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Anti-predator behaviour of Sahamalaza sportive lemurs, *Lepilemur sahamalazensis*, at diurnal sleeping sites

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Abstract

In response to predation pressure by raptors, snakes, and carnivores, primates employ anti-predator behaviours such as avoiding areas of high predation risk, cryptic behaviour and camouflage, vigilance and group formation (including mixed-species associations), and eavesdropping on other species' alarm calls. After detecting a predator, primates can produce alarm calls, show predator-specific escape strategies or even mob the predator. It remains unclear how solitary nocturnal primates respond to diurnal predation pressure while they sleep or rest. The aim of this study was to investigate the diurnal anti-predator behaviour of the nocturnal and solitary Sahamalaza sportive lemur, *Lepilemur sahamalazensis*, which regularly rests in exposed locations. We observed the responses of 32 Sahamalaza sportive lemurs to playbacks of territorial calls of an aerial predator (Madagascar harrier hawk), mating calls of a terrestrial predator (fossa), and the contact calls of a medium-sized bird (crested coua) as a control, at different diurnal sleeping sites. Lemurs never showed a flight response after replays of predator or control calls, but regularly froze after harrier hawk calls. Lemurs scanned the sky immediately after playback of harrier hawk calls, and the ground or trees after fossa calls. Lemur vigilance increased significantly after both predator calls. After crested coua calls the animals became significantly less vigilant, suggesting that contact calls of this bird serve as indicators of predator absence. We found no response differences between different types of sleeping sites. Our results show that resting Sahamalaza sportive lemurs recognise predator vocalisations as indicators of increased predation risk, discern vocalizations of different predators, and employ anti-predator behaviours specific for different predator classes. Their behavioural responses while resting or sleeping are comparable to those of active primates, and their response rate of 80% shows that this solitary and nocturnal primate is constantly aware of its environment.

Contents

Introduction

The influence of predation on morphology, behaviour and ecology of animals has long been recognized (Altmann, 1956; Hamilton, 1971; Kruuk, 1972; Curio, 1976; Burtt, 1981). Many reports on mammals and birds illustrate the crucial role of predation pressure on the evolution of anti-predator behaviours (Thompson *et al*., 1980; Cheney and Wrangham, 1987; Sih, 1987; Lima and Dill, 1990; Seyfarth and Cheney, 1990; Curio, 1993; Zuberbühler, 2000; Caro, 2005; Gursky and Nekaris, 2007; Scheumann *et al*., 2007; Fichtel, 2012). Raptors, snakes, and carnivores pose a predation risk for most wild primates (Cheney and Seyfarth, 1981; Cheney, 1987; Cowlishaw, 1994; Janson and van Schaik, 1993; Isbell, 1994; Hill and Dunbar, 1998; Treves, 1999; Bearder *et al*., 2002; Gursky, 2002a, b; Shultz and Noë, 2002). In response to predation pressure, primates use anti-predator behaviours such as crypsis, camouflage, and avoidance of areas of high predator density to reduce detection risk, and individual and group vigilance (even in mixed-species associations) to improve predator detection, which can include eavesdropping on other species' alarm calls (Vine, 1973; Seyfarth *et al*., 1980; van Schaik and van Hooff, 1983; Terborgh and Janson, 1986; Janson, 1992; Cowlishaw, 1994; Wright, 1998; Fallow and Magrath, 2010). After being detected by a predator, primates have been reported to mob the predator, show predator-specific escape strategies and emit alarm calls (Seyfarth *et al*., 1980; van Schaik and van Hooff, 1983; Sullivan, 1984; Isbell, 1994; Bshary and Noë, 1997; Zuberbühler *et al*., 1999; Fichtel and Kappeler, 2002; Stanford, 2002; Karpanty and Wright, 2007; Scheumann *et al*., 2007).

Responses of nocturnal primates to predation pressure have not been studied in as much depth as those of diurnal species, despite the former making up nearly one third of the primate order. Cryptic behaviour and camouflage have been assumed to be the main anti-predator strategies of nocturnal primates (Vine, 1973; Terborgh and Janson, 1986; Janson, 1992; Cowlishaw, 1994; Wright, 1998). In the past decade, however, experimental studies revealed that nocturnal primates exhibit predator-specific escape strategies as well as alarm calls, and that they make use of anti-predator strategies such as early detection, warning of approaching predators and mobbing behaviour - anti-predator strategies that also are common in diurnal primates (Fichtel, 2007; Rahlfs and Fichtel, 2010). Indeed, nocturnal primates might not only face high predation pressure while active at night, but also are exposed to predation from diurnal or cathemeral predators while inactive and resting in their shelters during the day (Wright, 1998; Schülke and Ostner, 2001; Karpanty, 2006). In Madagascar, a harrier hawk (*Polyboroides radiatus* Scopoli, 1786) for example has been observed extracting a nocturnal lemur (*Lepilemur ruficaudatus* Grandidier, 1867) from its daytime sleeping tree holes by pulling it through cracks using its beak (Schülke and Ostner, 2001). Fossas (*Cryptoprocta ferox* Bennett, 1833) and boas (*e.g. Boa manditra* Kluge, 1991), which also hunt during day and night, have been reported to successfully prey on different nocturnal species (Wright, 1998; Goodman, 2003; Karpanty, 2006).

Due to the diversity of their social systems (solitary, dispersed pairs, harems) and their exposed resting locations, the sportive lemurs (*Lepilemur* spp.) of Madagascar lend themselves to the study of anti-predator strategies of nocturnal prosimians (Tattersall, 1982; Harcourt and Thornback, 1990; Groves, 2001; Mittermeier and Nash, 2006). To date, anti-predator behaviour has been studied in one pair-living sportive lemur species, the red-tailed sportive lemur (*L. ruficaudatus* Fichtel, 2007), which distinguished between different predator types, increased vigilance and usually showed predator-specific flight responses. Solitary-living species, which rest and forage on their own, cannot profit from group benefits of predator avoidance (Stanford, 2002), either during activity or during resting periods (Radespiel *et al*., 1998, 2003). Mobbing of predators was also observed in solitary animals, though, and can be successfully used to confuse and discourage

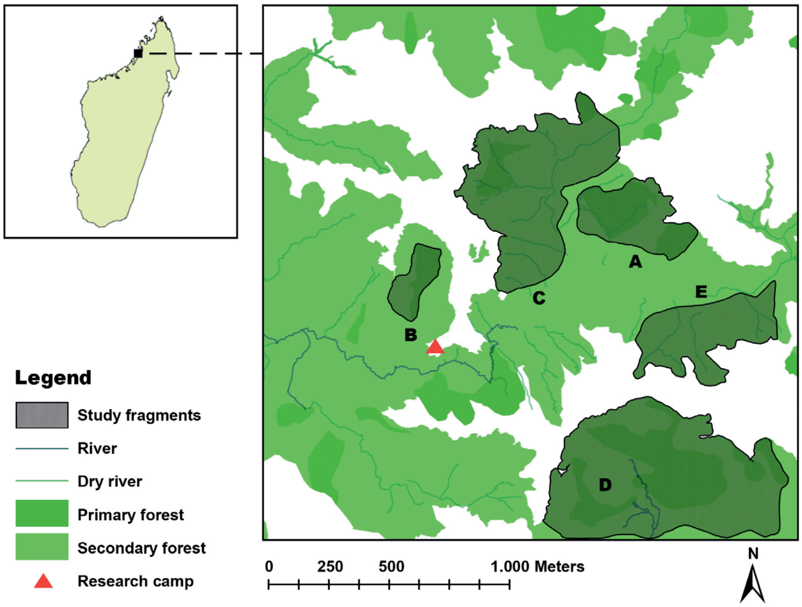

Fig. 1. Habitat map indicating study fragments in the Ankarafa Forest, Sahamalaza Peninsula, northwest Madagascar.

the predator (Zuberbühler *et al*., 1999; Clark, 2005). Studies on how solitary-living sportive lemurs respond to high predation pressure during the day have as yet not been carried out.

Here, we investigate the diurnal anti-predator behaviour of the Sahamalaza sportive lemur, *Lepilemur sahamalazensis* (Andriaholinirina *et al*., 2006), from northwestern Madagascar, using the species as a model for a solitary-living nocturnal prosimian. Since its recognition as a species, the Sahamalaza sportive lemur has been included on the list of the World's Top 25 Most Endangered Primates 2006 - 2008 (Mittermeier *et al*., 2007) and listed as Critically Endangered by the IUCN (C. Schwitzer, pers. comm.). During daylight hours the Sahamalaza sportive lemur rests in tree holes or in tree tangles. Individuals resting in tree holes usually sit at the entrance rather than inside the hole, possibly to increase sun exposure (Seiler *et al*., 2013a). Therefore, they are more accessible to predators like the Madagascar harrier hawk, the fossa, and possibly the Madagascar tree boa, as well as poachers, as each of these predators hunt during sportive lemur resting periods. During our own diurnal observations, 5-14% of resting sportive lemurs behaviours were considered active, usually including a high proportion of vigilance (Seiler *et al*., 2013a). To investigate anti-predator responses in the Sahamalaza sportive lemur, we conducted playback experiments during daytime hours on individual sportive lemurs resting in the entrance of tree holes and tree tangles in their natural habitat. To elicit anti-predator behaviour, the vocalisations of two potential and abundant predators, the fossa (mating calls) and the harrier hawk (territorial calls), were played to the sportive lemurs. Contact calls of the abundant crested coua (*Coua cristata* Linnaeus, 1766) were used as non-predator control calls.

Due to the high level of diurnal exposure and their relatively high level of activity during the day, we hypothesized that the Sahamalaza sportive lemur relies on early detection of predators, a strategy that also is used in other sportive lemur species (Fichtel, 2007). Therefore, we predicted them to increase vigilance after playbacks of possible predators, but not after control calls. Regarding predator class specific responses we predicted them to scan the sky after playbacks of aerial predator calls and to scan the ground or surrounding trees after playback of terrestrial predator calls. We predicted that in response to playbacks of predator calls, the lemurs immediately would either drop into the tree hole/canopy or to freeze. No change in behaviour was predicted in response to the contact calls of the crested coua, as the presence of this non-predatory bird species represents no danger to sportive lemurs. We predicted stronger reactions from animals resting in tree holes because individuals resting in tree tangles are less visible/exposed to predators, and because their diurnal activity level is lower compared to individuals resting in tree holes (Seiler *et al*., 2013a).

Material and methods

Study site

The Ankarafa Forest is situated in the UNESCO Biosphere Reserve and National Park on the Sahamalaza Peninsula and is part of the Region Sofia, NW Madagascar. It extends between 13°52'S and 14°27'S and 45°38'E and 47°46'E (WCS/DEC, 2002; Figure 1). The climate is strongly seasonal, with a cool, dry season from May to October and a hot, rainy season from November to April. The Ankarafa Forest lies in a transition zone between the Sambirano region in the North and the western dry deciduous forest region in the South, harbouring semi-humid forests with tree heights of up to 30 m (Schwitzer *et al*., 2006). The forests in this area include a mixture of plant species typical of the western dry deciduous forest as well as some typical of the Sambirano domain (Birkinshaw, 2004) and comprise primary and secondary forest fragments.

No large connected areas of intact primary forest are left on the Sahamalaza Peninsula, and the remaining fragments all show some degree of anthropogenic disturbance and/or edge effects (Schwitzer *et al*., 2007a, b). The forests and forest fragments are separated by grassland with shrubs. The Sahamalaza sportive lemur is found exclusively in this area. Other lemur species in Sahamalaza include the blue-eyed black lemur (*Eulemur flavifrons* Gray, 1867), the aye-aye (*Daubentonia madagascariensis* Gmelin, 1788), the western bamboo lemur (*Hapalemur occidentalis* Rumpler, 1975), the northern giant mouse lemur (*Mirza zaza*) and the fat-tailed dwarf lemur (*Cheirogaleus medius* Geoffroy, 1812). All lemur species living in Sahamalaza are threatened by hunting and deforestation (Schwitzer *et al*., 2006).

Study subjects

Between April and October 2010, a total of 461 playback experiments were conducted on 32 individual sportive lemurs. 26 animals were resting in tree holes, 6 in tree tangles. The first week of the field season was used to walk four adjacent forest fragments during the day to find mature sportive lemurs in their sleeping sites, and to identify them individually by their facial masks. We only chose individuals whose sleeping site/ resting position allowed us to clearly see their faces and thus to observe their behaviour in response to the playback experiments. Before we started conducting playback experiments with the animals we did diurnal observations of all individuals for three days each (6 am to 6 pm) to reduce the possible effect of our presence on their behaviour. As this *Lepilemur* species is not very abundant in the forest (between 0.07 and 0.23 ind/ha; Seiler *et al.*, in press) and individuals occasionally change sleeping sites or disappear, we also conducted playback experiments on previously untested mature sportive lemurs that were first found at least one month before the end of the field season. Due to differences in site fidelity we were not able to play all predator or control calls to all individuals, therefore numbers of sportive lemurs tested in the different categories differ (N=29 for harrier hawk; N=26 for fossa; N=27 for crested coua). Sportive lemurs were resting in tree holes located in dead trees of the species *Bridelia pervilleana*. Tree tangle sleeping sites were located in the species *Sorindeia madagascariensis*. Sportive lemurs resting in tree holes rested at the entrance of the tree hole at a height of 3.25 (2.5-4.4) metres (median with interquartile range), animals resting in tree tangles rested slightly higher at 5.65 (5.38-5.98) metres. Tree hole trees had a larger diameter at breast height (22.1 centimetres, range 14.7-24.9) than tree tangle trees (13.5 centimetres, 7.5-25.7), while tree tangles trees were higher (10 metres, 7-14) than tree hole trees (8.3 metres, 3.9-11.3) and also had a higher canopy cover (87%, 83-91) than tree hole trees 79%, 71-89 (see Seiler *et al.*, 2013a).

Playback stimuli

Territorial calls of harrier hawks and contact calls of crested coua were obtained from the online archive of the Macaulay Library (http://macaulaylibrary.org). Mating calls of fossas were recorded at the study site using a directional microphone (K6 power module and ME67 recording head, Sennheiser electronic GmbH & Co. KG, Wennebostel, Germany) and a PMD-670 digital recorder (Marantz Japan Inc., Sagamihara, Japan). We used mating calls of six different fossas, territorial calls of six different harrier hawks and contact calls of six different crested couas. Though territorial calls as well as mating calls are not associated with the hunting behaviour of predators, we considered these calls as sufficient for our experiments as they inform the sportive lemur about the presence of a potential predator. All recordings used for playback were equipped with 10 seconds fade in and fade out using SASLAB Pro (Avisoft Bioacoustics, Berlin, Germany). Table 1 summarises acoustic parameters of the calls used, and figure 2 shows example spectrograms of each call type (generated in SASLAB Pro; 1024-point

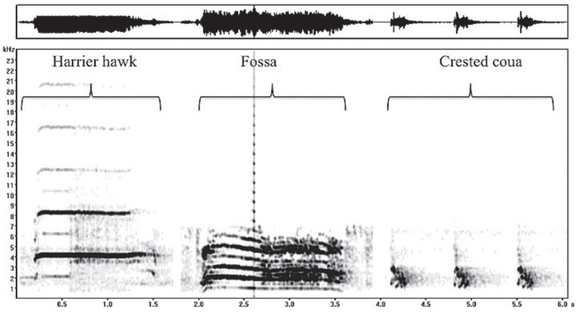

Fig 2. Spectrogram (lower panel) and oscillogram (upper panel) of one of the six copies of calls of harrier hawk, fossa, and crested coua used for playback.

Table 1. Median (interquartile range; Q1 – Q3) stimulus length (start of first call unit to end of last call unit), call duration (duration from call onset to call offset), inter call interval (time gap between call offset and successive call onset), peak frequency of call (measured from power spectrum), and source level (in dB peSPL re 1 m) of harrier hawk, fossa and crested coua recordings used as playback stimuli.

species	N	call type	stimulus length (s)	call duration (s)	inter call interval (s)	mean peak frequency (Hz)	source level (dB peSPL)
Fossa	6	mating	7.7 (5.7-9.3)	0.77 (0.4-1.2)	0.93 (0.7-2.8)	1120 (930-1310)	70.6 (70.2-72.4)
Harrier hawk	6	territorial	16.12 (15.3-17.4)	1.32 (1.2-1.4)	5.62 (5-8.9)	3460 (3370-4165)	67.8 (65.2-68.9)
Crested coua	6	contact	4.65 (4.5-4.9)	0.28 (0.2-0.3)	0.69 (0.6-0.8)	1960 (1730-2200)	70.4 (70.1-74.7)

Hamming window, 48 kHz sampling rate with 50% window overlap resulting in 47 Hz frequency resolution, and 10.7 ms temporal resolution).

Playback calibration

The calls were played back using an iPod nano, model A1320 (Apple Inc., Cupertino, CA) and wireless loudspeaker (JBL On Stage Micro II; Harman International Industries, Inc., Stamford, CT; Frequency range 80 Hz-20 kHz). The sound pressure level of call playbacks was measured in a semi-anechoic chamber in Bristol using 40BF microphone, 26AB preamplifier and 12AA power module (all G.R.A.S. Sound & Vibration, Holte, Denmark) calibrated by D1411E acoustic calibrator (Dawe Instruments, Brentford, UK). Mean sound pressure levels (SPL) were 67–71 dB peak-equivalent SPL re 1 m (see Table 1).

As a field test we played all stimuli in the absence of lemurs in the research camp to check for responses from harrier hawks, fossas or crested couas. We played the harrier hawk territorial calls when buzzards and harrier hawks where in hearing distance, and attracted several individuals of both species. To avoid drawing attention to the resting lemur, we never played back harrier hawk calls if we realized a real harrier hawk or other raptor was close by. We obtained vocal responses from crested couas to their species-specific playbacks, and twice individuals approached us after playbacks. These conspecific responses confirm that our replays in the field were of sufficient quality and adequate sound pressure level. No response from the rare and elusive fossa was ever noted.

Playback procedure

Playback equipment was either hidden behind a bush or in a tree at a horizontal distance of about five metres from the sportive lemurs sleeping site. The observer was seated at a different position at least five metres away from the playback equipment. The equipment was placed on the ground for the playback of a fossa and on a branch of at least 0.5 metres in height for playbacks of harrier hawk and crested coua. Occurrence, frequency, and duration of responses (see Table 2, Categories I) were documented using focal animal sampling for five minutes each before and after the playback. Where needed, binoculars were used to observe the animals' behaviour. Notepad and timer were used to note down the animals behaviour. Before starting the five minutes pre-playback observation, we waited for the tested individual to settle to the observer's presence. Sportive lemurs that are not habituated to human presence are vigilant and constantly stare at the potential predator, but return to their usual behaviour (Seiler *et al*., 2013a) after some minutes if the researcher remains calm and does not further approach the animal. During the five minutes observation interval, the exact time (mm:ss) of the onset and offset of each behaviour was noted. After five minutes, a pre-selected call was played back using a remote control, and the five minutes post-playback observation was started. Additionally, immediate behavioural responses (within 5 s) to playback were noted (see Table 2, Categories II). The experimental approach was adapted after Fichtel (2007).

The six different versions of harrier hawk calls were played back between 23 and 39 times resulting in a total of 173 playbacks to 29 different individuals (Table 3,

Table 2. Diurnal ethogram of the Sahamalaza sportive lemur as observed during playback experiments. Durations (in seconds) of category I behaviors were determined within the five minute intervals before and after each playback. Category II was used to quantify behavior immediately (within 5 s) after each playback.

I – Behavioral categories in the five minutes before and after call playback	
rest	Animal sits or lies inactively; eyes closed or open, but without attentive scanning
vigilance	Animal fixates a specific direction/component or scans the environment; eyes are wide open; some movement possible
autogroomig	Animal grooms itself; licking or gnawing its fur
out of sight	Animals is out of sight in the tree hole or canopy
II – Behavioral categories immediately (within 5 s) after call playback	
scanning up	Animal is vigilant and looks up into sky or trees
scanning down	Animal is vigilant and looks down to the ground
hide	Animal drops into tree hole or climbs into dense canopy; swift
freeze	Animal stops any movement but stays vigilant; gaze directed at sky or ground; eyes wide open and not blinking; muscles tense

Table 3. Overview of numbers of playback-experiments conducted with six different versions of harrier hawk territorial call, fossa mating call and crested coua contact call with sportive lemur resting at two types of sleeping sites (tree hole: TH; tree tangle: TT).

	Harrier hawk						Fossa						Crested coua						Total
Call Nr.	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6	
TH (n=26)	33	29	25	20	21	23	26	18	19	19	20	16	32	23	22	21	19	15	401
TT (n=6)	6	3	3	3	4	3	3	2	2	4	2	4	4	4	4	3	3	3	60
Total	39	32	28	23	25	26	29	20	21	23	22	20	36	27	26	24	22	18	461

raw data in On-line Supplementary Material Table S1). The six different fossa calls were presented a total of 135 times to 26 individuals. The six different crested coua calls were played back a total of 153 times to 27 study subjects. All calls were presented in a randomised order to individual lemurs avoiding repeats of the same call recordings. We presented only one playback stimuli per individual per day. Depending on the site fidelity of individual sportive lemurs between one and 48 playback experiments were conducted over a period of six month. As fossas were spotted roaming the forests only at certain times of day, we presented their calls between 6:00 and 9:00 am and between 4:30 and 6:00 pm only. The calls of harrier hawks and crested coua were presented between 6:00 am and 6:00 pm.

Data analyses

To test for overall differences in response to the different playback stimuli, a Friedman test was used with each individuals mean difference in vigilance during the five-minute periods before and after the playback of stimuli. To test for differences in the duration of individual lemurs' vigilance (measured as seconds of vigilant behaviour) before and after the playback of predator and control calls, we performed a Wilcoxon signed rank test ($P \leq 0.05$) with each individuals' mean vigilance duration in the five-minute periods before and after the playback of each stimulus type with Holm's Sequential Bonferroni corrections as post-hoc tests.

To test for response differences between sleeping site types (tree holes vs. tree tangles), we calculated the mean difference in vigilance during the five-minute periods before and after the playback of stimuli of each individual and used Mann-Whitney-U tests ($P \leq 0.05$) with Holm's Sequential Bonferroni corrections as post-hoc tests.

To test for immediate responses, scanning or movement directions were either rated as appropriate ('scanning up', 'freeze' and/or 'hide' after harrier hawk calls, 'scanning down', 'freeze' and/or 'hide' after fossa calls; no change/reaction after crested coua calls; compare Table 2) or inappropriate (no change / reaction after harrier hawk and fossa calls; 'freeze' or 'hide' after crested coua calls). χ^2 tests with Yates-correction on numbers of appropriate and inappropriate behaviours were used to test for differences in reactions of lemurs (random=50%; $P \leq 0.05$), separately for scanning and movement reactions. χ^2 tests also were used to test for behavioural changes between immediately before and immediately after the playbacks, using total numbers of different behaviours of each individual as unit of analysis.

To exclude the possibility that habituation had an influence on our results, we tested for variation in the difference of duration of vigilance before and after playbacks between the first and the last quarter of playback-experiments conducted on each animal, using a Wilcoxon signed rank test ($P \leq 0.05$). No change in the reactions towards presentation of predator and control calls was found ($F=0.005$; $P=0.943$).

Results

Duration of vigilance

The tested individuals displayed an overall difference in response to the different playback stimuli (Friedman-test: $\chi^2=24.970$, $P<0.001$). The duration of vigilance increased after playbacks of fossa and harrier hawk calls (Table 4). Although in 82% of the cases the individuals calmed down during the five minutes after the playback treatment, in 18% the individuals remained vigilant for more than five minutes. In 47% the lemurs did not increase vigilance after the control playback treatment with calls of crested couas. In 47% the individuals' vigilance was found to even decrease (Table 4). The animals never vocalised in response to the calls of potential predators.

Table 4. Vigilance in seconds (median with interquartile range, Q1-Q3) within five minutes before and after the playback of harrier hawk (N=29), fossa (N=26) and crested coua calls (N=27) (Wilcoxon signed ranks test; P≤0.05)

	Harrier hawk	Fossa	Crested coua
vigilance before call (s)	78 (0-162.5)	82.75 (23.9-185.9)	111 (35.3-268)
vigilance after call (s)	256.5 (98.5-300)	267.5 (161.3-300)	79.5 (8.8-160)
Wilcoxon Signed Ranks Test	Z=-3.731 P<0.001	Z=-3.749 P<0.001	Z=-2.581 P=0.01

Table 5. Percentages of behaviour observed immediately before and after presentation of territorial calls of harrier hawk, mating calls of fossa and contact calls of crested couas. χ^2 test (rate 50%; P≤0.05).

	rest %	vigilance %	autogrooming %
Harrier hawk			
before	73	23	7
after	24	74	2
	χ^2=43.506 P<0.05	χ^2=46.095 P<0.05	χ^2=2.778 P>0.1
Fossa			
before	73	22	5
after	24	76	0
	χ^2=37.565 P<0.05	χ^2=39.273 P<0.05	χ^2=27.895 P<0.005
Crested coua			
before	65	28	7
after	65	32	4
	χ^2=0.115 P>0.1	χ^2=0.269 P>0.1	χ^2=1.000 P>0.1

Immediate behavioural changes

78% of the tested sportive lemurs for fossa calls and 81% for harrier hawk calls immediately became vigilant in response to the playbacks of predator calls, whilst only 13% of the tested individuals changed behaviour to vigilance after coua calls. The percentage of vigilance increased from 22% and 23% immediately before to 76% and 74% immediately after the playback of fossa and harrier hawk calls, respectively (Table 5). In contrast, vigilance did not change in response to the presentation of crested coua calls (28% vs 32%).

Immediate scanning responses

In 73% of harrier hawk calls and in 100% of fossa calls, individual sportive lemurs showed appropriate scanning behaviour. In immediate response to playbacks of harrier hawk calls, lemurs scanned the sky, but not the ground or trees (df=22; χ^2=70.35, P<0.001, Table 6). The lemurs never looked directly at the speaker, but tended to scan the sky above the speaker. After playback of fossa calls, individuals scanned the ground (toward the speakers) or trees significantly more often than the sky (df=17; χ^2=220.85, P<0.001,Table 6). In response to crested coua call playbacks the sportive lemurs displayed an immediate change of scanning direction during only 9% of calls, and in all of those cases the lemurs reacted in response to real crested couas or other birds (df=21; χ^2=197.21, P<0.001; Table 6) who entered the area attracted to the calls.

Immediate movements

With regard to movements, sportive lemurs showed significantly more appropriate behaviour, (freezing in 92% of the cases) after playbacks of harrier hawk calls (df=22; χ^2=34.47, P<0.05, Table 6). In response to the call, individuals rapidly looked up, and then froze in that position. Interestingly, on two occasions they hid in the tree hole after real harrier hawks flew by. After playbacks of fossa calls however the animals showed appropriate and inappropriate responses in similar frequencies (df=17; χ^2=23.75, P>0.1, Table 6). In response to crested coua calls individuals showed significantly more appropriate behaviour, though, that meant they did not react except in one case where a real crested coua approached the lemur (df=21; χ^2=284.43, P<0.001, Table 6).

Tree hole vs tree tangle

There were no significant differences in vigilance during the five minutes before and after the playbacks between lemurs resting in tree holes (N=24 for harrier hawk calls; N=22 for fossa calls; N=24 for crested coua calls) and those resting in tree tangles (N=5 for harrier hawk calls, N=4 for fossa calls; N=3 for crested coua calls; Mann-Whitney U-test F=1503.0 P=0.442 for

Table 6. Appropriate reactions (APP: look up for harrier hawk, look down for fossa, no change for crested coua) and inappropriate reactions (INAPP: look down/no change for harrier hawk, look up/no change for fossa, look up/look down for crested coua) of scanning direction of tested Lepilemurs and APP (freeze/hide in canopy or tree hole for harrier hawk and fossa, no change for crested coua) and INAPP (out of tree hole/canopy or no change for harrier hawk and fossa, freeze/hide in tree hole/canopy for crested coua) of tested Lepilemurs. χ^2 test (rate 50%; P≤0.05); Degrees of freedom (Df) = 22 for harrier hawk, 17 for fossa, 21 for crested coua.

	Harrier hawk			Fossa			Crested coua		
	APP	INAPP		APP	INAPP		APP	INAPP	
scanning direction									
Σ	113	55	χ^2=70.35 P<0.001	121	4	χ^2=220.8 P<0.001	132	145	χ^2=197.21 P<0.001
movement									
Σ	97	71	χ^2=34.47 P<0.05	67	56	χ^2=23.75 P>0.1	145	1	χ^2=284.43 P<0.001

harrier hawk calls; F=942.5, P=0.687 for fossa calls; F=1418.5; P=0.916 for crested coua calls).

Discussion

We present the first data on the diurnal anti-predator behaviour of a nocturnal, solitary-living sportive lemur species. As individuals of this Critically Endangered species rest relatively exposed during the day, they may have evolved an effective strategy to avoid predation by aerial and terrestrial predators that are hunting during the day. Generally, our results corroborate similar previous research on diurnal as well as nocturnal primates by showing that the studied Sahamalaza sportive lemurs increase vigilance after playbacks of predator calls and show initial responses that are specific for a predator class (Macedonia and Polak, 1989; Macedonia, 1990; Zuberbühler *et al*., 1999; Fichtel and Kappeler, 2002; Fichtel, 2007; Karpanty and Wright, 2007, Rahlfs and Fichtel, 2010). After replay of fossa and harrier hawk calls vigilance behaviour of tested individuals increased and sometimes even lasted for over five minutes, suggesting that the Sahamalaza sportive lemur uses early acoustic detection of predators. After playbacks of the crested coua contact calls that were used as a control, the animals reduced vigilance, most likely because the presence of these calls indicates that no predator had been spotted by the crested coua. Lemurs scanned the sky after calls of harrier hawks, and scanned the ground or trees after calls of fossas, indicating that they were able to recognize and distinguish between calls of different predators and respond adequately to the different hunting strategies of aerial and terrestrial predators. As tested sportive lemurs responded adequately to all three call stimuli throughout the whole testing period and repeated presentation of the playback stimuli, we ruled out bias by habituation to our presence or the replays.

Similar responses to predator calls are known from playback experiments on different primate species: brown-mantled tamarin (*Saguinus fuscicollis* Spix, 1823) and mustached tamarin (*S. mystax* (Spix, 1823); Heymann, 1990; Peres, 1993); Diana monkey (*Cercopithecus diana* (Linnaeus, 1758); Zuberbühler *et al*., 1997) and Campbell's monkey (*C. campbelli* (Waterhouse, 1838); Zuberbühler, 2001); in lemurs: the cathemeral red-fronted lemur (*Eulemur rufus* Audebert, 1799) and eastern lesser bamboo lemur (*Hapalemur griseus* Link, 1795), the diurnal Milne-Edwards' sifaka (*Propithecus edwardsi* (Grandidier, 1871); Karpanty and Wright, 2007) and Verreaux's sifaka (*P. verreauxi* (Grandidier, 1867); Brockman, 2003). Similar to the Sahamalaza sportive lemur, these primates discriminated between aerial and terrestrial predators and became more vigilant after call playbacks. Contrary to our results, in all previous studies the animals showed distinct flight responses to different types of predators. The brown-mantled tamarin and the mustached tamarin (Heymann, 1990; Peres, 1993) for example looked upwards and quickly descended in response to aerial predators, while in response to terrestrial predators, they looked downwards and sometimes approached the predator. Similar to the Sahamalaza sportive lemur, active nocturnal primates were able to distinguish between different predator types and increased their vigilance, but additionally they usually showed flight responses (red-tailed sportive lemur: Fichtel, 2007; spectral tarsiers, *Tarsius tarsier* (Erxleben, 1777); Gursky, 2006; Gursky and Nekaris, 2007). Spectral tarsiers, which are secondarily nocturnal (Martin and Ross, 2005), are reported to freeze and sometimes show mobbing behaviour in response to a raptor model, and to climb upwards and mob carnivore or snake models. They also produce different types of alarm calls in response to aerial or terrestrial predators (Gursky, 2006; Gursky and Nekaris, 2007).

Active red-tailed sportive lemurs that lived in dispersed pairs, remained stationary and scanned the sky in response to harrier hawk calls, and fled or climbed up, scanned the ground and increased their scanning rate in response to fossa calls (Fichtel, 2007). The author suggested that vigilance is an important anti-predator behaviour of sportive lemurs, which is corroborated by our observations on Sahamalaza sportive lemurs. Contrary to our study, Fichtel (2007) conducted playbacks at night while the lemurs were active, which might explain the stronger flight responses of individuals compared to our findings on diurnal resting. Even though it could profit from warning pair-partner and offspring, the red-tailed sportive lemur did not produce alarm calls (Fichtel, 2007), like the solitary Sahamalaza sportive lemur in our study. Other studies on pair-living sportive lemur species report on loud vocalisation during periods of activity (Rasoloharijaona *et al*., 2006; Méndez-Cárdenas *et al*., 2008; Méndez-Cárdenas and Zimmermann, 2009), as found in the Sahamalaza sportive lemur (Seiler, 2012), and Rabesandratana *et al*. (2006) reported that a Milne-Edwards' sportive lemur emitted loud bark sequences when being chased by a fossa. The lemur changed its' vocalisation to louder shrill and chatter calls when the fossa had nearly grabbed it, and other sportive lemurs were attracted by the vocalisations. Similarly, a red-tailed lemur resting in a tree hole that was attacked by a Madagascar harrier hawk emitted loud distress calls (Schülke and Ostner, 2001). In comparison, both other *Lepilemur* species are more vocal than the Sahamalaza sportive lemur, which might be due to the fact that they live in dispersed pairs, whilst the Sahamalaza sportive lemur is a solitary species (Seiler, 2012). Lemurs might specifically use loud vocalisations when under attack to startle the predator (Scheumann *et al*., 2007). In the case of the Sahamalaza sportive lemur, we have never observed a predator attack and therefore do not know whether it uses vocalisations in that situation. In general, it would be counterproductive for a solitary lemur to use alarm calls in response to predator vocalisation, as this might draw the predator's attention. If the predator already detected the lemur, it might be advantageous for the individual to mob the predator, as shown in other solitary animals (Zuberbühler *et al*., 1999; Clark, 2005).

So far, only individually caged grey mouse lemurs (*Microcebus murinus* Miller, 1777) have been reported to not show flight responses when presented with predator models of fossas and raptors, but to increase vigilance towards the predator replicas (Rahlfs and Fichtel, 2010). The latter suggested that the observed vigilance behaviour is adapted to the hunting strategy of their predators, as many terrestrial predators, including the fossa, are stalking or sit-and-wait predators, relying on an element of surprise to capture their prey (Schaller, 1968, 1972). Once prey detects a predator, the latter usually is monitored in order not to grant another chance to strike (Schaller, 1967). This might also be the case for the Sahamalaza sportive lemur. A sportive lemur detecting a fossa could calmly keep track of the predator and decide to flee only if it becomes likely to attack. Similar to the reactions of Sahamalaza sportive lemurs after the playbacks of harrier hawk calls, the raptor model in the study of Rahlfs and Fichtel (2010) did elicit freezing behaviour in grey mouse lemurs. That is probably due to the hunting techniques used by birds of prey, which either actively search in flight or perch-hunt (Jaksić and Carothers, 1985). As raptors rely heavily on visual or acoustic cues to detect their prey, moving animals are perceived more easily than stationary ones (Rice, 1983). Thus, it should be advantageous for prey to remain immobile and freeze as soon as an avian predator is detected (Fitzgibbon, 1990; Caro *et al*., 2004).

The Sahamalaza sportive lemurs in this study did not show specific flight behaviour, unlike most diurnal and active nocturnal primates, but seem to use a similar strategy as described for mouse lemurs by Rahlfs and Fichtel (2010). Only twice after harrier hawk call playbacks did an individual flee into its tree hole, but only when a bird incidentally flew close by. In most other cases the animals froze. As individual Sahamalaza sportive lemurs are well camouflaged it might be sufficient to freeze when hearing but not yet seeing a raptor. During diurnal qualitative observations individuals usually dropped down in their tree hole as soon as a large bird, not necessarily a predator, flew by. This hints at a graded response strategy where it is adequate to initially assess from where the predator approaches, to look into the respective direction(s), and to decide what to do based on further observations (Kirchhof and Hammerschmidt, 2006). This would be adaptive as it reduces the costs of unnecessary responses to such frequent signals as the territorial calls of harrier hawks that can be heard regularly all day. It should be particularly relevant for this species to control energetic costs, as red-tailed sportive lemurs reportedly have some of the lowest resting metabolic rates of all mammalian folivores, about 50% below that predicted for their body mass (Schmid and Ganzhorn, 1996).

We furthermore tested for differences in vigilance between Sahamalaza sportive lemurs occupying different sleeping site types (tree holes vs. tree tangles). Our previous study (Seiler *et al.,* 2013a) found a significantly higher diurnal vigilance in lemurs resting in tree holes and we argued that this might be due to the increased risk of being detected by raptors. Individuals in tree holes might be easier to spot for raptors as they rest in the entrance of the holes and because such trees that have poorer canopy cover compared to tree tangle trees (Seiler *et al*., 2013a). The additional investment in vigilance suggests a compensating probably thermoregulatory benefit from exposed resting at tree hole entrances. Animals usually presented as much body surface as possible to direct sunlight. Furthermore, multiple flight routes are available to animals resting in tree tangles whilst individuals in tree holes could just hide in their tree holes, which often had sizeable cracks. Nonetheless, Sahamalaza sportive lemurs resting in tree holes did not respond more strongly to predator calls than animals resting in tree tangles, suggesting that individuals in both sleeping site types face a similar predation risk once a predator is close by. Even though individuals resting in tree tangles might face a lower risk of being detected by a predator compared to individuals in tree holes, they should keep track of the predator to be able to flee fast enough in case of detection by the predator.

Generally, the high amount of vigilance during the day might suggest that a certain degree of cathemerality is of advantage for this nocturnal lemur species. As we have never seen the animals travelling or feeding during the day it cannot be classified as purely cathemeral, though. Tattersall (1987) defines cathemerality as follows: “The activity of an organism may be regarded as cathemeral when it is distributed approximately evenly throughout the 24 h of the daily cycle, or when significant amounts of activity, particularly feeding and/or travelling, occur within both, the light and dark portions of that cycle.” Nonetheless, we suggest a high amount of vigilance during the day might not only be of advantage for the Sahamalaza sportive lemur, but also for every other nocturnal animal species that rests in rather open sites and has predators with reversed activity patterns.

In conclusion, our results suggest that resting Sahamalaza sportive lemurs respond to the diurnal predation pressure by relatively energy-saving predator-specific behaviours that include early acoustic detection, crypsis and keeping track of predators. These behaviours have previously been known from active diurnal or nocturnal primate species, but not for resting primates. The finding that even resting nocturnal lemurs show anti-predator behaviour that is specific for either terrestrial or aerial predators and increased vigilance, has important implications for their daily time and energy budgets, and might similarly apply to other primate species that have predators with reverse activity patterns.

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On-line Supplementary Information (SI)

S1. Numbers of playback-experiments conducted with six different versions of harrier hawk territorial call, fossa mating call and crested coua contact call with sportive lemur resting at two types of sleeping sites (tree hole: TH; tree tangle: TT).