives and exotics indicating the potential for increased interactions and competition. The greatest overlap in temporal activity occurred between both ring-tail *Galidia elegans* and brown-tail vontsira *Salanoia concolor* and exotic dogs *Canis familiaris*. *Cr. ferox*, falanouc *Eupleres goudotii* and spotted fanaloka *Fossa fossana* also overlapped in activity with the nocturnal, exotic Indian civet *Viverricula indica*. *Cr. ferox* avoided humans and *Ca. familiaris* across all seasons. Unexpectedly, carnivore body size and ecological niche were not important predictors of temporal overlap. Previous research has shown these native and exotic carnivores overlap spatially and these new findings of temporal overlap among native and exotic carnivores add urgency to the need to manage exotic carnivores across Madagascar.

Introduction

Understanding the mechanisms driving community structure is important for sound conservation and management of wildlife species. Community structure is shaped by a multitude of spatiotemporal, intra- and interspecies interactions including competition, predation, mutualism, parasitism, commensalism or ammenalism. For sympatric species that fill similar ecological roles, partitioning of the temporal niche dimension may be an important mechanism enabling coexistence as this may reduce the potential for direct competitive interactions for food or space (Kronfeld-Schor & Dayan, 2003; Santos & Presley, 2010). Therefore, investigating temporal activity patterns can aid in understanding co-existence (Pianka, 1973) especially for carnivores of similar body size and diet. Tem-

poral avoidance may be a primary driver in reducing competition, leading to increased co-existence and thus enhanced biodiversity (Kronfeld-Schor & Dayan, 2003).

Madagascar's Eupleridae carnivores arguably are both the least studied and most threatened family of Carnivora in the world (Brooke *et al.*, 2014). They represent a monophyletic radiation (Yoder *et al.*, 2003), thus making comparisons of niche utilization simplified compared with other carnivore families. Eupleridae, therefore, provide a straightforward model for understanding community structure including the influence of exotic species. Recent work has confirmed the presence of six endemic (hereafter 'native') and three exotic carnivore species (Appendix S1) across north-eastern Madagascar (Farris *et al.*, 2012). The overall ecological niche (e.g. temporal activity, habitat use and diet) as currently

understood for these six native carnivores is variable (Table 1). However, there are similarities in habitat, body size and resource use between falanouc *E. goudotii*, the spotted fanaloka *F. fossana* and among the three vantsira carnivores (Goodman, 2012). Our understanding of temporal activity patterns among Madagascar carnivores comes from anecdotal accounts and a single quantitative study from Ranomafana National Park (RNP) (Gerber, Karpanty & Randrianantenaina, 2012a). Gerber *et al.* (2012a) highlighted the negative relationship between domestic and/or feral dogs *Canis familiaris* and exotic Indian civets *Viverricula indica* on

native carnivore activity patterns. Opposite activity patterns between native and exotic carnivores could result from exploitative competition or interference competition (including intraguild predation) (Salo *et al.*, 2007; Clout & Russell, 2008; Vanak & Gompper, 2010). Of particular concern is our limited understanding of activity patterns of exotic and feral carnivores given their negative impacts on native wildlife in Madagascar (Gerber *et al.*, 2012a; Gerber, Karpanty & Randrianantenaina, 2012b; Farris, 2014; Farris *et al.*, 2014) and in other habitats worldwide (Gompper, 2013). The similar body size between multiple native and exotic carnivores across

Table 1 Characteristics and background of the six native and three exotic (in bold) carnivore species compared for this study

Species (common name)	IUCN classification ^a	Weight (kg) ^{b,c}	Activity pattern (primary–secondary)	Habitat preference	Diet
Large carnivores					
Domestic dog <i>Canis familiaris</i>	–	Variable ^m	Variable ^{b,d}	Degraded/fragmented forest, near anthropogenic areas ^{b,c}	Poorly studied (lemurs, small mammals likely)
Fossa <i>Cryptoprocta ferox</i>	Vulnerable	5.5–9.9	Nocturnal-crepuscular ^{b,e,f,g}	Contiguous, degraded dry and humid forest ^{b,c}	Lemurs, small mammals, small vertebrates ^c
Feral cat <i>Felis species</i>	–	3.5–8.0	Variable ^b	Variable ^{b,c,d}	Poorly studied (lemurs, small mammals likely)
Medium carnivores					
Falanouc <i>Eupleres goudotii</i>	Near threatened	1.5–4.6	Crepuscular-nocturnal ^{b,e,g}	Contiguous, degraded humid forest and marsh/aquatic areas ^{b,c,d}	Small vertebrates and invertebrates ^c
Indian civet <i>Viverricula indica</i>	–	2.0–4.0	Nocturnal ^{b,h}	Degraded/fragmented forest, near anthropogenic areas ^{b,c,d}	Poorly studied (small mammals likely)
Spotted fanaloka <i>Fossa fossana</i>	Near threatened	1.3–2.1	Nocturnal ^b	Contiguous humid forest, near marsh/aquatic areas ^{b,c,d}	Small mammals, amphibians, crustaceans, invertebrates ^c
Small carnivores					
Ring-tail vantsira <i>Galidia elegans</i>	Least concern	0.76–1.10	Diurnal-crepuscular ^{b,c,i}	Contiguous/degraded humid forests, near anthropogenic areas ^{b,c,d}	Highly variable (lemurs, small mammals, birds, reptiles, fish) ^c
Broad-stripe vantsira <i>Galidictis fasciata</i>	Near threatened	0.6–1.0	Nocturnal ^{b,j}	Contiguous/degraded humid forest ^{b,c,d}	Small vertebrates (rodents, reptiles, amphibians and invertebrates) ^c
Brown-tail vantsira <i>Salanoia concolor</i>	Vulnerable	0.55–0.75 ^c	Diurnal ^{k,l}	Contiguous/degraded humid forest ^{b,c,d}	Invertebrates ^c

We used body weight to categorize all carnivore species as large (≥ 3.5 kg), medium (1.3–3.5 kg) and small (≤ 1.1 kg). Exotic carnivores are provided in bold font.

^a(IUCN, 2014).

^b(Gerber *et al.*, 2012b; Goodman, 2012).

^c(Goodman, 2012).

^d(Farris, 2014).

^e(Albignac, 1972).

^f(Hawkins, 1998).

^g(Dollar, 1999).

^h(Su & Sale, 2007).

ⁱ(Goodman, 2003a).

^j(Goodman, 2003b).

^k(Britt & Virkaitis, 2003).

^l(Farris *et al.*, 2012).

^mWeight of domestic and feral dogs recorded in literature and observed by our team in Madagascar are highly variable and range from less than 5 kg to more than 10 kg.

the landscape (Table 1) is of great concern because exotic and feral species may competitively exclude native species as exotic carnivores continue to increase in distribution and perhaps abundance across the landscape. Determining the temporal activity patterns of exotic and native carnivores across habitat types and seasons is important to predict whether it may be necessary to remove exotic animals from protected areas to protect native species.

The effect of season on Malagasy carnivore activity patterns, including the overlap in activity among exotic and native species across seasons, has not been investigated. Variation in seasonal activity patterns may occur if seasonal variation in temperature, precipitation and photoperiod drive behavioral shifts. Moreover, seasonal changes in activity may result from changes in reproductive status, prey availability and/or competition (Kavanau & Ramos, 1975; Clutton-Brock & Harvey, 1978). For example, the breeding season of *Cryptoprocta ferox* is October through December when females advertise via vocalizations and scent marking from a fixed location and mate with many males multiple times over several days (Goodman, 2012). We currently lack information on how carnivores might alter their temporal activity across seasons in Madagascar.

Our goal was to explore activity patterns of Madagascar's native and exotic carnivores to determine how activity patterns vary among native carnivores of similar body size and niche (defined by habitat use and diet), by season and in relation to exotic carnivores. To achieve this goal we (1) quantified activity patterns (day, dawn, dusk and night) for six native and three exotic carnivores across the landscape; (2) investigated effects of season and site on native and exotic carnivore activity patterns throughout the diel cycle; (3) investigated the effects of body size and ecological niche on overlap in temporal activity among all carnivore pairings. We hypothesized that (1) native and exotic carnivores would demonstrate

variation in activity patterns across seasons due to variability in temperature, resource availability and mating behavior; (2) native carnivores would avoid sites where exotic carnivore activity is high based on our findings of lack of co-occurrence among native and exotic carnivores (Farris, 2014), which may result from competition, predation and/or harassment; (3) native and exotic carnivores of similar body size and ecological niche would demonstrate divergence in activity patterns indicating division of the temporal niche to allow for co-existence. In particular we expected to see temporal segregation among the three small-bodied vantsira carnivores (ring-tail *Galidia elegans*, broad-stripe *Galidictis fasciata* and brown-tail vantsira *S. concolor*); the three medium-sized carnivores (falanouc *E. goudotii*, spotted fanaloka *F. fossana* and exotic Indian civet *V. indica*); and the three large-bodied carnivores (fossa *Cr. ferox*, dog *Ca. familiaris* and feral cat *Felis* sp.).

Methods

Study site

We photographically surveyed carnivores from 2008 to 2013 across Madagascar's largest protected area complex, the Masoala-Makira landscape (Fig. 1). This landscape consists of Masoala National Park (240 000 ha) (Kremen, 2003) and Makira Natural Park (372 470 ha of protected area and 351 037 ha of community management zone). The Masoala-Makira landscape has the highest estimated levels of biodiversity in Madagascar but faces numerous anthropogenic pressures threatening the endemic wildlife therein (Golden, 2009; Farris, 2014). We surveyed a total of seven study sites across the Masoala-Makira landscape of which two were surveyed repeatedly for a total of 12 surveys. Study sites were selected to capture wide variation in habitat degradation and

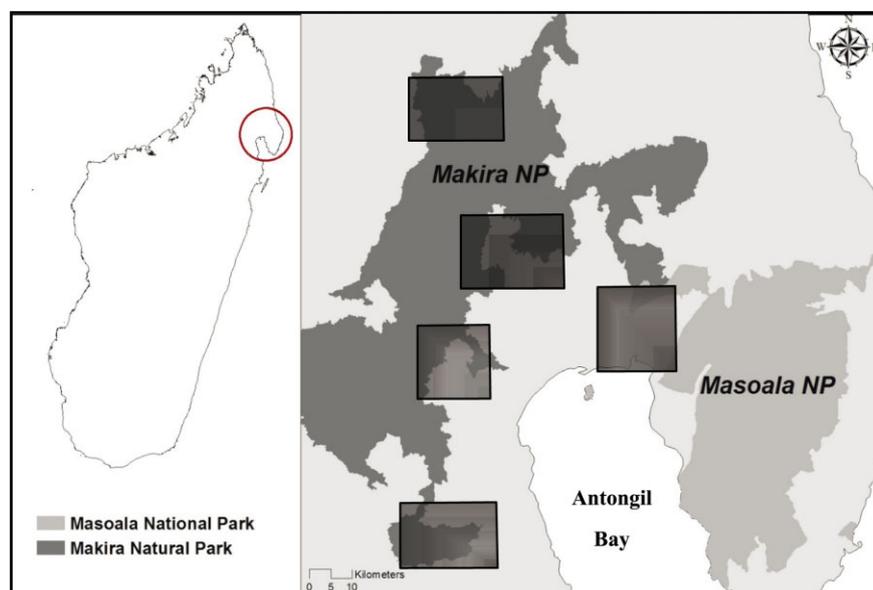


Figure 1 Map of the Masoala-Makira landscape including the outline of the regions in which the surveys were conducted at seven study sites. Photographic surveys occurred from 2008 to 2012. Map used with permission from Farris, 2014.

fragmentation as part of an ongoing research project (Farris *et al.*, 2012; Farris, 2014; Farris *et al.*, 2014.) Additional published research using this expansive dataset, regarding hunting and bushmeat consumption, required us to keep village and/or forest site names anonymous. As a result, we ranked and labeled sites based on their level of degradation (01 = least degraded; 07 = most degraded; Appendix S2) using principal components and cluster analyses rather than using the village or forest names (Farris, 2014).

Seasons

We defined climatic seasons using daily measurements of temperature and rainfall and from existing studies on seasonal patterns for this region (Sterling, 1993). These climatic seasons were consistent with those found at RNP where Gerber *et al.* (2012a) conducted their investigation of carnivore temporal activity patterns (Tecot, 2007). We recorded rainfall and temperature measurements at 06:00, 12:00 and 18:00 each day during the course of the photographic surveys from locations within the camera grid/study site.

Of the 12 total surveys, we conducted two surveys ($n = 2$ different sites) during the hot-wet season [February–May; mean temperature = $23.0^{\circ}\text{C} \pm$ standard deviation (SD) 1.5; mean rainfall = $4.3 \text{ cm} \pm$ SD 7.3], seven surveys ($n = 5$ different sites, one site surveyed three times) during the cool-wet season (June–September; mean temperature = $16.1^{\circ}\text{C} \pm$ SD 2.3; mean rainfall = $3.7 \text{ cm} \pm$ SD 5.2) and three surveys ($n = 2$ different sites, one site surveyed twice) during the hot-dry season (October–January; mean temperature = $21.3^{\circ}\text{C} \pm$ SD 3.7; mean rainfall = $5.4 \text{ cm} \pm$ SD 9.0). Given the high variability in rainfall data collected during our study, resulting from numerous cyclone events, we also used existing historical climate data (<http://data.worldbank.org>) and additional studies measuring climate patterns within this region to validate the categorization of seasonal periods. Our two sites with repeated surveys (sites S02 and S05) were sampled over different seasons.

Carnivore sampling

We established 18–25 remote camera stations (with two cameras per station) at each study site using both digital (Reconyx PC85 & HC500, Moultrie D50 & D55, Cuddeback IR) and film-loaded (DeerCam DC300) cameras. We placed cameras on either side of human (0.5–2.0 m wide) and wildlife (<0.5 m wide) trails, at 20–30 cm off the ground, and used no bait or lure. Camera stations were approximately 500 m apart in a grid pattern (Gerber *et al.*, 2012b). Cameras operated 24 h a day for an average of 67 days (SD = 8.10) per study site and we checked each camera station every 5–10 days between the hours of 06:00 and 17:00 to change memory cards or film and batteries, and to ensure cameras were functioning properly.

Analysis of temporal activity data

We defined an independent capture event as all photos of a given carnivore species within a 30-min period (Di Bitetti,

Paviolo & De Angelo, 2006). We defined the ‘dawn’ and ‘dusk’ time periods as 1 h prior to and 1 h post sunrise and sunset, respectively. Species primarily active during dawn and dusk are referred to as crepuscular. We defined ‘day’ time period (denoted diurnal) as between dawn and dusk, whereas ‘night’ time period (denoted nocturnal) was between dusk and dawn. This resulted in approximately 10 h of available time for both day and night time periods and 2 h of available activity each for dusk and dawn time periods.

Hierarchical Bayesian Poisson analysis

We investigated carnivore activity patterns by modeling captures (capture events/available hours; hereafter photographic rate) for each time category. We modeled the daily count y_{ijk} (e.g. capture event), on each sampling day i , at study site k , for each time category j using a hierarchical Bayesian Poisson model using an offset equal to the number of hours available. To make inference about each study site and the activity of species across sites, we treated each time category as a random effect, allowing us to simultaneously make inference about activity at each study site and summarize species-level activity across study sites for each of the nine carnivore species of interest.

Kernel density analysis

To evaluate alternative hypotheses of how season, study site and season by study site influence carnivore temporal activity throughout the diel cycle, we assumed that photographic times (converted to radians) followed the circular von Mises distribution with parameters κ (concentration) and a mean direction of linear predictors following $\mu + 2 \cdot \text{atan}(\beta \cdot \mathbf{X})$, where μ and β are unknown coefficients to be estimated via maximum likelihood and \mathbf{X} is a matrix of predictor variables (Fisher & Lee, 1992). We used the R package ‘circular’ to fit these models (Agostinelli & Lund, 2013). We conducted model selection using Akaike’s information criterion (Akaike, 1973) and made inference from the most simple model (no variation by camera survey) and from the most parsimonious model by estimating the probability density of temporal activity distribution for each species using nonparametric kernel density analyses (Ridout & Linkie, 2009).

For each species we determined its dominant activity pattern as diurnal, nocturnal or crepuscular by examining its continuous activity throughout the diel cycle (i.e. kernel density analysis) and noting any preference for a given time period (i.e. Poisson analysis). Preference was described as a higher expected number of photographs per hour of available time.

To assess the effect of ecological niche and body size on temporal overlap, we estimated the coefficient of overlap between all paired carnivore species’ probability densities using an estimator supported for small sample size [Δ_1] (Ridout & Linkie, 2009). We compared the overlap coefficient, Δ_1 , between all species pairings to determine if their Δ_1 was lower, indicating temporal avoidance, than between more dissimilar species.

Results

Our surveys resulted in a total of 15 253 trap nights (mean = $1270 \pm \text{SD} = 229$ per study site) and provided a total of 2991 photographic captures of carnivores (1639 captures of six native carnivores and 1352 captures of three exotic carnivores; Table 2; Appendix S2). Based on kernel analysis and the resulting mean photographic rates (i.e. expected capture events per available hours), we found variation or flexibility in how a carnivore used the 24-h period. Overall we found that *Cr. ferox*, *E. goudotii*, *F. fossana*, *Galidic. fasciata* and *V. indica* were nocturnal while *Galidia elegans*, *S. concolor* and *Ca. familiaris* were diurnal (Table 3; Fig. 2a,b). However, *Cr. ferox*, *E. goudotii* and *V. indica* also used additional time periods to a lesser extent (photographic rate ≤ 0.06), suggesting these carnivores may exhibit some crepuscular activity but are primarily nocturnal across the landscape (Fig. 2a). The exotic *Felis* sp. had wide-ranging activity patterns across the landscape, slightly preferring day time (Table 3; Fig. 2b).

Our model selection from the kernel density estimates revealed the null model, combining all captures across the landscape and across seasons, was best for explaining activity patterns for three carnivores (*Cr. ferox*, *E. goudotii* and *Ca. familiaris*; Appendix S3). For three other species we found site (i.e. *Galidia elegans*), season (i.e. *Felis* sp.) and site by season (i.e. *F. fossana*) were also important for explaining activity patterns (Appendix S3). *Galidia elegans* was exclusively diurnal at study site S04 during the cool-wet season; but at study sites S02 (hot-dry, cool-wet) and S05 (cool-wet) we observed moderate levels of crepuscular activity and even limited nocturnal activity (Fig. 3a). *Felis* sp. decreased nocturnal activity during hot-wet and hot-dry seasons compared with the cool-wet season where activity peaked at midnight, dusk and dawn (Fig. 3b). Despite the consistent nocturnal activity throughout all surveys for *F. fossana*, this nocturnal carnivore appears to shift its peak activity from early evening (18:00–0:00) during the cool-wet season to early morning (0:00–06:00) during the two hot seasons (Fig. 3c). This is supported further by our repeated surveys at study site 02 where *F. fossana* greatly altered its nocturnal activity from hot-dry to cool-wet season (Fig. 3c).

Table 3 Relative preference of activity period (dawn, day, dusk and night) based on number of photographic captures, mean photographic capture rate (photos/available hours) ordered from highest to lowest activity and probability of overlap with the most active time period

Common name	Time period – ordered by use			
<i>Cryptoprocta ferox</i>	Night	Day	Dawn	Dusk
# captures	182	68	54	32
Photo. rate (SE)	0.13 (0.06)	0.07 (0.02)	0.02 (0.02)	0.02 (0.01)
Prob. overlap	–	0.48	0.09	0.05
<i>Fossa fossana</i>	Night	Dusk	Dawn	Day
# captures	617	67	49	4
Photo. rate (SE)	0.65 (0.49)	0.03 (0.02)	0.02 (0.02)	0.01 (0.01)
Prob. overlap	–	0.07	0.06	0.01
<i>Eupleres goudotii</i>	Night	Dawn	Day	Dusk
# captures	99	52	24	20
Photo. rate (SE)	0.16 (0.08)	0.06 (0.04)	0.03 (0.02)	0.01 (0.01)
Prob. overlap	–	0.28	0.04	0.01
<i>Galidictis fasciata</i>	Night	Dawn	Dusk	Day
# captures	67	11	3	0
Photo. rate (SE)	0.19 (0.04)	0.02 (0)	0 (0)	0 (0)
Prob. overlap	–	0.09	0	0
<i>Galidia elegans</i>	Day	Dawn	Dusk	Night
# captures	132	13	2	0
Photo. rate (SE)	0.24 (0.14)	0.01 (0.02)	0.01 (0.01)	0 (0)
Prob. overlap	–	0.06	0.03	0.01
<i>Salanoia concolor</i>	Day	Dawn	Dusk	Night
# captures	54	4	2	0
Photo. rate (SE)	0.16 (0.09)	0.01 (0.01)	0.01 (0.01)	0 (0)
Prob. overlap	–	0.05	0.03	0.01
<i>Canis familiaris</i>	Day	Dawn	Dusk	Night
# captures	851	73	61	44
Photo. rate (SE)	0.32 (0.14)	0.02 (0.02)	0.02 (0.01)	0.01 (0.01)
Prob. overlap	–	0.22	0.20	0.15
<i>Felis species</i>	Day	Dusk	Night	Dawn
# captures	73	30	33	37
Photo. rate (SE)	0.14 (0.08)	0.08 (0.06)	0.05 (0.04)	0.04 (0.04)
Prob. overlap	–	0.58	0.34	0.27
<i>Viverricula indica</i>	Night	Dusk	Day	Dawn
# captures	33	4	4	2
Photo. rate (SE)	0.33 (0.07)	0.06 (0.03)	0.05 (0.02)	0.03 (0.02)
Prob. overlap	–	0.01	0	0

The number of hours available in each time category is corrected using an offset and carnivores having <15 captures at a given study site were excluded from analysis.

Table 2 Summary of independent photographic 'captures' by season across the landscape from 2008 to 2013

Scientific name	# photographic captures by season			Total photographic captures
	Hot-dry (n = 2 sites)	Hot-wet (n = 2 sites)	Cool-wet (n = 5 sites)	
<i>Cryptoprocta ferox</i>	98	112	142	352
<i>Fossa fossana</i>	377	88	302	767
<i>Eupleres goudotii</i>	76	5	121	202
<i>Galidia elegans</i>	46	61	47	154
<i>Galidictis fasciata</i>	61	5	32	98
<i>Salanoia concolor</i>	25	0	41	66
<i>Canis familiaris</i>	357	395	383	1135
<i>Felis species</i>	3	24	146	173
<i>Viverricula indica</i>	8	2	34	44

The camera trapping sampling effort varied by season with 201, 125 and 374 trap nights during the hot-dry, hot-wet and cool-wet, respectively.

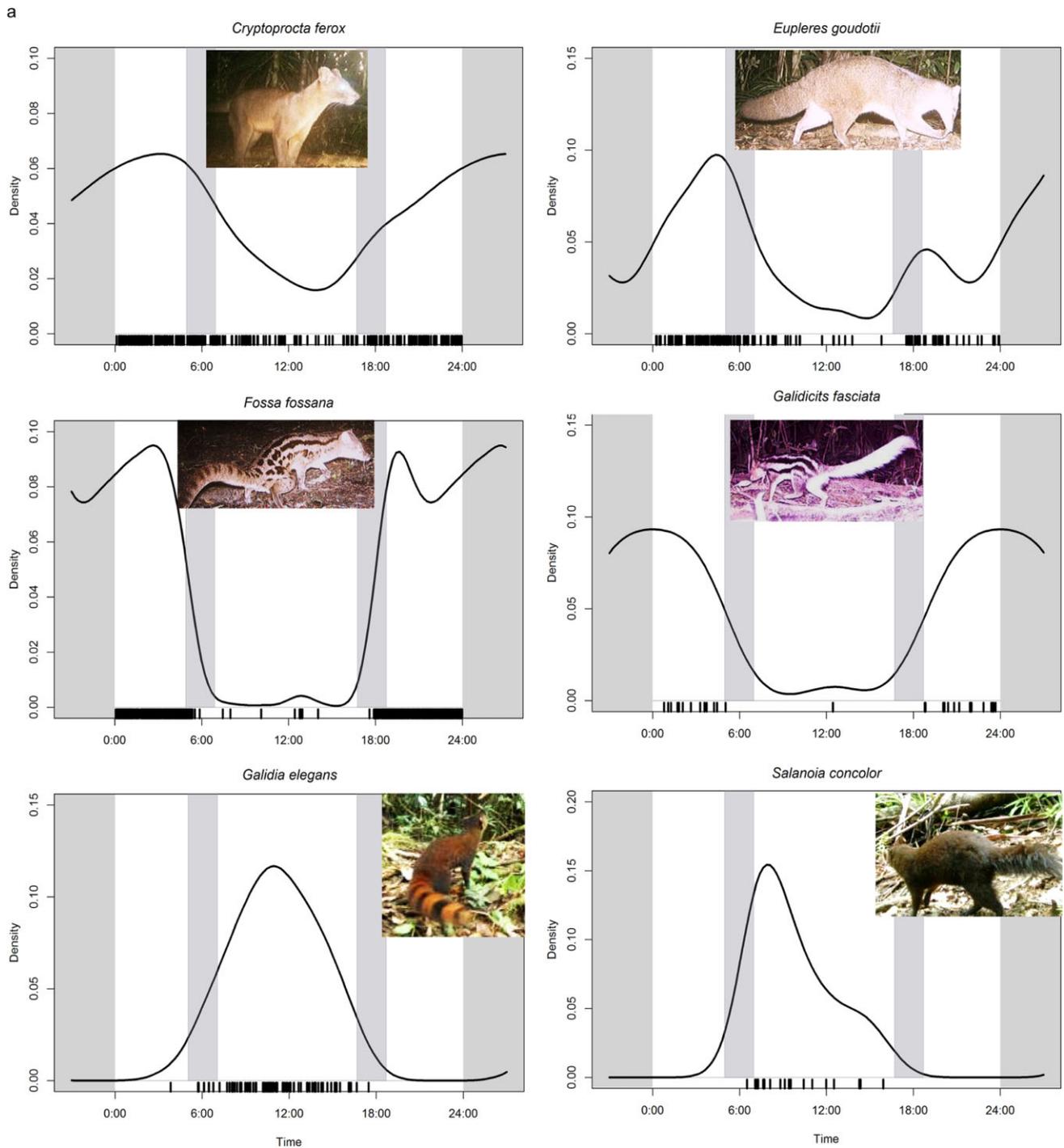


Figure 2 Temporal activity patterns resulting from Poisson regression analysis including the number of photographic captures (black bars on x-axis) across diel cycle (dawn and dusk in gray bars; day and night in white) plotted by the density of temporal activity (y-axis), where higher density represents increased activity, for (a) six native and (b) three exotic carnivores across the Masoala-Makira landscape. Photographic sampling occurred from 2008 to 2013.

Despite the null model being highest ranking for three carnivore species, we still found striking trends for these carnivores in activity patterns across season and/or site, with moderate model weights suggesting some support (Appen-

dix S3). For example, during the hot-dry season we found *Ca. familiaris* greatly diminished activity during midday and increased crepuscular activity (Fig. 3d) while *Cr. ferox* exhibited a decrease in nocturnal activity and a slight increase in

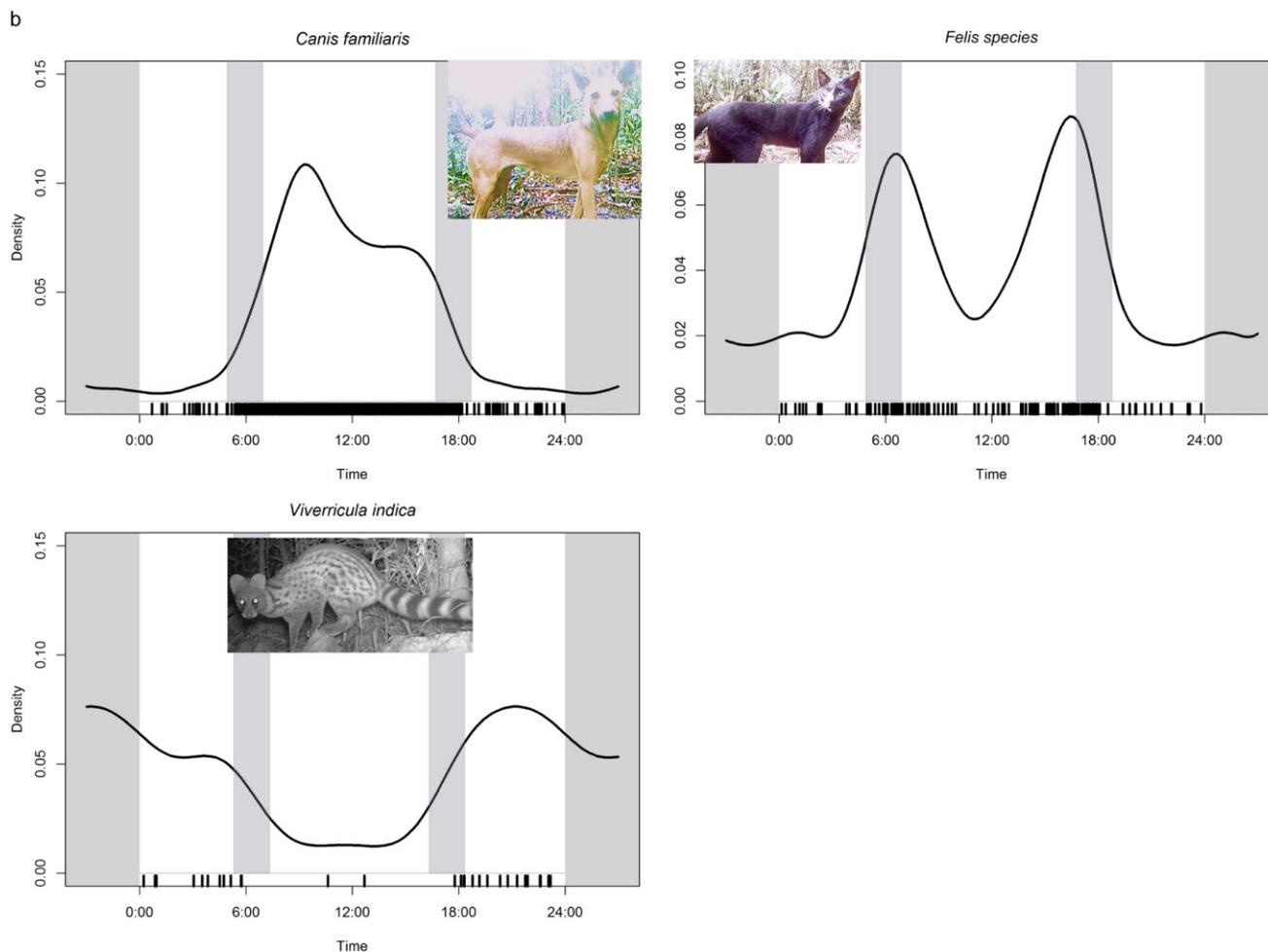


Figure 2 Continued

activity during dusk hours (Fig. 3e). This altering of activity during the hot-dry season for *Cr. ferox* occurred during their breeding season (October to December). During the hot-dry season *E. goudotii* showed more variable activity across all four time periods rather than the strong peaks in crepuscular activity during the cool-wet (Fig. 3f).

We found evidence of native carnivores shifting their temporal activity patterns in the presence of exotic carnivores. The shift in *F. fossana* activity during the hot seasons occurred at study sites S02 and S05 where human and *Ca. familiaris* activity was very high (Fig. 3c; Appendix S2). Additionally, *Cr. ferox* exhibited nocturnal activity where humans and similar-sized *Ca. familiaris* were highly active (study site S07), and diurnal activity where they were rare (study site S02). We found no *S. concolor* at study sites having very high captures rates of *Ca. familiaris*, which exhibits strong temporal overlap with this rare native carnivore ($\hat{\Delta}_1 = 0.88$; Table 4). *Felis* sp. showed exclusively crepuscular and almost no nocturnal activity at study site S06 where co-occurring carnivore occupancy

and activity was very low and small mammal activity was high (Farris, 2014; Appendix S2).

Carnivore body size and niche requirements were not strong predictors of temporal overlap among carnivore pairings (Table 4). The average degree of overlap among all carnivore pairings was $\hat{\Delta}_1 = 0.57 \pm \text{SD } 0.23$ (median = 0.61). We observed a high degree of overlap in activity patterns between numerous carnivore pairings. In particular, the small-bodied diurnal *Galidia elegans* and *S. concolor* demonstrated the greatest overlap among native carnivores ($\hat{\Delta}_1 = 0.91$; Table 4; Fig. 4a), but limited overlap with the similar-sized nocturnal *Galidic. fasciata* ($\hat{\Delta}_1 = 0.21$ and $\hat{\Delta}_1 = 0.19$, respectively; Fig. 4b,c). The ecological niche requirements and diet of *Galidic. fasciata* and *S. concolor* appear very similar but show strong divergence with *Galidia elegans* (Table 1). Further, *Cr. ferox* and *E. goudotii*, which show night-day and night-dawn activity (respectively) have considerable overlap in activity ($\hat{\Delta}_1 = 0.86$; Table 4); however, these two native carnivores demonstrate strong differences in body size, diet and habitat preference (Table 1). The similar-sized *E. goudotii* and

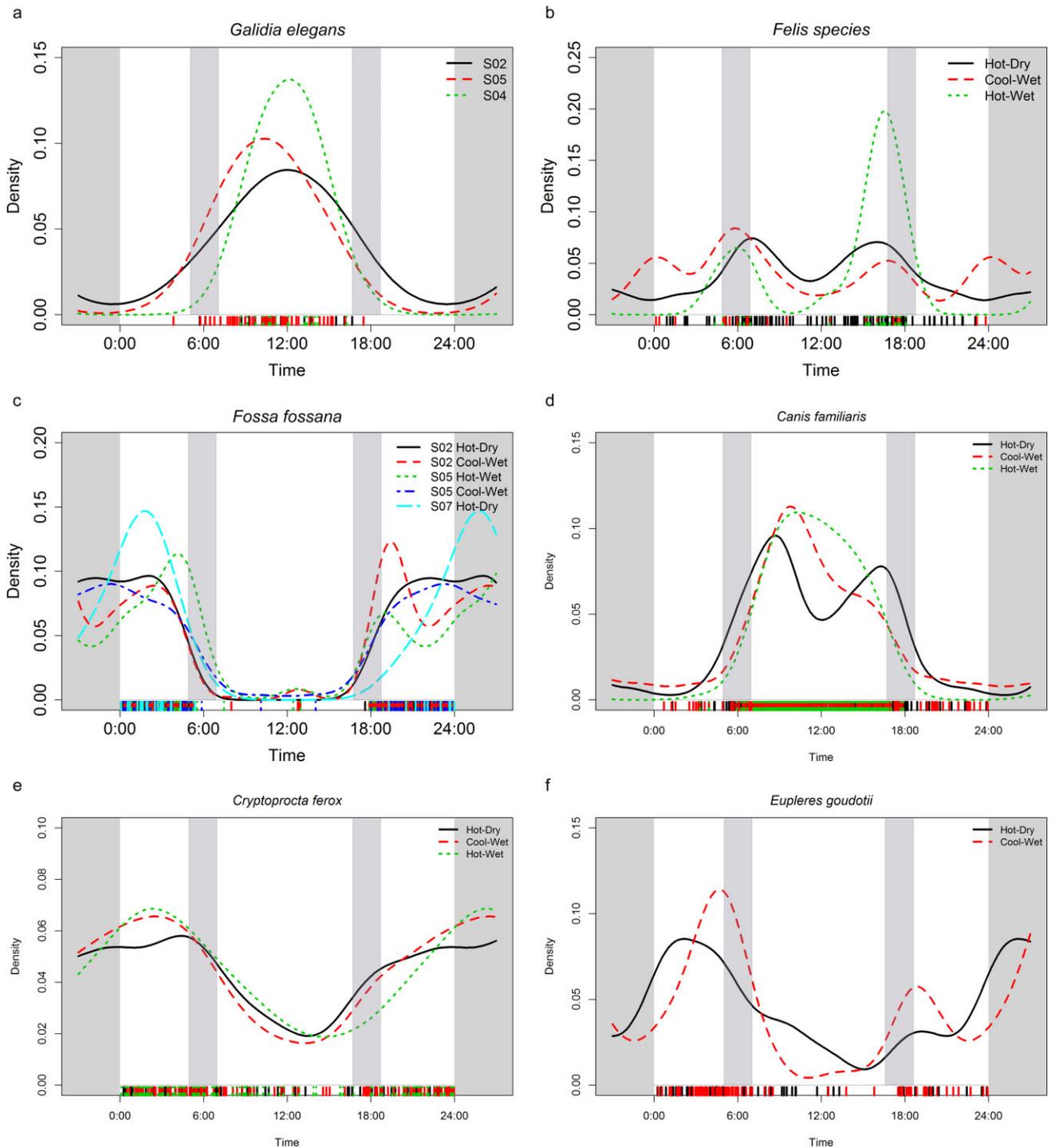


Figure 3 Temporal activity patterns revealed by number of photographic captures across diel cycle (x-axis) plotted by density of temporal activity (y-axis) for (a) *Galidia elegans* across study sites 02, 04 and 05; (b) *Felis species* across three seasons (hot-dry, hot-wet and cool-wet); (c) *Fossa fossana* across five site and season combinations; (d) *Canis familiaris* across three seasons; (e) *Cryptoprocta ferox* across three seasons; and (f) *Eupleres goudotii* across two seasons (hot-dry and cool-wet). Activity patterns for *Galidia elegans*, *Felis sp.* and *F. fossana* represent the highest ranking model from the kernel density estimation. We did not estimate activity patterns for target carnivore species at individual study sites and seasons having fewer than 15 captures.

Table 4 Temporal overlap, based on $\hat{\Delta}_1$ estimates from kernel density analyses, among native and exotic (bold) carnivore pairings with similarities (+) and differences (–) in niche (habitat use and diet) and body size listed from highest to lowest amount of temporal overlap

Species 1	Species 2	Niche	Body size	$\hat{\Delta}_1$
<i>Salanoia concolor</i>	<i>Galidia elegans</i>	–	+	0.91
<i>S. concolor</i>	<i>Canis familiaris</i>	–	–	0.88
<i>Galidia elegans</i>	<i>Ca. familiaris</i>	+	–	0.87
<i>Eupleres goudotii</i>	<i>Cryptoprocta ferox</i>	–	–	0.86
<i>Galidictis fasciata</i>	<i>Viverricula indica</i>	–	–	0.83
<i>Cr. ferox</i>	<i>V. indica</i>	–	–	0.82
<i>Fossa fossana</i>	<i>V. indica</i>	–	+	0.80
<i>Cr. ferox</i>	<i>Galidic. fasciata</i>	–	–	0.76
<i>Eupleres goudotii</i>	<i>V. indica</i>	–	+	0.74
<i>Eupleres goudotii</i>	<i>Galidic. fasciata</i>	–	–	0.72
<i>F. fossana</i>	<i>Cr. ferox</i>	–	–	0.70
<i>Eupleres goudotii</i>	<i>F. fossana</i>	+	+	0.68
<i>Felis species</i>	<i>Ca. familiaris</i>	+	+	0.67
<i>Cr. ferox</i>	<i>Felis species</i>	–	+	0.65
<i>Eupleres goudotii</i>	<i>Felis species</i>	–	–	0.63
<i>S. concolor</i>	<i>Felis species</i>	–	–	0.61
<i>Galidia elegans</i>	<i>Felis species</i>	+	–	0.56
<i>Felis species</i>	<i>V. indica</i>	+	–	0.56
<i>Cr. ferox</i>	<i>Ca. familiaris</i>	–	+	0.44
<i>Galidic. fasciata</i>	<i>Felis species</i>	–	–	0.42
<i>Cr. ferox</i>	<i>Galidia elegans</i>	–	–	0.42
<i>Cr. ferox</i>	<i>S. concolor</i>	–	–	0.41
<i>Eupleres goudotii</i>	<i>Ca. familiaris</i>	–	–	0.39
<i>Eupleres goudotii</i>	<i>Galidia elegans</i>	–	–	0.37
<i>Eupleres goudotii</i>	<i>S. concolor</i>	–	–	0.36
<i>Ca. familiaris</i>	<i>V. indica</i>	+	–	0.33
<i>S. concolor</i>	<i>V. indica</i>	–	–	0.29
<i>Galidia elegans</i>	<i>V. indica</i>	+	–	0.23
<i>Galidic. fasciata</i>	<i>Ca. familiaris</i>	–	–	0.23
<i>Galidia elegans</i>	<i>Galidic. fasciata</i>	–	+	0.21
<i>S. concolor</i>	<i>Galidic. fasciata</i>	+	+	0.19

Photographic sampling for kernel density estimation took place from 2008 to 2013.

F. fossana, which also show great overlap in body size and habitat preference (Table 1), have only moderate overlap in activity ($\hat{\Delta}_1 = 0.67$; Table 4).

Among native–exotic pairings, the diurnal native carnivores *Galidia elegans* and *S. concolor* have high overlap with larger bodied *Ca. familiaris* ($\hat{\Delta}_1 = 0.87$ and $\hat{\Delta}_1 = 0.88$, respectively; Table 4; Fig. 5a,b) and moderate overlap with *Felis* sp. ($\hat{\Delta}_1 = 0.56$ and $\hat{\Delta}_1 = 0.61$, respectively; Table 4). There is high overlap in niche requirements between *Galidia elegans* and these two exotic carnivores (Table 1). Moreover, the nocturnal *E. goudotii* and *F. fossana* demonstrate high overlap in activity with the similar sized, exotic *V. indica* ($\hat{\Delta}_1 = 0.74$ and $\hat{\Delta}_1 = 0.80$, respectively; Table 4; Fig. 5c); however, there is substantial divergence in niche requirements between these two native carnivores and the exotic *V. indica* (Table 1). *Cryptoprocta ferox* was most similar in body size to the three exotic carnivores and showed high overlap with *V. indica* ($\hat{\Delta}_1 = 0.82$; Fig. 5d), moderate overlap with *Felis* sp. ($\hat{\Delta}_1 = 0.65$) and little overlap with *Ca. familiaris* ($\hat{\Delta}_1 = 0.44$;

Table 4). However, the niche requirements and diet of *Cr. ferox* are quite different from the three exotic carnivores (Table 1). Finally, among the exotic carnivores the medium-sized, nocturnal *V. indica* showed the greatest number of overlapping relationships with native carnivores (Table 4).

Discussion

Quantifying activity patterns

Our findings regarding native carnivore activity patterns across the Masoala-Makira landscape are congruent with Gerber *et al.* (2012a) from RNP for most of the carnivore species. However, important differences exist, including the primarily crepuscular activity of *E. goudotii* in this study compared with the strictly nocturnal activity from RNP (Gerber *et al.*, 2012a). In addition, *Ca. familiaris* appear to be strictly diurnal across our seven study sites compared with the highly variable activity found at RNP. The widespread negative impacts of *Ca. familiaris* have been documented worldwide (Gompper, 2013) and their activity may vary based on a host of variables, particularly the activity of humans. Variation in activity across seasons, which was not investigated by Gerber *et al.* (2012a), may provide an explanation for this discrepancy in activity patterns for these carnivore species. Finally, the highly variable activity of *Cr. ferox*, the largest native species including its activity across all four time periods (dawn, day, dusk and night), provides evidence of their generalist behavior. This finding, along with their differences in diet from co-occurring carnivores, and their ability to climb and use the forest canopy provides evidence of limited niche overlap among *Cr. ferox* and co-occurring carnivore species.

Influence of season and site on activity patterns

We found mixed results relative to our first hypothesis that native and exotic carnivores will show variation in temporal activity across seasons. In particular, we found that *Cr. ferox* may increase dusk activity during their mating season (hot–dry season). Their noisy, conspicuous and localized mating behavior is likely to influence activity patterns during this period, particularly among males who travel long distances and sometimes fight over females (Goodman, 2012). We also found seasonal influences on activity for *E. goudotii* and *F. fossana*, which both exhibited increased nocturnal activity during the hot–dry season compared with the cool–wet season. We observed this change in activity across seasons for both carnivores at study site S02, one of our repeated survey sites, which signifies that this slight shift in activity likely results from seasonal change alone. However, we have observed a substantial increase in *Felis* sp. occupancy from 2008 to 2013 at this study site (Farris, unpubl. data) and this may be influencing native carnivore activity at this study site. For *F. fossana* this change in activity, particularly at study site S07, may also be influenced by increased human and *Ca. familiaris* activity. Additionally, we observed similar

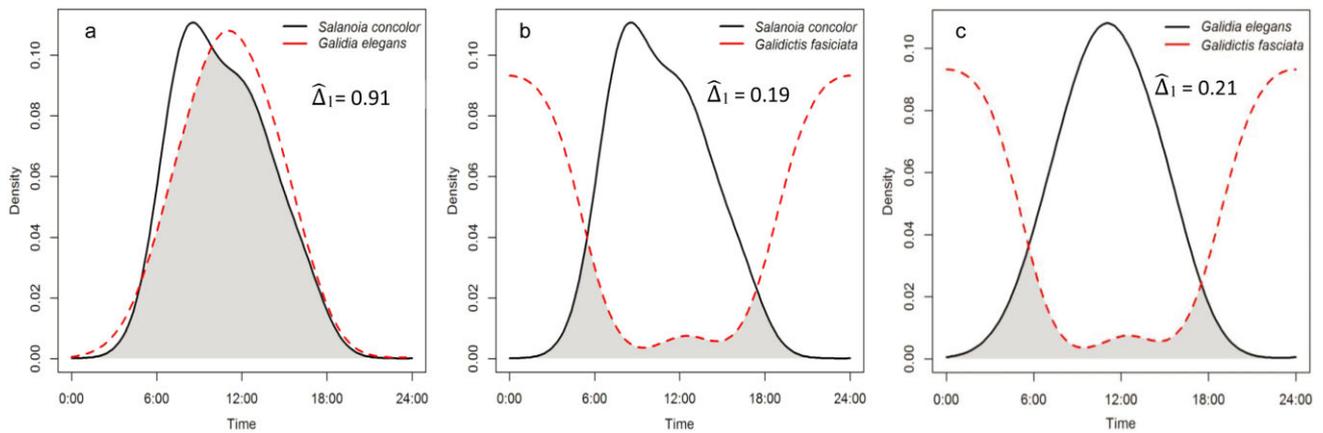


Figure 4 Level of overlap measured by $\hat{\Delta}_1$ estimate and shaded in gray for activity patterns, resulting from number of photographic captures across diel cycle (x-axis) plotted by density of temporal activity (y-axis), for the similar small-bodied vantsira carnivores measured by $\hat{\Delta}_1$ estimate based on kernel density estimates between (a) *S. concolor* and *Galidia elegans*; (b) *S. concolor* and *Galidictis fasciata*; and (c) *Galidia elegans* and *Galidictis fasciata*.

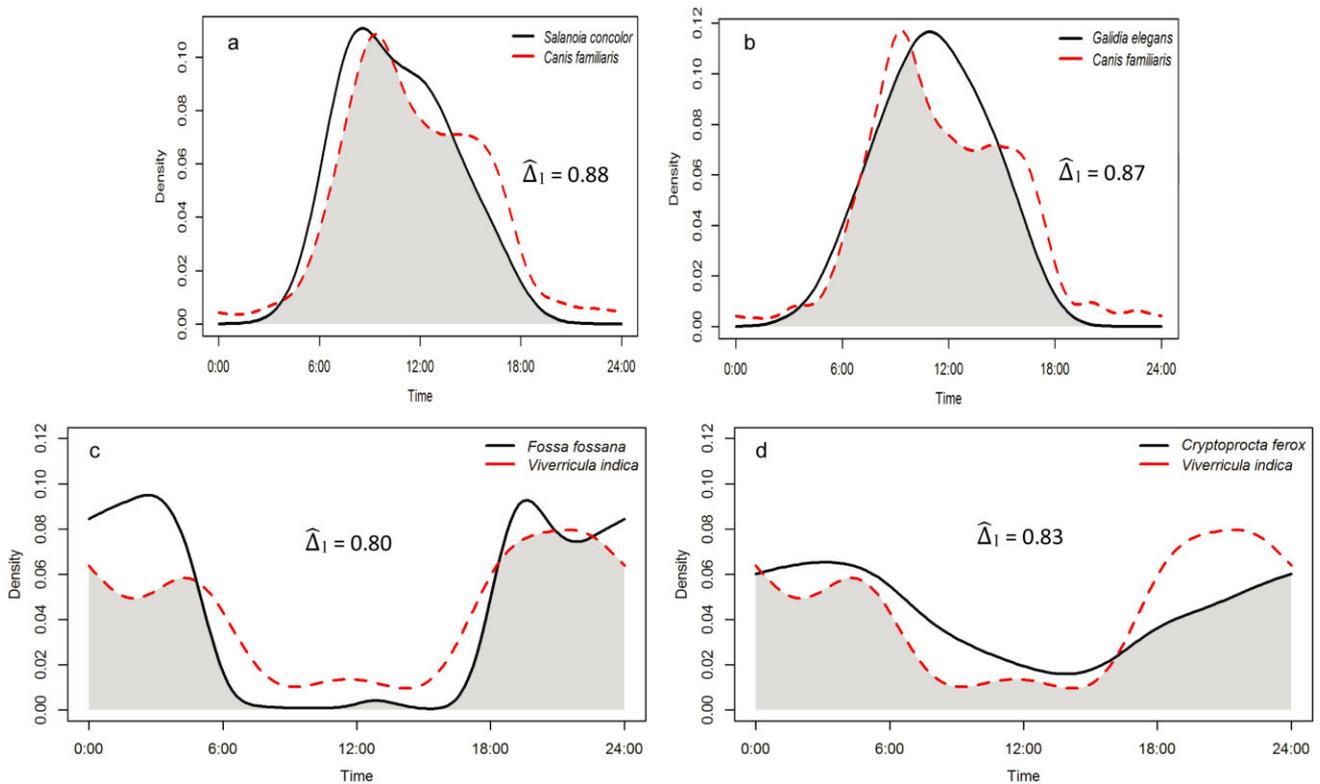


Figure 5 Level of overlap, measured by $\hat{\Delta}_1$ estimate and shaded in gray, for activity patterns of native and exotic carnivores resulting from number of photographic captures across diel cycle (x-axis) plotted by density of temporal activity (y-axis), including (a) *S. concolor* and *Ca. familiaris*; (b) *Galidia elegans* and *Ca. familiaris*; (c) *F. fossana* and *V. indica*; (d) *Cr. ferox* and *V. indica*.

seasonal changes in activity patterns for exotic carnivores. Both *Ca. familiaris* and *Felis* sp. showed slight changes in activity during the hot-dry and hot-wet seasons, respectively. In the case of *Ca. familiaris*, the strong decrease in activity during midday hours during the hot-dry season likely result

from the strong correlation with human activity/captures, given that most humans were not active during the hottest part of the day during this season. The shift in activity for *Felis* sp. during the hot-wet season is believed to result from seasonal change, rather than co-occurring species, given repeated

surveys of site S05 over different seasons show great variation in activity patterns.

We found some support for our second hypothesis that native carnivores alter their activity patterns at sites where exotic carnivore activity is high. The highest overlap between native and exotic carnivores occurred between *Galidia elegans* and *S. concolor* with *Ca. familiaris*. This overlap between *S. concolor* and *Ca. familiaris* may explain the absence of *S. concolor* from study sites S03, S04 and S05, where suitable low elevation rainforest habitat occurs but *Ca. familiaris* occupancy was extremely high. Despite the high temporal overlap between the two carnivores, we found little support for the effect of *Ca. familiaris* on the variation in *Galidia elegans* activity across study sites, as was observed at RNP (Gerber *et al.*, 2012a). Activity of *Cr. ferox* appears to be influenced by human and *Ca. familiaris* activity. *Cryptoprocta ferox* demonstrated more nocturnal activity at sites having exceptionally high human and *Ca. familiaris* activity (study sites S04, S05 and S07), while they exhibited more diurnal activity at sites where human activity was low (study site S02; Appendix S2) regardless of season. We were unable to determine any difference in *Cr. ferox* response toward humans versus *Ca. familiaris* because captures of humans and *Ca. familiaris* were highly correlated (Farris, 2014); however, the negative impacts of *Ca. familiaris* on native wildlife are likely to diminish if local people did not bring *Ca. familiaris* with them into the forest.

The decrease in *E. goudotii* dusk activity from the hot-dry season and nocturnal activity during the cool-wet season may result from interactions with exotic carnivores as *Ca. familiaris* showed more dusk activity during the hot-dry season and *Felis* sp. showed more nocturnal activity during the cool-wet season. Recent research has demonstrated that increases in habitat degradation and fragmentation in Madagascar have resulted in decreases in native carnivore occupancy and density as well as increases in exotic carnivore occupancy (Gerber *et al.*, 2012b; Farris, 2014), and habitat alteration is likely resulting in increased temporal overlap among native and exotic carnivores.

Overlap of temporal activity

Our findings reveal strong temporal overlap among carnivores (both native and exotic); however, we did not find support for our third hypothesis that body size and niche requirements (habitat use and diet) are strong predictors of temporal overlap, as has been found in other studies of co-occurring carnivores (Sunarto *et al.*, in press). The ecological niche of these carnivores likely encompasses more dimensions than we are currently familiar with (Goodman, 2012) or were able to investigate, thus including additional niche dimensions in future analyses may explain temporal overlap patterns among these carnivores. The strongest temporal overlap for any species combination within this study occurred between the small-bodied, diurnal *Galidia elegans* and *S. concolor*, although both had little overlap with the sympatric, nocturnal *Galidic. fasciata*. This study represents the first quantitative comparison of the three sympatric, smaller bodied vantsira

species (*Galidia elegans*, *S. concolor* and *Galidic. fasciata*) including the first study, to our knowledge, to confirm the co-existence of these three native carnivore species (Farris *et al.*, 2012). We suggest the sympatric relationship among the three vantsira carnivores results from the division of the temporal niche (nocturnal activity by *Galidic. fasciata* and diurnal activity by both *Galidia elegans* and *S. concolor*) and the habitat selection and potential dietary differences between *Galidia elegans* and *S. concolor* (Goodman, 2012). We found that while *Galidia elegans* and *S. concolor* co-occurred at study sites S02 and S07, they rarely were captured at the same camera stations within those survey sites. These two native vantsira carnivores are sympatric in general distribution but do not appear to be at the micro-habitat level. Further, we also observed temporal overlap for the crepuscular *Cr. ferox* and *E. goudotii* and the nocturnal *F. fossana* and *Galidic. fasciata*. We suggest the limited temporal overlap in activity and segregation in diet between the medium body-sized native carnivores *F. fossana* and *E. goudotii* allows for their sympatric co-occurrence across eastern rainforest habitat.

This study represents the first investigation of carnivore seasonal activity patterns in Madagascar, including both effects of season and exotic carnivore activity on native carnivore temporal activity patterns. We also provide additional evidence of the burgeoning threat posed to Madagascar's native carnivores, believed to be the world's least studied and most threatened family of Carnivora (Brooke *et al.*, 2014), from the influx of exotic carnivores across eastern rainforest habitat.

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References

- Agostinelli, C. & Lund, U. (2013). Circular: circular statistics, 2013. <http://CRAN.R-project.org/package=circular>. R package version 0.4-7.

- Akaike, H. (1973). *Information theory and an extension of the maximum likelihood principle*. In Second international symposium on information theory: 267–281. Budapest: Akademiai Kiado.
- Albignac, R. (1972). The carnivora of Madagascar. In *Biogeography and ecology in Madagascar*: 667–682. Battistini, R. & Richard-Vindard, G. (Eds). the Netherlands: Springer.
- Britt, A. & Virkaitis, V. (2003). Brown-tailed mongoose *Salanoia concolor* in the Betampona Reserve, eastern Madagascar: photographs and an ecological comparison with ring-tailed mongoose *Galidia elegans*. *Sm. Carniv. Cons.* **28**, 1–3.
- Brooke, Z.M., Bielby, J., Nambiar, K. & Carbone, C. (2014). Correlates of research effort in carnivores: body size, range size and diet matter. *PLoS ONE* **9**, e93195.
- Clout, M.N. & Russell, J.C. (2008). The invasion ecology of mammals: a global perspective. *Wildl. Res.* **35**, 180–184.
- Clutton-Brock, T. & Harvey, P.H. (1978). Mammals, resources and reproductive strategies. *Nature* **273**, 191–195.
- Di Bitetti, M., Paviolo, A. & De Angelo, C. (2006). Density, habitat use and activity patterns of ocelots (*Leopardus pardalis*) in the Atlantic forest of Misiones, Argentina. *J. Zool. (Lond.)* **270**, 153–163.
- Dollar, L. (1999). Preliminary report on the status, activity cycle, and ranging of *Cryptoprocta ferox* in the Malagasy rainforest, with implications for conservation. *Sm. Carniv. Cons.* **20**, 7–10.
- Farris, Z.J. (2014). *Response of Madagascar's endemic carnivores to fragmentation, hunting, and exotic carnivores across Masoala-Makira landscape*. Blacksburg: Virginia Polytechnic Institute and State University.
- Farris, Z., Kelly, M.J., Karpanty, S.M., Ratelolahy, F., Andrianjakarivelo, V. & Holmes, C. (2012). Brown-tailed vontsira *Salanoia concolor* (Eupleridae) documented in Makira Natural Park, Madagascar: new insights on distribution and camera-trap success. *Sm. Carniv. Cons.* **47**, 82–86.
- Farris, Z.J., Karpanty, S.M., Ratelolahy, F. & Kelly, M.J. (2014). Predator-primate distribution, activity, and co-occurrence in relation to habitat and human activity across fragmented and contiguous forests in northeastern Madagascar. *Int. J. Primatol.* **35**, 859–880.
- Fisher, N. & Lee, A. (1992). Regression models for an angular response. *Biometrics* **48**, 665–677.
- Gerber, B.D., Karpanty, S.M. & Randrianantenaina, J. (2012a). Activity patterns of carnivores in the rain forests of Madagascar: implications for species coexistence. *J. Mammal.* **93**, 667–676.
- Gerber, B.D., Karpanty, S.M. & Randrianantenaina, J. (2012b). The impact of forest logging and fragmentation on carnivore species composition, density and occupancy in Madagascar's rainforests. *Oryx* **46**, 414–422.
- Golden, C.D. (2009). Bushmeat hunting and use in the Makira forest, north-eastern Madagascar: a conservation and livelihoods issue. *Oryx* **43**, 386.
- Gompper, M.E. (2013). *Free-ranging dogs and wildlife conservation*. Oxford and New York: Oxford University Press.
- Goodman, S. (2003a). Carnivora: *Galidia elegans*, ring-tailed mongoose, vontsira mena. In *The Natural History of Madagascar*: 1351–1354. Goodman, S. & Benstead, J.P. (Eds). Chicago: The University of Chicago Press.
- Goodman, S. (2003b). Carnivora: *Galidictis fasciata*, broad-striped mongoose, vontsira fotsy. In *The Natural History of Madagascar*: 1354–1357. Goodman S. & Benstead J.P. (Eds). Chicago: The University of Chicago Press.
- Goodman, S.M. (2012). *Les carnivora de Madagascar*. Antananarivo: Association Vahatra.
- Hawkins, C.E. (1998). Behaviour and ecology of the fossa, *Cryptoprocta ferox* (Carnivora: Viverridae) in a dry deciduous forest, western Madagascar. Aberdeen: University of Aberdeen.
- IUCN (2014). The IUCN red list of threatened species version 2014.1. <http://www.iucnredlist.org>.
- Kavanau, J.L. & Ramos, J. (1975). Influences of light on activity and phasing of carnivores. *Am. Nat.* **109**, 391–418.
- Kremen, C. (2003). The Masoala peninsula. In *The natural history of Madagascar*: 1459–1466. Goodman, S.M. & Benstead, J.P. (Eds). Chicago: University of Chicago Press.
- Kronfeld-Schor, N. & Dayan, T. (2003). Partitioning of time as an ecological resource. *Annu. Rev. Ecol. Evol. Syst.* **34**, 153–181.
- Pianka, E.R. (1973). The structure of lizard communities. *Annu. Rev. Ecol. Syst.* **4**, 53–74.
- Ridout, M.S. & Linkie, M. (2009). Estimating overlap of daily activity patterns from camera trap data. *J. Agric. Biol. Environ. Stat.* **14**, 322–337.
- Salo, P., Korpimäki, E., Banks, P.B., Nordström, M. & Dickman, C.R. (2007). Alien predators are more dangerous than native predators to prey populations. *Proc. Roy. Soc. Lond. Ser. B.* **274**, 1237–1243.
- Santos, G.M.D.M. & Presley, S.J. (2010). Niche overlap and temporal activity patterns of social wasps (hymenoptera: Vespidae) in a Brazilian cashew orchard. *Sociobiology* **56**, 121–131.
- Sterling, E.J. (1993). *Behavioral ecology of the aye-aye (Daubentonia madagascariensis) on Nosy Mangabe, Madagascar*. New Haven: Yale University.
- Su, S. & Sale, J. (2007). Niche differentiation between common palm civet *Paradoxurus hermaphroditus* and small Indian civet *Viverricula indica* in regeneration degraded forest, Myanmar. *Sm. Carniv. Cons.* **36**, 30–34.
- Sunarto, S., Kelly, M.J., Parakkasi, K. & Hutajulu, M.B. (in press). Felid coexistence in central Sumatra: ecological characteristics, spatial and temporal overlap, and implications for management. *J. Zool. (Lond.)* ••, ••–••.
- Tecot, S.R. (2007). *Seasonality and predictability: the hormonal and behavioral responses of the red-bellied lemur, Eulemur rubriventer, in southeastern Madagascar*. Ann Arbor: ProQuest.

Vanak, A.T. & Gompper, M.E. (2010). Interference competition at the landscape level: the effect of free-ranging dogs on a native mesocarnivore. *J. Appl. Ecol.* **47**, 1225–1232.

Yoder, A.D., Burns, M.M., Zehr, S., Delefosse, T., Veron, G., Goodman, S.M. & Flynn, J.J. (2003). Single origin of Malagasy Carnivora from an African ancestor. *Nature* **421**, 734–737.

Supporting Information

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

Appendix S1. Photographic captures of the six native (endemic), from largest to smallest body size, and three exotic (in bold) carnivore species captured during our surveys from 2008 to 2013 across the Masoala-Makira landscape, Madagascar, including (A) fosa *Cryptoprocta ferox*; (B) falanouc

Eupleres goudotii; (C) spotted fanaloka *Fossa fossana*; (D) ring-tail vontsira *Galidia elegans*; (E) broad-stripe vontsira *Galidictis fasciata*; (F) brown-tail vontsira *Salanoia concolor*; (G) **domestic dog** *Canis familiaris*; (H) **feral cat** *Felis species*; and (I) **Indian civet** *Viverricula indica*.

Appendix S2. Survey details for the seven study sites (camera trapping grids), ranked from least degraded (S01) to most degraded (S07), across the Masoala-Makira landscape, including the trap success and standard error (TS, SE) for each of the six endemic and three exotic carnivore species.

Appendix S3. Kernel density estimation model results including AIC value, delta AIC, model likelihood, AIC weight and number of parameters (K). Species *Galidictis fasciata*, *S. concolor* and *V. indica* had <15 captures for all study sites which excluded them from analysis. Photographic sampling for kernel density estimation took place across seven study sites (Site) and three seasons (Season) from 2008 to 2013.