

Activity patterns of carnivores in the rain forests of Madagascar: implications for species coexistence

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Temporal partitioning of activity among sympatric species can be an important mechanism for species coexistence. Further, if exotic and native species overlap temporally, there is potential for direct competition and antagonism, which may lead to native species extirpation. We first assessed if ecologically similar native carnivores of Madagascar demonstrated activity pattern overlap and then explored whether overlap in activity might lead to negative impacts of exotic carnivores on native carnivores. We used photographic sampling to quantify the temporal activity patterns of carnivores at 4 study sites. The activity of the 2 smaller-bodied native species, *Galidia elegans* and *Galidictis fasciata*, overlapped minimally; these 2 carnivores share a similar generalist diet, which may drive their divergent temporal activity. In contrast, the medium-sized native species, *Fossa fossana* and *Eupleres goudotii*, were both highly nocturnal; these 2 species appear segregated in their diets. The largest native carnivore, *Cryptoprocta ferox*, selectively used crepuscular hours, but overall was cathemeral; it was notably absent or basically so at sites where dogs were most abundant and active throughout the diel cycle. We found *G. elegans* to shift from preferred activity periods in the presence of dogs and the exotic *Viverricula indica*. Our results suggest that the presence and activity of exotic carnivores can negatively impact native carnivores in fragmented rain forests.

Key words: activity pattern, carnivore, cathemeral activity, *Cryptoprocta ferox*, Eupleridae, Madagascar, niche, predation risk

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How an animal uses time and distributes its activity within the diel cycle is an important niche dimension (Norris et al. 2010; Pianka 1973). Animals may reduce intraguild competition and predation risk, and thus increase niche segregation, by minimizing temporal overlap with similar species (Kronfeld-Schor and Dayan 2003). Carnivores are no exception. Temporal niche segregation by ecologically similar carnivores has been demonstrated in diverse systems (Chen et al. 2009; Di Bitetti et al. 2009; Hayward and Slotow 2009; Lucherini et al. 2009).

Activity patterns of native carnivores of Madagascar have been described only anecdotally and never quantified (Albignac 1972; Dollar 1999a, 1999b; Hawkins 1998). Of the 10 extant carnivore species within the endemic family Eupleridae (Durbin et al. 2010; Goodman and Helgen 2010; Yoder et al. 2003), all are listed on the *IUCN Red List* (International Union for the Conservation of Nature and Natural Resources 2011) and 5 occupy the central-eastern rain forests (in descending body size: fossa [*Cryptoprocta ferox*], small-toothed civet [*Eupleres goudotii*], Malagasy civet [*Fossa fossana*], ring-tailed mongoose [*Galidia elegans*], and broad-striped mongoose [*Galidictis fasciata*])—Gerber et al. 2010; International Union

for the Conservation of Nature and Natural Resources 2011). The activity patterns of *C. ferox* and *G. elegans* are of particular conservation importance, because both species are predators of lemurs (Colquhoun 2006; Karpanty and Wright 2007), many of which are also listed by the International Union for the Conservation of Nature and Natural Resources, and *C. ferox* has extirpated lemurs from continuous and from fragmented rain forests (Irwin et al. 2009). Malagasy carnivore species are all monophyletic; they diverged from a single colonization event approximately 18–24 million years ago (Yoder et al. 2003).

Because the native carnivores of Madagascar's rain forests are sympatric at protected sites that experience minimal human use (Gerber et al., in press), temporal activity separation may be one possible mechanism behind the coexistence of species that may otherwise affect each other via predation or competition. We expect that a high degree of overlap in 1 niche dimension that might lead to interference or exploitative competition, or even intraguild predation, should be associated with a low



degree of overlap in other niche dimensions for coexisting species (Schoener 1974). Because similar-sized carnivores often have high dietary overlap, it is informative to explore patterns of temporal niche separation by comparing similar-body-sized carnivores (Donadio and Buskirk 2006; Woodward and Hildrew 2002). Our 1st objective was to assess if ecologically similar native carnivores demonstrated temporal segregation. All Malagasy carnivore species are thought to be generalist predators, except for the 2nd largest native species, *E. goudotii*, which is thought to specialize on earthworms and insects (Albignac 1974; Hawkins 1994). We predicted that the generalist native species would temporally segregate from those species closest in body size to minimize competition.

Dramatic loss and fragmentation of Madagascar's forests over the last 50 years (Harper et al. 2007) has facilitated the introduction of exotic carnivores, which may negatively impact native carnivores. Madagascar's altered forests have lower diversity and density of native carnivores and increased diversity and density of exotic carnivores (domestic dog [*Canis familiaris*], feral and exotic cats [*Felis catus* and *Felis silvestris*], and small Indian civet [*Viverricula indica*])—Gerber et al., in press). Competitive or predatory interactions between native and exotic carnivores may lead to extirpations, altered activity patterns, or changes in resource use (Mitchell and Banks 2005). The introduction of exotic carnivores that are ecologically similar to native carnivores also may alter dynamics of predation and competition between native carnivores, especially if there is temporal overlap between native and exotic carnivores that results in temporal or spatial shifts in the native species (Hunter and Caro 2008; Palomares and Caro 1999; Phillips et al. 2007; Vanak and Gompfer 2010). Interactions between native and exotic carnivores in Madagascar have not yet been explored beyond documenting coexistence of native and exotic species in areas degraded by various human activities such as logging (Gerber et al., in press). Our 2nd objective was to explore activity pattern overlap between native and exotic carnivores to assess potential negative impacts of exotic carnivores on native carnivores.

MATERIALS AND METHODS

Study area.—We worked in the eastern rain forests of Madagascar at 4 study sites; 2 sites were part of and 2 sites were disconnected from the larger continuous rain-forest corridor along the east coast of Madagascar (Fig. 1). We expected that the 4 sites might vary in the presence of native and exotic carnivores. These 4 sites were selected as part of an ongoing study of carnivore and lemur ecology in continuous versus fragmented rain forests (Gerber et al. 2010, 2011, in press; Kotschwar 2010). We sampled 2 sites located in the continuous eastern rain-forest corridor in Ranomafana National Park: Valohoaka-Vatoharanana (5.28-km² sample grid; elevation 753–1,205 m) and Sahamalaotra (6.53-km² sample grid; elevation 1,056–1,161 m). We sampled 2 sites that were fragments and thus disconnected from the continuous eastern

forest corridor: Tsinjoarivo (6.72-km² sample grid; elevation 1,469–1,643 m) and Ialatsara Forest Station (6.22-km² sample grid; elevation 1,308–1,563 m).

Other than the presence of *C. familiaris* from nearby villages, the Valohoaka-Vatoharanana site had minimal present or past human use (Wright 1997). The Sahamalaotra site had both a lower basal area of trees and lower tree density than Valohoaka-Vatoharanana due to selective logging before Ranomafana National Park was established in 1991 (Razafimahaimodison 2004); however, both were still closed-canopy forests (Gerber et al., in press). The Tsinjoarivo site was 150 km north of Ranomafana National Park; the sample grid was placed within a group of 28 rain-forest fragments ranging in size from 7 to 192 ha that were in close proximity to each other yet separate from the continuous rain-forest corridor. The Ialatsara Forest Station site was 15 km northwest of Ranomafana National Park; the sample grid was placed across a group of 10 rain-forest fragments ranging in size from 2 to 240 ha. Forest structure was similar between the Tsinjoarivo and Ialatsara Forest Station, but was much altered compared to the other 2 sites in Ranomafana National Park, with reduced basal area of trees and a more open canopy cover (Gerber et al., in press). At both Tsinjoarivo and Ialatsara Forest Station, fragments were surrounded by a matrix of shrub, nonvegetated areas that had been recently slashed and burned, exotic trees (e.g., *Pinus* sp. or *Eucalyptus* sp.), and agriculture. Local people used Tsinjoarivo and Ialatsara Forest Station for travel and forest products, but only in Tsinjoarivo did people live between the forest fragments.

Sampling took place over 2 years (2008–2009). Valohoaka-Vatoharanana and Sahamalaotra were sampled in the cold-dry season (April–October) and Tsinjoarivo and Ialatsara Forest Station in the warm-dry season (October–December). As characterized by weather monitoring at Ranomafana National Park, which is at a mid-elevation similar to all of our 4 sites, from 2005 to 2009 the cold-dry season was characterized by an average minimum to maximum daily temperature of 13–19°C and a daily rainfall \pm SD of 6.4 ± 4.3 mm. The minimum to maximum daily temperature in the warm-dry season was 16–25°C with a daily rainfall of 7.4 ± 12.1 mm during this same time period.

Activity pattern sampling.—We used a random starting point to establish a grid of camera stations along existing trail networks to photographically sample carnivores at each site (Fig. 1). Tsinjoarivo and Ialatsara Forest Station included camera stations within and between forest fragments. We deployed 26–31 camera stations for 52–61 days at each site. The average spacing \pm SD among adjacent stations was 555 ± 100 m. Camera stations consisted of 2 independently operating passive-infrared cameras, mounted on opposite sides of a trail. This provided a photograph of both flanks for each animal, thus improving individual identification in recaptures (i.e., repeated photographs) for *C. ferus* and *F. fossana*; these 2 species were the only 2 carnivore species that were individually identifiable (Gerber et al. 2010) and for which selection of time periods could be analyzed at the individual

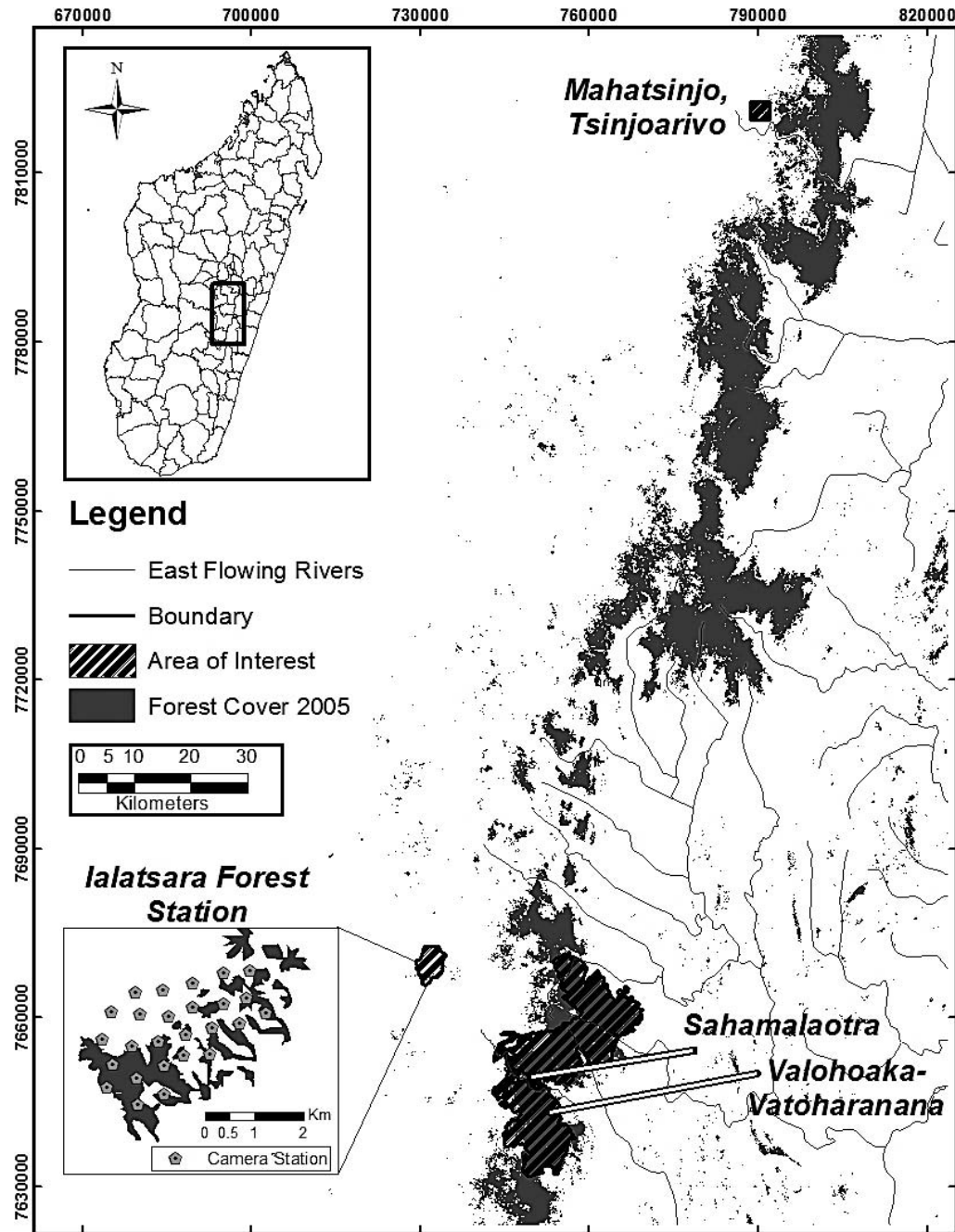


FIG. 1.—Four rain-forest study sites at which we sampled activity patterns of carnivores in eastern Madagascar from May to December 2008 and October to December 2009 (from south to north: Valohoaka-Vatoharanana, Sahamalaotra, Ialatsara Forest Station, and Tsinjoarivo). Top insert map shows political provinces and location on the island of Madagascar, whereas the bottom insert map shows the camera station sampling layout among rain-forest fragments at Ialatsara Forest Station as an example. Rain-forest extent is from Conservation International (2011).

level. We attached cameras 20 cm above the ground and set them to be active for 24 h/day. Camera types included DeerCam DC300s (DeerCam, Park Falls, Wisconsin), which were set to a 1-min delay between consecutive photographs, and Reconyx PC85s (Reconyx, Inc., Holmen, Wisconsin), which were set with no time delay. Each photograph recorded the date and time. We used chicken meat wrapped in wire mesh, hung above the camera stations, as a scent lure. Scent lure was used for the total sampling periods at

Valohoaka-Vatoharanana and Ialatsara Forest Station, whereas at Sahamalaotra and Tsinjoarivo, we used scent lure for only about half of the sampling period, which allowed us to evaluate the effect of scent lure on our ability to accurately describe carnivore activity patterns. We checked camera stations every 3–5 days to ensure continued operation, and replaced batteries, scent lure, film, and memory cards when necessary. Our study was approved by the Institutional Animal Care and Use Committee at Virginia Tech (protocol 08-051

FIW) and followed guidelines of the American Society of Mammalogists (Sikes et al. 2011).

Temporal activity patterns.—We defined an activity sample as the median time of all photographs of the same species or individual (*C. ferrox* and *F. fossana*) detected at a camera station within a 0.5-h period, thus minimizing the nonindependence of consecutive photographs (Ridout and Linkie 2009). To assess whether this effectively reduced temporal dependency of activity samples within our data sets, we calculated the median time between consecutive samples of individuals within a rain-forest site, or consecutive samples of individually unidentifiable species at each camera station. We conservatively assumed that a median time of less than 4 h suggested considerable autocorrelation (Jauhiainen and Korhonen 2005). To evaluate the effect of scent lure on our ability to accurately quantify carnivore activity, we tested if species' activity distributions (over total diel cycle) from data collected with and without scent lure were different using the nonparametric circular Mardia–Watson–Wheeler statistical test (Batschelet 1981). All analyses using this test were restricted to data sets with ≥ 10 activity samples (Fisher 1993). If scent lure had no effect, we pooled data sets. Throughout, we used an alpha level of 0.05 to determine statistical significance and when performing multiple pairwise tests, we controlled the experiment-wise error rate using Bonferroni corrections (Zar 1998).

We then tested for effects of individual, sex, and study site on activity distributions using Mardia–Watson–Wheeler tests. If no differences were observed among individual *C. ferrox* and *F. fossana* within a site, we pooled data sets at each site and tested for differences among sites and sexes. For carnivores that could not be individually identified, we were unable to test for individual variation and thus recognize the pooling of activity samples at each site is possibly pseudoreplication, if individuals did vary in their activity patterns (Aebischer et al. 1993). However, we still used these pooled data to test for differences between the activity patterns of species among sites.

For all species, we then pooled data sets when activity distributions were not different across sites, or sites and sexes. We used Rao's test of uniformity on these pooled or unpooled activity distributions to evaluate whether each species exhibited a uniform activity pattern over the diel cycle using the R package Circular (R Development Core Team 2011). To quantify the diel activity pattern of each species, we utilized a kernel density analysis (Ridout and Linkie 2009). Kernel density estimation is a nonparametric method for evaluating the probability density function of a random variable (Worton 1989), which in this case was temporal activity.

Relative preference of time periods.—We categorized the diel cycle based on times of sunrise and sunset at each study site into dawn, day, dusk, and night. We defined the crepuscular hours of dawn and dusk as ± 1 h from sunrise and sunset. For *C. ferrox* and *F. fossana*, we could identify the sexes, thus we used a generalized multinomial model (Proc Logistic; SAS Institute Inc., Cary, North Carolina) to test whether the proportion of use among dawn, day, dusk, and

night differed by site and sex. For other species for which we could not identify the sexes, we tested whether the proportion of use among dawn, day, dusk, and night differed by site using a likelihood-ratio chi-square test in a contingency table (Zar 1998). If differences were found, we used partial chi-square cell values to interpret the contribution of individual cells to overall significance. If there were no differences among sites or sites and sex, we pooled data sets.

We used the pooled data sets to examine whether carnivores selected dawn, day, dusk, and night given the availability of these 4 time periods. We used preference as a relative measure among defined time periods to indicate the level of disproportionality between use and availability (Manly et al. 2002). For *C. ferrox* and *F. fossana*, we were able to use the individual as the sampling unit and used a design II resource selection function, where selection of time periods is considered at the individual animal level (Manly et al. 2002). For all other species, we were unable to distinguish individuals and thus used a design I resource selection function, thus selection is measured at the population level. As before, we are unable to account for individual variation and recognize that this is possibly pseudoreplication (Aebischer et al. 1993). Resource selection analyses were done using the R package adehabitat (Calenge 2006); raw and standardized selection ratios were calculated to evaluate selection of the different time periods.

RESULTS

Temporal activity patterns.—Species presence and number of activity samples at the 4 study sites varied (Table 1). The limited data sets (< 10 activity samples) of *C. ferrox* in Tsinjoarivo, and *C. familiaris* and *E. goudotii* in Valohoaka-Vatoharanana, prevented us from including those sites in species-specific tests of site effects, or in tests of relative preference of time periods. The median time between consecutive photographs of individuals of *C. ferrox* and *F. fossana* at a site was > 17.5 h, whereas for the individually unidentifiable species at a camera station it was > 19 h, except at Valohoaka-Vatoharanana where *G. elegans* was observed at a median time of every 7 h. We found that activity distributions of native and exotic carnivores sampled with and without scent lure were not statistically different (all species Mardia–Watson–Wheeler test: $P > 0.05$, $d.f. = 1$).

For *C. ferrox* and *F. fossana*, we found no differences among the activity patterns of individuals within sites (*C. ferrox*: Valohoaka-Vatoharanana: $W_6 = 6.90$, $P = 0.14$, Sahamalaoatra: $W_6 = 5.46$, $P = 0.24$; *F. fossana*: Valohoaka-Vatoharanana: $W_{28} = 39.86$, $P = 0.11$, Sahamalaoatra: $W_{32} = 17.97$, $P = 0.59$) and thus pooled individuals at each site. We found that most species demonstrated a nonuniform activity pattern ($P < 0.05$; Fig. 2), with the exceptions of *C. familiaris* in Ialatsara Forest Station ($U_1 = 144.03$, $P = 0.07$) and *Felis* sp. in both Ialatsara Forest Station and Tsinjoarivo ($U_1 = 148.75$, $P = 0.44$), where both species showed considerable activity across the diel cycle. The native species

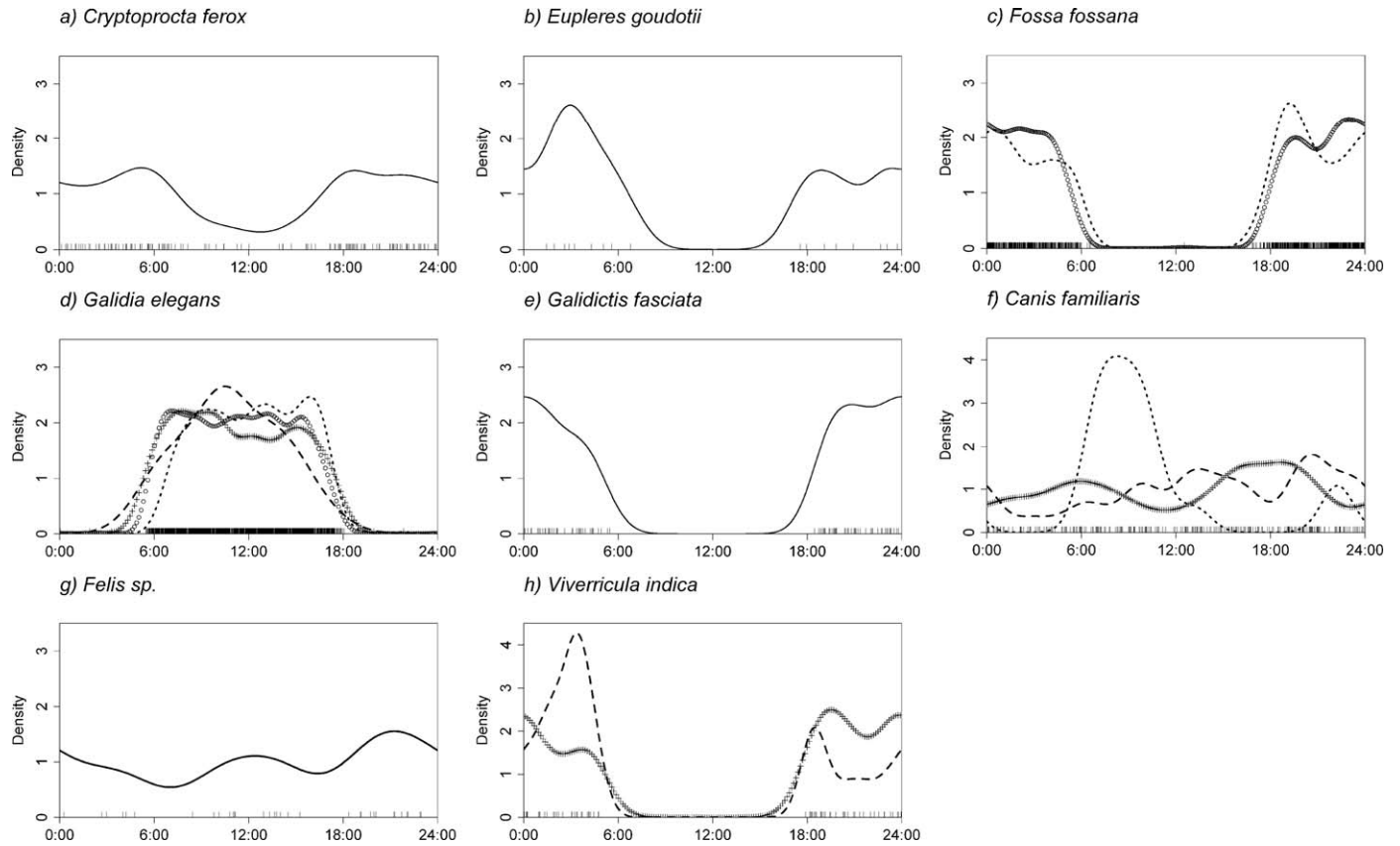


FIG. 2.—Temporal activity of rain-forest carnivores of Madagascar. Activity samples for each species were collected at 4 rain-forest sites within Madagascar’s eastern forests; data were pooled across sites when activity distributions were not different. Solid (—) lines indicate the use of pooled data from all relevant sites for the species, circles (○) indicate data from Valohoaka-Vatoharanana, dotted (···) lines indicate data from Sahamalaotra, dashed (—) lines indicate data from Tsinjoarivo, and plus signs (+) indicate data from Ialatsara Forest Station. Tick marks on the x-axis represent all activity samples for each species. The y-axis range is the kernel density and is not consistent among all graphs. Species are grouped 1st by native versus exotic, then by decreasing body size within the native versus exotic grouping.

TABLE 1.—The number of photographic-activity samples for native and exotic (denoted by a dagger [†]) carnivores from 4 sites in Madagascar’s eastern rain forests. Activity patterns of *Canis familiaris*, *Fossa fossana*, and *Galidia elegans* differed by site. NA = not applicable.

Species ^a	Weights (kg) ^b	Valohoaka-Vatoharanana	Sahamalaotra	Tsinjoarivo	Ialatsara Forest Station	Data set ^c	Mardia–Watson–Wheeler test	
							<i>W</i> _{d.f.}	<i>P</i>
<i>Cryptoprocta ferox</i>	6–8	91	51	2	—	Sex/site	1.84 ₂ /0.69 ₂	0.40/0.71
<i>Eupleres goudotii</i>	1.5–4.6	2	16	—	—	Site	NA	NA
<i>Fossa fossana</i>	1.3–2.1	780 A	460 B	—	—	Sex/site	3.64 ₂ /27.76 ₂	0.80/0.002
<i>Galidia elegans</i>	0.76–1.1	1,554 AB	427 A	28 AC	185 BC	Site	10.03 ₆	0.04
<i>Galidictis fasciata</i>	0.6–1.0	52	10	10	27	Site	1.23 ₆	0.98
<i>Canis familiaris</i> †	Variable	7	17 A	169 B	97 B	Site	18.98 ₄	<0.001
<i>Felis sp.</i> †	3.5–8	—	—	23	16	Site	4.53 ₂	0.11
<i>Viverricula indica</i> †	2–4	—	—	22 A	49 B	Site	7.64 ₂	0.02

^a Activity samples were the median time of all photographs of the same species or individual (*Cryptoprocta ferox* and *F. fossana*) detected at a camera station within a 0.5-h period; thus, there were 7 activity samples total of *C. familiaris* at the Valohoaka-Vatoharanana site. A dash (—) indicates that the species was absent from the site. The same letter next to the activity samples within a species indicates that the activity distributions were not statistically different across sites for that species. Multiple-comparison tests were done using the Mardia–Watson–Wheeler test, but controlling for an experiment-wise alpha of 0.05 using a Bonferroni correction. For example, the activity distributions of *C. familiaris* at Tsinjoarivo and the Ialatsara Forest Station both contain the letter “B” and are thus not statistically different from each other, but are different from the activity distribution at Sahamalaotra. Species are grouped 1st by native versus exotic (denoted by a dagger [†]), then by decreasing body size within the native versus exotic grouping.

^b Weight ranges for each carnivore species are taken from Alagnac (1974), Dollar (2006), Dunham (1998), Goodman (2003b), Hawkins (1998), Kerridge et al. (2003), and Nowak (2005).

^c Species’ activity distributions were tested for differences across sites, or sites and sex, as noted here.

C. ferox, *E. goudotii*, and *F. fossana* were absent or only observed a few times and assumed to be simply passing through the site (Table 1).

Relative preference for time periods.—We found that the proportion of activity during the dawn, day, dusk, and night time periods for *C. familiaris* ($\chi^2_6 = 15.28$, $P = 0.02$) and *G. elegans* ($\chi^2_9 = 34.94$, $P < 0.001$) differed significantly across sites with different carnivore species composition. For *C. familiaris*, we found less than expected use of night (use: 6.25%, available: 45.6%) in Sahamalaotra where all native carnivores, including the crepuscular–nocturnal *C. ferox*, were present, accounting for 40% of the total chi-square value (χ^2_1 of night = 6.12, and total $\chi^2_6 = 15.28$). Otherwise, there were no differences; thus, we pooled data from Ialatsara Forest Station and Tsinjoarivo ($\chi^2_3 = 5.9$, $P = 0.12$) for *C. familiaris*. For *G. elegans*, we found less than expected use of dawn (use: 5.85%, available: 8.33%) and greater use of dusk (use: 9.84%, available: 8.33%) in Sahamalaotra compared to the other sites, accounting for 70% of the total chi-square value (dawn $\chi^2_1 = 6.19$, dusk $\chi^2_1 = 18.36$, and total $\chi^2_9 = 34.94$). At this same site only, *C. familiaris* used dawn more than expected, and avoided dusk, in direct contrast to the activity patterns of *G. elegans* (Table 2). Otherwise, there were no differences; thus, we pooled data from the 3 other sites for *G. elegans* ($\chi^2_6 = 5.55$, $P = 0.67$). All other species showed no site differences, thus we pooled all data sets in which they were detected for analyses of relative preference.

All native and exotic species exhibited nonrandom use of the dawn, day, dusk, and night time periods when considering availability of each of these time periods (Table 2). *C. ferox* preferred the crepuscular hours with no difference between activity at dawn and dusk; *C. ferox* also was active during the day and night, but daytime hours were used less than available. We found *F. fossana* to be predominantly nocturnal, but these animals also used dusk in proportion to its available hours. At all sites, *G. elegans* was highly diurnal, but preferred the crepuscular and day hours differently in Sahamalaotra than at the other sites. Both *G. fasciata* and *E. goudotii* were highly nocturnal; they used the crepuscular hours in proportion to their availability and exhibited no diurnal activity. *C. familiaris* preferred the day hours except for at Sahamalaotra, where it preferred dawn and then day hours. *Felis* sp. preferred the night and used the crepuscular hours in proportion to their availability. We found *V. indica* to prefer dusk and night, while avoiding the daytime.

DISCUSSION

The activity of the 2 smaller-bodied native species, *G. elegans* and *G. fasciata*, overlapped minimally at all sites because the former is primarily active during dawn or day, and the latter at night. Examination of available data on *G. elegans* and *G. fasciata* suggests that they share a similar generalist diet (Goodman 2003a, 2003b), which may explain why these 2 native carnivores have such divergent temporal activity. By contrast, both of the native medium-sized species, *F. fossana* and *E. goudotii*, were highly nocturnal. However, these 2

species appear segregated in their diets because *E. goudotii* has a unique dietary specialization on earthworms and insects (Albignac 1974, 1984), whereas *F. fossana* is a generalist predator (Goodman et al. 2003). The larger-bodied *C. ferox* may have limited dietary overlap with the other native Malagasy carnivores because of its size, thus negating any effects of temporal niche overlap with all other native species related to its activity during crepuscular, night, and day hours.

The interactions of exotic *C. familiaris*, *Felis* sp., and *V. indica* with native carnivores are more difficult to understand and may vary by study site. We found that native Malagasy carnivores that were present at multiple sites that differed in exotic carnivore presence showed no dramatic shifts in their temporal activity patterns among the sites. These findings are consistent with mammal studies outside of Madagascar, which have shown only subtle changes in activity patterns due to human activity, resource availability, or other types of habitat disturbance (Ngoprasert et al. 2007; Norris et al. 2010; Presley et al. 2009; Zielinski 1988). A marked change, such as a mammal shifting its activity from primarily diurnal to nocturnal, appears rare (Griffiths and Schaik 1993; Kitchen et al. 2000). This may be due to disturbance tolerance, adjustment of behavior in another niche dimension (i.e., diet or space), or morphological or physiological constraints.

Although we did not find dramatic changes in temporal activity, we did observe shifts in activity by native and exotic carnivores that may be related to, or causal factors behind, variation in species composition among sites. At the Sahamalaotra site, where all 5 native carnivores were present with 2 exotic carnivores, *C. familiaris* preferred dawn whereas *G. elegans* avoided it, despite the finding that *G. elegans* selected dawn for its activity at all other sites. At both Ialatsara Forest Station and Tsinjoarivo, *G. elegans* avoided dusk because the exotic *V. indica* preferred dusk at that site; however, where *V. indica* was absent (e.g., Sahamalaotra), *G. elegans* used dusk more than twice as often. At both Ialatsara Forest Station and Tsinjoarivo, where the native carnivore community was greatly reduced, both *C. familiaris* and *Felis* sp. exhibited fairly uniform activity throughout the diel cycle. This pattern of constant activity by *Felis* sp. is particularly important, because in a concurrent study, the ability of *G. elegans* to occupy an area declined as *Felis* sp. increased its use of that area (Gerber et al., in press). With the population of *Felis* sp. constantly active, *G. elegans* may be unable to adjust its activity to significantly reduce temporal overlap, as may be necessary to reduce competition or even predation.

Viverricula indica and *F. fossana* are both nocturnal and are similar in size, and appear to have similar diets of vertebrates and invertebrates (Chuang and Lee 1997; Goodman et al. 2003). The slightly larger *V. indica* may competitively dominate *F. fossana* when resources are constrained such as in a rain-forest fragment, thus partially explaining the absence of *F. fossana* from 2 study sites located in fragmented rain forests where *V. indica* was present.

Given that dogs are known to kill medium-sized civets in Asia (Vanak and Gompper 2009) and have been observed to

TABLE 2.—The relative preference, selection ratios, and test of random use of the dawn, day, night, and dusk time periods given their availability by native and exotic (denoted by a dagger [†]) carnivores across 4 sites within the eastern rain forests of Madagascar. Preference is relative to the other time periods and indicates the level of disproportionality between use and availability.

Species (sites) ^a	Random use test ^b	P	Relative preference ^c (selection and avoidance) ^{d,e}						
			Dusk	—	Dawn	>>>	Night	>>>	Day
<i>Cryptoprocta ferox</i> (Valohoaka-Vatoharanana + Sahamalaotra)	25.90	<0.01	Dusk	—	Dawn	>>>	Night	>>>	Day
Use (%)			15.1		13.9		50.7		20.3
Selection ratio			1.81		1.67		1.16*		0.51
Standard selection ratio (%)			35.18		32.39		22.45		9.98
<i>Eupleres goudotii</i> (Sahamalaotra)	19.43	<0.01	Night	>>>	Dawn	—	Dusk	>>>	Day
Use (%)			80.0		10.0		10.0		0.0
Selection ratio			1.86		1.20*		1.20*		0.00
Standard selection ratio (%)			43.66		28.17		28.17		0.00
<i>Fossa fossana</i> (Valohoaka-Vatoharanana + Sahamalaotra)	1,202.30	<0.01	Night	>>>	Dusk	—	Dawn	>>>	Day
Use (%)			88.2		6.7		4.9		0.1
Selection ratio			2.01		0.80*		0.12		0.00
Standard selection ratio (%)			68.37		27.33		4.22		0.09
<i>Galidia elegans</i> (Valohoaka-Vatoharanana + Ialatsara Forest Station + Tsinjoarivo)	2,254.93	<0.01	Day	>>>	Dawn	>>>	Dusk	>>>	Night
Use (%)			84.9		10.5		4.1		0.5
Selection ratio			1.97		1.26		0.49		0.01
Standard selection ratio (%)			52.75		33.74		13.18		0.33
<i>Galidia elegans</i> (Sahamalaotra)	502.29	<0.01	Day	>>>	Dusk	>>>	Dawn	>>>	Night
Use (%)			83.8		9.8		5.9		0.5
Selection ratio			2.08		1.18*		0.71		0.01
Standard selection ratio (%)			52.30		29.59		17.82		0.29
<i>Galidictis fasciata</i> (all 4 sites)	136.19	<0.01	Night	>>>	Dawn	—	Dusk	>>>	Day
Use (%)			90.2		5.4		4.3		0.0
Selection ratio			2.22		0.65*		0.52*		0.00
Standard selection ratio (%)			65.57		19.17		15.26		0.00
<i>Canis familiaris</i> † (Sahamalaotra)	14.12	<0.01	Dawn	—	Day	>>>	Night	>>>	Dusk
Use (%)			17.6		70.6		11.8		0.0
Selection ratio			2.11		1.75		0.27		0.00
Standard selection ratio (%)			51.05		42.32		6.63		0.00
<i>Canis familiaris</i> † (Ialatsara Forest Station + Tsinjoarivo)	455.70	<0.01	Day	>>>	Dusk	—	Dawn	>>>	Night
Use (%)			83.8		9.1		6.4		0.6
Selection ratio			1.83		1.09*		0.77*		0.02
Standard selection ratio (%)			49.43		29.44		20.70		0.43
<i>Felis</i> sp.† (Ialatsara Forest Station + Tsinjoarivo)	10.74	0.01	Night	>>>	Day	—	Dawn	>>>	Dusk
Use (%)			55.0		35.0		10.0		0.0
Selection ratio			1.47		0.76*		1.20*		0.00
Standard selection ratio (%)			42.73		22.28		34.99		0.00
<i>Viverricula indica</i> † (Ialatsara Forest Station + Tsinjoarivo)	90.58	<0.01	Dusk	>>>	Night	—	Dawn	>>>	Day
Use (%)			19.2		68.5		12.3		0
Selection ratio			2.30		1.82		1.48*		0.00
Standard selection ratio (%)			41.11		32.56		26.33		0.00

^a Species are grouped 1st by native versus exotic (denoted by a dagger [†]), then by decreasing body size within the native versus exotic grouping. Data were pooled (+) when proportional use of time periods was not different among sites. Individual *Cryptoprocta ferox* and *Fossa fossana* were used as the sampling unit; thus, resource selection functions were analyzed using a design II framework. Individuals of all other species could not be individually identified, thus resource selection functions were analyzed using a design I framework.

^b Log-likelihood statistical test of random resource use of time periods given their availability, where a significant *P*-value indicates a nonrandom use of time, *d.f.* = 3. Use values are the observed percentage of activity samples in each time period (dawn, day, dusk, and night).

^c Relative preference of time classes indicates the level of disproportionality between use and availability, ranked from the most preferred to the least, a dash (—) indicates a nonsignificant difference between 2 classes and >>> indicates a significant difference (experiment-wise *P* < 0.05).

^d Selection ratios (the proportion of use/availability) > 1 indicate that the time period is selectively used more than available, whereas those < 1 indicate that the time period is avoided. An asterisk (*) indicates when the selection ratio is not statistically different than 1 and use is proportional to availability.

^e Standardized selection ratios are the probability that an animal would choose a time period over all others, assuming that all time periods are equally available (Manly et al. 2002).

interact antagonistically with *C. ferox* within Ranomafana National Park (S. Arrigo-Nelson, pers. obs.), *C. familiaris* may be a considerable threat to native carnivores. This potential for antagonism may at least partially explain the absence, or transient status, of observations of *C. ferox* in both Ialatsara Forest Station and Tsinjoarivo, where we found greater probability of occupancy of *C. familiaris* than in the Sahamalaotra site (Gerber et al., in press). Although examination of our data can provide insight into the possible role of temporal activity overlap in the absence of some of these native species from fragmented habitats, other factors such as direct hunting, disease, reduced area, and Allee effects might play a role in altered community structure and also should be examined in future studies. For example, even though *E. goudotii* overlaps temporally with *V. indica* and *Felis* sp., the diet of *E. goudotii* is unique; thus, temporal overlap with exotic carnivores alone is unlikely to explain its absence from the fragmented habitats.

The International Union for the Conservation of Nature and Natural Resources “Vulnerable” *C. ferox* is a known lemur predator (Hawkins and Racey 2008) that has been documented to cause the extirpation of the endangered Milne-Edwards’s sifaka (*Propithecus edwardsi*) and diademed sifaka (*Propithecus diadema*) from continuous and fragmented forests, respectively (Irwin et al. 2009). Quantifying the temporal activity of *C. ferox* allows an evaluation as to whether cathemerality in some lemur species (e.g., *Eulemur* sp.) developed as an antipredator strategy, such that lemurs are temporally cryptic and thus unavailable to *C. ferox* (Colquhoun 2006). Although *C. ferox* has previously been described as nocturnal, crepuscular, and cathemeral depending on the study (Albignac 1972; Dollar 1999a), we found it to prefer crepuscular activity and secondly to select night over the daytime. Lemurs described as cathemeral often exhibit a peak activity at the crepuscular hours (Donati and Borgognini-Tarli 2006), which if *C. ferox* is cueing in on prey activity would suggest a high predation risk for cathemeral lemurs given our findings of crepuscular activity patterns by *C. ferox*. However, predator temporal activity often generally corresponds to when prey are most vulnerable, which is a function of detectability and catchability (Zielinski 2007). As such, high temporal activity overlap between predator and prey in a given time period may not necessarily correspond with high predation risk. Predation risk is no doubt a strong selective force on prey behavior; however, the relationship between lemur predation risk and temporal activity patterns of *C. ferox* and lemurs is likely more complex than simple temporal activity avoidance through crypticity. To evaluate whether lemur cathemerality is an effective antipredator tactic against *C. ferox*, it is necessary to understand how predation rates of *C. ferox* on lemurs vary throughout the diel cycle, which is currently unknown.

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