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Activity patterns and temporal avoidance by prey in response to Sunda clouded leopard predation risk

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Abstract

Little is known about the activity patterns of Bornean ungulates, or the temporal interactions of these species with the Sunda clouded leopard *Neofelis diardi*. In this study, we use photographic capture data to quantify the activity patterns for the Sunda clouded leopard and six potential prey species: bearded pig *Sus barbatus*, Bornean yellow muntjac *Muntiacus atherodes*, red muntjac *Muntiacus muntjak*, lesser mouse deer *Tragulus kanchil*, greater mouse deer *Tragulus napu*, and sambar deer *Rusa unicolor*, and to calculate the overlap in activity patterns between these species. This is the first insight into the temporal interactions between the Sunda clouded leopard and its potential prey. Sunda clouded leopards' activity patterns overlapped most with those of sambar deer and greater mouse deer. In the absence of clouded leopards, we report a significant difference in activity patterns for bearded pigs which show greater nocturnal activity in the absence of this predator. This suggests that bearded pigs may be prey species for clouded leopards and they are capable of altering their activity pattern in response to this risk.

Introduction

Temporal interactions between predators and prey can be complex. Predators are expected to maximize their hunting efficiency (their intake per unit effort) by exploiting periods of prey vulnerability, while at the same time limiting competition with other predators. For example, carnivores specialized in burrowing such as badgers *Meles meles* dig prey from their underground refuges, the same prey species being hunted above ground by predators relying on speed (red fox, *Vulpes vulpes*) or stealth (European lynx, *Lynx pardinus*) (Fedriani, Palomares & Delibes, 1999). Prey species have to trade optimal feeding opportunities, finding mates and reducing competition with conspecifics against avoiding encounters with predators. Prey may avoid predators by temporal or spatial shifts. Valeix *et al*. (2009) describe how African ungulates altered their space use in response to the risk of lion predation; likewise, Fedriani *et al*. (1999) report that the red fox avoids conflict with the larger European lynx by a differential use of space. Bowyer *et al*. (1999) describe how female ungulates move to areas of lower predation risk before giving birth. Avoidance by shifting activity patterns is described, for example, by Eccard *et al*. (2008) and Gliwicz & Drabowski (2008) who found that bank voles *Myodes glareolus* and root voles *Microtus oeconomus*, respectively, became nocturnal in the presence of the diurnal least weasel (*Mustela nivalis*). A similar shift was described by Fenn & Macdonald (1995) who reported that a population of Norway rats *Rattus norwegicus* was diurnal (rather than the typical nocturnal) when facing a high risk of nocturnal predation by red foxes.

However, as Valeix *et al*. (2009) observed, prey species' behavioural plasticity varies and therefore, conversely, and provided the effect of competition is not dominant, we might expect predator activity to be often in phase with the periods when those potential prey species are most vulnerable to their method of predation. For some predators, this may result in their activity patterns mirroring those of their prey; while we would not expect this to be a general phenomenon, it may be commonest for felids that hunt principally using visual cues (Sunquist & Sunquist, 2002). Harmsen *et al.* (2011), for example, have reported this mirroring effect of predator and prey for both jaguar *Panthera onca* and *Puma concolor* and their respective main prey species in a rainforest environment. Jenny & Zuberbuhler (2005) report that leopard *Panthera pardus* activity patterns, although varying across Africa, remain in phase with its main prey. Likewise, Kawanishi & Sunquist (2004) found that tigers (*Panthera tigris*) in Taman Negara National Park, Malaysia, were mainly diurnal, an activity pattern that corresponds with that of their most important prey species. There are some conspicuous counter-examples however, for example, the lion *Panthera leo* is a primarily nocturnal hunter but is principally dependent on plains zebra *Equus quagga* and common wildebeest *Connochaetes taurinus* as prey (Mills & Shenk, 1992), species that are active diurnally.

Like all felids, the Sunda clouded leopard *Neofelis diardi* (hereafter clouded leopard) is an obligate carnivore, and is predominantly nocturnal, with some crepuscular activity (Cheyne & Macdonald, 2011; Hearn *et al.*, in press). In the absence of any larger carnivore in Borneo, this time tabling may function to maximize hunting opportunities rather than as a tactic to avoid interspecific conflicts.

While detailed information is currently lacking, the clouded leopard's diet is known to include sambar deer *Rusa unicolor*, muntjacs *Muntiacus* spp., bearded pig *Sus barbatus*, mouse deer *Tragulus* spp. (Rabinowitz, Andau & Chai, 1987; Mohamed, Samejima & Wilting, 2009), porcupines (Gordon & Stewart, 2007) and primates (Yeager, 1991; Matsuda, Tuuga & Higashi, 2008). The patterns of activity for most of these ungulate prey species in Borneo remain unclear as do the temporal interactions with clouded leopards. Elsewhere, the ungulate guild composition differs as does predation pressure, potentially shaping different patterns of activity for these ungulates. Across their ranges, the sambar deer is nocturnal (Schaller, 1967; Payne & Francis, 1998; Kawanishi & Sunquist, 2004), the red muntjac *Muntiacus muntjak* is diurnal (Payne & Francis, 1998; Kawanishi & Sunquist, 2004) or nocturnal (Kamler *et al.*, 2012), the yellow muntjac *Muntiacus atherodes* is diurnal (Payne & Francis, 1998), the lesser mouse deer *Tragulus kanchil* is crepuscular (Matsubayashi, Bosi & Kohshima, 2003) or arrhythmic (Payne & Francis, 1998), and the bearded pig mostly diurnal (Payne & Francis, 1998). In this study, we use photographic capture data from Borneo to quantify the activity patterns for six ungulate species: bearded pig *S. barbatus*, Bornean yellow muntjac *M. atherodes*, red muntjac *M. muntjak*, lesser mouse deer *T. kanchil*, greater mouse deer *Tragulus napu*, and sambar deer *R. unicolor*, and investigate the temporal segregation between them. Temporal partitioning among sympatric species of Muridae has been reported by Meek, Zewe & Falzon (2012) who speculate that this may reduce competition for food resources, but this has not previously been investigated for an ungulate guild. We compare activity cycles between males and females for clouded leopards and also for bearded pigs. For the other ungulate species, this subdivision was not possible. Either we could not reliably distinguish males from females in the photographs while retaining sufficient sample sizes, or in the case of the yellow muntjac, males and females do not travel independently of one another. We then compare the activity patterns of Sunda clouded leopard with those of the sympatric ungulates to draw inferences about principal prey species. Finally, we compare ungulate activity cycles in forests where clouded leopards were detected with those in which this predator appears to be absent. Clouded leopards may exert a top-down effect on the activity cycles of ungulates. In the absence of this apex predator, some species may be released from a predominantly diurnal activity cycle with consequences for the balance of competition with other ungulates.

We hypothesize firstly (Hypothesis 1) that if ungulates are vulnerable to predation by clouded leopards they will be more diurnal in areas where clouded leopards are present, compared with areas where clouded leopards are not present. If ungulate activity is not affected by the presence of clouded leopards, one plausible explanation is that the prey are not vulnerable because, for example, they are too small or too large to be hunted efficiently. Secondly (Hypothesis 2), we hypothesize that contest competition among ungulates will lead to lower temporal overlap for those species that exploit similar food resources that are patchily distributed, such as fruit.

Methods

Study sites

As part of an ongoing assessment of Sunda clouded leopard abundance and responses to habitat modification, six forest areas (Danum Valley Conservation Area, Ulu Segama, Malua and Kabili-Sepilok Forest Reserves, Tabin Wildlife Reserve, and the Lower Kinabatangan Wildlife Sanctuary) in Sabah, Malaysian Borneo, were surveyed with camera traps between November 2006 and August 2011. Together, these areas cover primary and selectively logged lowland Dipterocarp rainforest and selectively logged predominantly riverine rainforest. Clouded leopards were detected in all survey areas except Kabili-Sepilok Forest Reserve (hereafter Sepilok), presenting the opportunity to investigate ungulate activity patterns in the absence of a natural predator.

Field methods

We established 363 camera stations across the study sites. We set up cameras on old logging roads and both animal and man-made trails; they were positioned *c.* 40–50 cm above the ground with locations separated by *c.* 1.5–2.0 km. In all areas, we used passive infrared digital camera traps of varying models: Snapshot Sniper P41 (Snapshot Sniper LLC, OK, USA), Cuddeback Capture (Non Typical Inc., WI, USA), Bushnell Trophycam 2010 (Bushnell Corporation, KS, USA), Reconyx HC500 (Reconyx Inc., WI, USA) and Panthera V3 (Panthera, New York, NY, USA). At all locations, we set the cameras to operate continuously for 24 h of each day with either a white Xenon flash (Snapshot Sniper, Cuddeback

Table 1 The number of independent records of Sunda clouded leopard *Neofelis diardi* and six presumed prey species from each survey area. The number of trap days in each area is indicated in parentheses. The area covered by camera traps in each site is indicated as is the sample size for males and females where relevant

	Survey area					
Species	Danum Valley (6228)	Ulu Segama (4154)	Malua (3343)	Tabin (6172)	Kinabatangan (3997)	Sepilok (3755)
Area of camera grid (km^2)	66.26	60.07	102.80	160.28	111.0	52.4
Bearded pig *Sus barbatus*	379 (153 male, 36 female)	619 (210 male, 185 female)	828 (215 male, 57 female)	1056 (202 male, 199 female)	1308 (120 male, 275 female)	167 (41 male, 19 female)
Bornean yellow muntjac *Muntiacus atherodes*	542	126	134	1189	6	112
Red muntjac *Muntiacus muntjak*	100	167	24	70	0	0
Lesser mouse deer *Tragulus kanchil*	526	43	207	952	32	340
Greater mouse deer *Tragulus napu*	308	162	202	173	17	250
Sambar deer *Rusa unicolor*	291	214	608	587	90	21
Sunda clouded leopard	22 (11 male, 10 female)	104 (87 male, 16 female)	10 (8 male, 2 female)	41 (36 male, 4 female)	14 (7 male, 6 female)	0

Capture and Panthera V3) or infrared LED flash (Bushnell Trophycam 2010 and Reconyx HC500) firing under low light levels. All models of camera recorded the time and date of each photographic event.

Data analysis

Following van Schaik & Griffiths (1996), we assumed that when an animal of a given species passed in front of the camera, the likelihood of obtaining a photo-capture was equal throughout both night and day. Additionally, we assumed that the manner in which clouded leopards hunt would not affect detections. The date and time of each event were extracted from the EXIF data of each photograph. To reduce bias caused by repeat detections of the same animal, one record of each species per hour per camera site was considered as a detection event for each 24-h period, and subsequent records were eliminated.

The timing of sunrise and sunset in Sabah is fairly consistent throughout the year and across study sites. Sunrise is roughly 06:00 h and sunset 18:00 h, local time (GMT + 8). We categorized nocturnal activity as that which fell between 19:00 and 05:00 h and diurnal as between 07:00 and 17:00 h; the remaining periods we classed as crepuscular.

Statistical modelling of activity patterns was effected using circular techniques (Zar, 1996). We constructed models predicting daily activity as a function of continuous trigonometric predictor variables describing one and two complete cycles in a 24-h period ($\mathrm{Sin}\Theta$, $\mathrm{Cos}\Theta$, and $\mathrm{Sin}2\Theta$, $\mathrm{Cos}2\Theta$ with $\Theta\ \pi t/24$, where t is time in hours). For sympatric species, we first tested whether activity cycles differed among species using a categoric predictor with levels indicating species. For models testing for an effect of the presence of clouded leopard, we used a categoric term indicating site (firstly using six levels, one of which, Sepilok, was thought to not have clouded leopards). To investigate this further, we compared all sites with known presence of clouded leopard using five levels and, finally, we pooled the data from these five sites to compare with Sepilok using two levels. Patterns were compared between the sexes for bearded pigs and clouded leopards using a similar method. In the presence of interaction (significance of trigonometric × categoric terms) indicating evidence for varying periodicity, we fitted separate models for each level of the category (e.g. species). These models identified the amplitude and number of cycles within each 24-h period (see de Bruyn & Meeuwig, 2001). Patterns were visualized using the package Plotrix in R (Lemon, 2006).

We also calculated a coefficient of overlap between the activity patterns of each ungulate and Sunda clouded leopard from pooled data, including a novel bootstrap procedure, to estimate the precision of this measure following Ridout & Linkie (2009) and Linkie & Ridout (2011).

Results

We accumulated a total of 27 649 trap days across all study areas. The numbers of independent photo-captures for each species (Table 1) were considerably higher than previously reported for similar studies (e.g. Linkie & Ridout, 2011).

Overall activity patterns

There was strong evidence that activity patterns differed among species (cosx1*species: F 5,114 = 25.7, $P < 0.001$; sinx1*species: F 5, 114 = 2.6, $P = 0.03$). We therefore examined the cycles separately for each species (Fig. 1). Sunda clouded leopards showed a strongly nocturnal pattern of activity. Greater mouse deer and sambar deer were also clearly nocturnal. In contrast, both yellow and red muntjacs were diurnal, although red muntjac showed a higher peak in activity at dawn than did yellow muntjac. The lesser mouse deer was largely crepuscular and the bearded pig showed no distinct

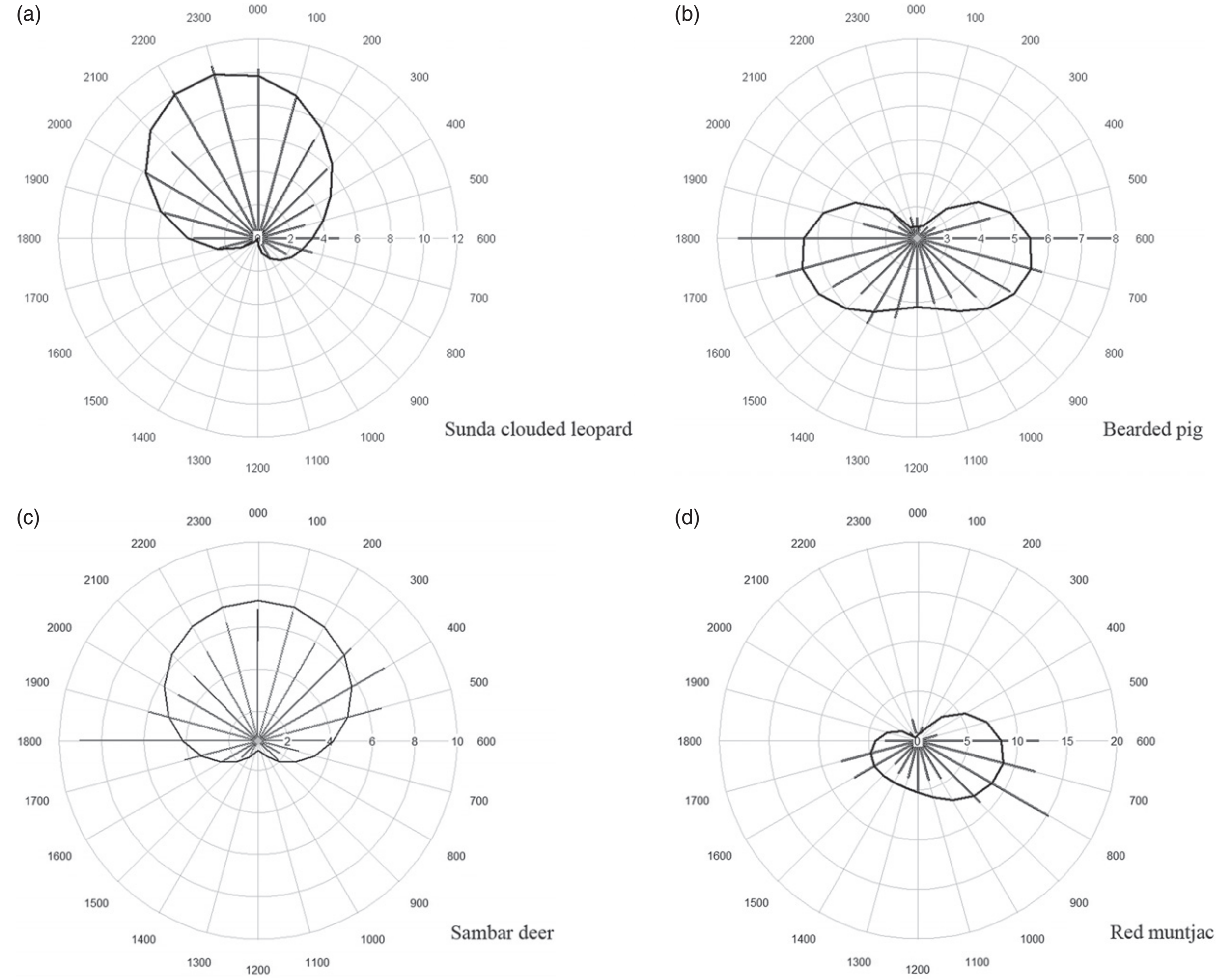


Figure 1 Periodic regression analysis of clouded leopard and ungulate activity patterns. Actual data are shown as bars and the model is plotted as a line. The plot is divided into hours with the response axis showing the percentage of detections in each hour. (a) Sunda clouded leopard *Neofelis diardi*, (b) bearded pig *Sus barbatus*, (c) sambar deer *Rusa unicolor*, (d) red muntjac *Muntiacus muntjak*, (e) Bornean yellow muntjac *Muntiacus atherodes*, (f) lesser mouse deer *Tragulus kanchil*, (g) greater mouse deer *Tragulus napu*.

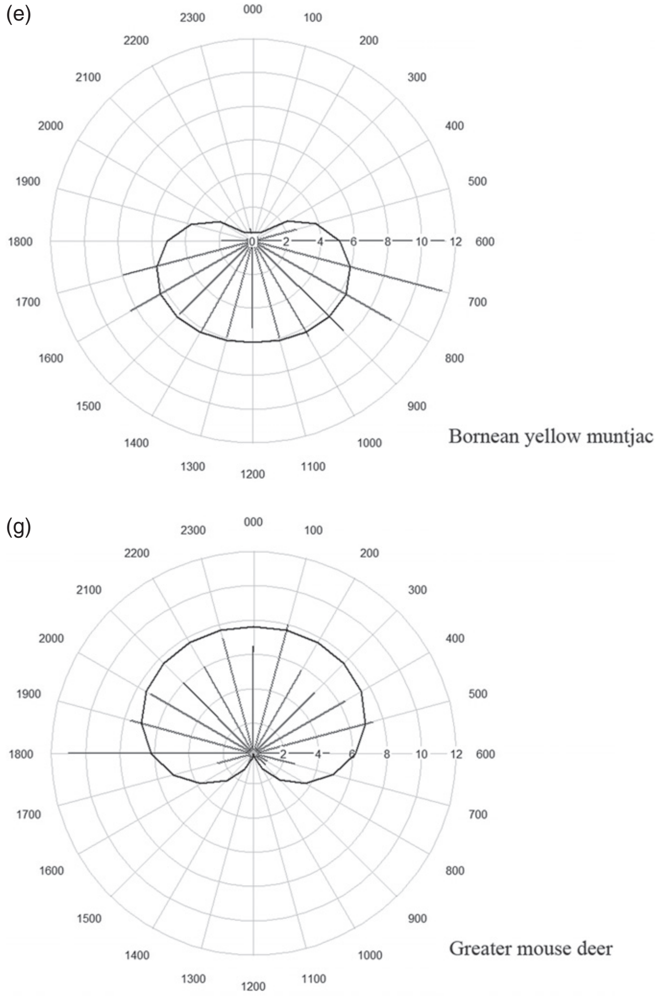
overall pattern. More detailed analyses of bearded pig activity, however, revealed patterns with clear cycles related to sex (Fig. 2).

Sex differences

Bearded pigs exhibited clear intersexual differences in activity (cosx1*sex: F 1, 38 = 11.1, $P = 0.002$) and there was weaker evidence for a difference between male and female clouded leopards (cosx2*sex: F 1, 38 = 4.0, $P = 0.054$). Male bearded pigs exhibited a bimodal, crepuscular activity cycle, whereas females were predominantly diurnal, with their activity peaking around midday. Both male and female clouded leopards showed predominantly nocturnal cycles, but the males were proportionally more active than females at dusk and dawn (Fig. 2).

Absence of clouded leopards

In Sepilok Forest Reserve, where clouded leopards were likely to have been absent, the activity cycles of bearded pigs differed from those in forests where clouded leopards were present, most markedly for male bearded pigs, to a lesser extent female bearded pigs and also greater mouse deer. Both male and female pigs showed a higher level of nocturnality in this area compared with the forests in which clouded leopards were present. Greater mouse deer were primarily nocturnal in both areas, but showed proportionally more activity at dusk and in the earlier part of the night in the absence of clouded leopards (Fig. 3). In contrast, there was little evidence that the other ungulate species were affected by the absence of clouded leopards (Fig. 3, Table 2). The comparisons between the remaining five sites where clouded leopards were present did not



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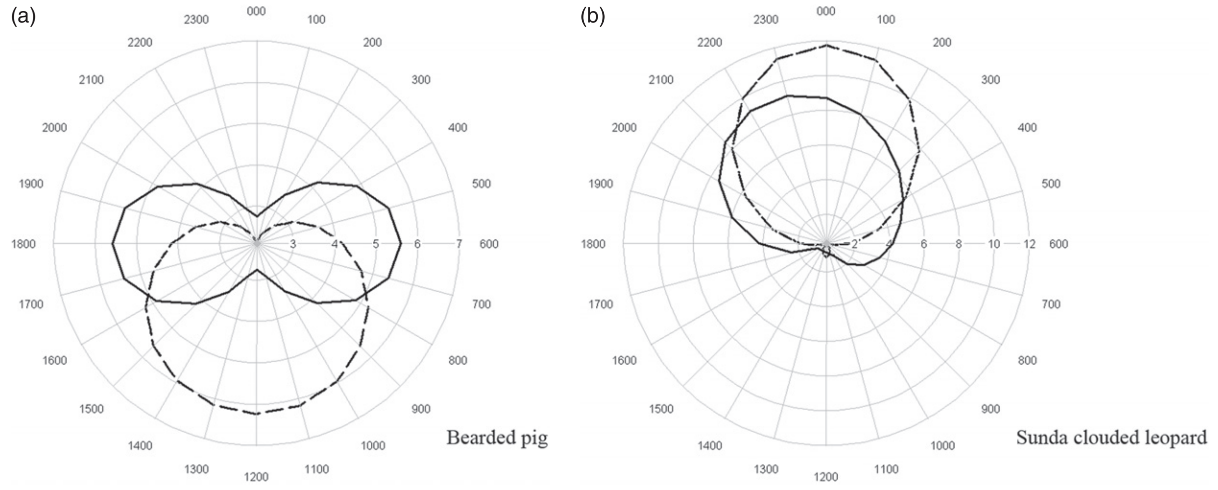

Figure 2 Differences in activity patterns between males (solid line) and females (dashed line) for (a) bearded pigs *Sus barbatus* and (b) Sunda clouded leopards *Neofelis diardi*. The plot is divided into hours with the response axis showing the percentage of detections in each hour.

Figure 3 Differences in ungulate activity patterns in areas with clouded leopards (solid line) and without (dashed line). (a) Male pigs, *Sus barbatus* (b) female pigs, *Sus barbatus* (c) greater mouse deer *Tragulus napu*, (d) lesser mouse deer *Tragulus kanchil*, (e) Bornean yellow muntjac *Muntiacus atherodes*, (f) sambar deer *Rusa unicolor*. The plot is divided into hours with the response axis showing the percentage of detections in each hour.

Table 2 Differences in ungulate activity patterns between areas with (pooled data) and without clouded leopards

Model	d.f.	Sum square	Mean square	*F*	*P*
Male bearded pigs					
sinx1*clouded leopard	1	2.606	2.606	0.537	0.468
sinx2*clouded leopard	1	24.082	24.082	4.962	0.032
cosx1*clouded leopard	1	91.464	91.464	18.847	<0.001
cosx2*clouded leopard	1	2.143	2.143	0.442	0.510
Residuals	38	184.417	4.853		
Female bearded pigs					
sinx1*clouded leopard	1	0.02	0.022	0.002	0.967
sinx2*clouded leopard	1	41.75	41.746	3.278	0.078
cosx1*clouded leopard	1	6.12	6.120	0.481	0.492
cosx2*clouded leopard	1	12.85	12.849	1.009	0.322
Residuals	38	483.96	12.736		
Greater mouse deer *Tragulus napu*					
sinx1*clouded leopard	1	12.340	12.340	3.313	0.077
sinx2*clouded leopard	1	12.621	12.621	3.389	0.073
cosx1*clouded leopard	1	1.597	1.597	0.429	0.517
cosx2*clouded leopard	1	3.651	3.651	0.980	0.328
Residuals	38	141.533	3.725		
Lesser mouse deer *Tragulus kanchil*					
sinx1*clouded leopard	1	10.84	10.838	0.779	0.383
sinx2*clouded leopard	1	0.20	0.197	0.014	0.906
cosx1*clouded leopard	1	21.24	21.239	1.526	0.224
cosx2*clouded leopard	1	0.64	0.641	0.046	0.831
Residuals	38	528.93	13.919		
Bornean yellow muntjac *Muntiacus atherodes*					
sinx1*clouded leopard	1	0.16	0.16	0.021	0.886
sinx2*clouded leopard	1	0.09	0.09	0.012	0.914
cosx1*clouded leopard	1	0.14	0.14	0.019	0.533
cosx2*clouded leopard	1	3.03	3.03	0.395	0.892
Residuals	38	291.64	7.67		
Sambar deer *Rusa unicolor*					
sinx1*clouded leopard	1	0.35	0.346	0.027	0.870
sinx2*clouded leopard	1	6.00	5.995	0.472	0.496
cosx1*clouded leopard	1	33.39	33.393	0.094	0.761
cosx2*clouded leopard	1	1.19	1.189	2.627	0.113
Residuals	38	482.96	12.710		

show any significant differences in activity patterns for yellow muntjac. There were significant differences for male and female bearded pigs, greater mouse deer and sambar deer (Table 3). In the presence of clouded leopards, the activity cycle of male pigs was either crepuscular or strongly diurnal and female pigs were predominantly diurnal, although in Malua the peak of activity was in the late afternoon and very early evening. Greater mouse deer maintained a predominantly nocturnal activity cycle across study areas, but showed a strongly bimodal pattern with peaks at dawn and dusk in Tabin. Similarly, sambar deer are nocturnal in all areas, but their activity peaks at dawn in Malua.

Activity overlap

The highest level of temporal overlap between ungulates (0.91) was observed for the greater mouse deer and sambar deer, which both showed a strongly nocturnal activity pattern (Fig. 4). The overlap between yellow and red muntjacs was also high (0.87). The lowest levels of overlap were between greater mouse deer and red muntjacs (0.32) and greater mouse deer and yellow muntjacs (0.27).

Both male and female clouded leopards overlapped most strongly with greater mouse deer, with overlap coefficients of 0.70 and 0.85, respectively (Fig. 4a and b). There was also high overlap between both male and female clouded leopards and sambar deer (0.67 with male clouded leopards and 0.79 with females). Conversely, there was low overlap between the predominantly nocturnal clouded leopards and the diurnal muntjacs (0.24 and 0.19 with yellow muntjac, and 0.29 and 0.23 with red muntjac, for male and female clouded leopards, respectively). Overlap was also low between male and female clouded leopards and the crepuscular lesser mouse deer, with coefficients of 0.48 and 0.41, respectively. The overlap coefficient was lower for female clouded leopards and female

Table 3 Differences in ungulate activity patterns between all areas where clouded leopards are present

Model	d.f.	Sum square	Mean square	*F*	*P*
Male bearded pigs					
sinx1*site	4	23.65	5.912	1.271	0.287
sinx2*site	4	10.77	2.693	0.579	0.679
cosx1*site	4	102.43	25.607	5.504	<0.001
cosx2*site	4	16.07	4.018	0.864	0.489
Residuals	95	442.02	4.653		
Female bearded pigs					
sinx1*site	4	66.77	16.694	2.697	0.035
sinx2*site	4	10.12	2.531	0.409	0.802
cosx1*site	4	32.92	8.229	1.330	0.265
cosx2*site	4	34.48	8.620	1.393	0.242
Residuals	95	587.96	6.189		
Greater mouse deer *Tragulus napu*					
sinx1*site	4	51.92	12.98	1.238	0.300
sinx2*site	4	20.53	5.13	0.489	0.744
cosx1*site	4	124.14	31.03	2.959	0.024
cosx2*site	4	44.24	11.06	1.055	0.383
Residuals	95	996.27	10.49		
Lesser mouse deer *Tragulus kanchil*					
sinx1*site	4	33.25	8.31	0.515	0.725
sinx2*site	4	27.62	6.91	0.428	0.788
cosx1*site	4	138.06	34.52	2.139	0.082
cosx2*site	4	61.19	15.30	0.948	0.440
Residuals	95	1533.17	16.14		
Sambar deer *Rusa unicolor*					
sinx1*site	4	4.94	1.24	0.323	0.862
sinx2*site	4	4.14	1.03	0.270	0.964
cosx1*site	4	50.39	12.60	3.293	0.014
cosx2*site	4	23.57	5.89	1.540	0.197
Residuals	95	363.44	3.83		
Bornean yellow muntjac *Muntiacus atherodes*					
sinx1*site	4	66.55	16.64	0.783	0.539
sinx2*site	4	28.92	7.23	0.340	0.850
cosx1*site	4	13.82	3.46	0.163	0.957
cosx2*site	4	30.16	7.54	0.355	0.840
Residuals	95	2017.70	21.24		
Red muntjac *Muntiacus muntjak*					
sinx1*site	4	25.93	8.64	0.616	0.607
sinx2*site	4	24.50	8.17	0.583	0.628
cosx1*site	4	7.24	2.41	0.172	0.915
cosx2*site	4	42.90	14.30	1.020	0.389
Residuals	95	1065.62	14.02		

bearded pigs than male pigs (0.40 and 0.47, respectively). Male clouded leopards overlapped more strongly with both male and female bearded pigs (0.64 and 0.52, respectively).

While the only species with statistically significantly different activity cycles between Sepilok and the other forest areas was bearded pig, and to a lesser extent greater mouse deer, the collective shifts in activity patterns resulted in some clearer differences in overlaps among the ungulates, there are numerous pairs of taxa where the confidence intervals for overlaps with and without clouded leopard do not overlap (Fig. 5). Sambar deer, for example, overlapped more with all other species apart from greater mouse deer in the absence of clouded leopards. Other clear effects included that in the absence of clouded leopards male and female pig activity and yellow muntjac overlapped less, and that conversely there were more overlaps between male pigs and greater mouse deer, and between greater mouse deer and yellow muntjac.

Discussion

This is one of the first studies to quantify the activity patterns of Bornean tropical forest ungulates and is the first to measure the overlap between the activity cycles of the Sunda clouded leopard and some of its potential prey species. We show a significant shift in bearded pig activity patterns in the absence of clouded leopards, suggesting that these activity cycles may be shaped, at least in part, by the risk of predation by clouded leopards. We also reveal a high temporal overlap between the clouded leopard and both sambar deer and greater mouse deer.

Activity patterns of Bornean ungulates and overlap with clouded leopards

We found bearded pigs to be predominantly diurnal (females) or crepuscular (males). A similar species, *Sus scrofa*, was also found to be diurnal in Sumatra (Linkie & Ridout, 2011). We found a significant shift in activity patterns for male pigs between areas of differing predation pressure. Male pigs were almost exclusively nocturnal where clouded leopards were absent. It may be more cost effective for pigs, in terms of energy expenditure, to forage and move at night when temperatures are lower, but the risk of predation may be a stronger driving force and prevent this in areas where clouded leopards are present. This driving force may be stronger for female than for male pigs. Female bearded pigs showed a higher proportion of diurnal activity than did male pigs and showed a weaker shift in cycle in the absence of clouded leopards. Most pigs identified as females in this study were recorded with young, or were lactating; diurnality may be a strategy to avoid encountering clouded leopards during the period when piglets are most vulnerable to predation from this felid.

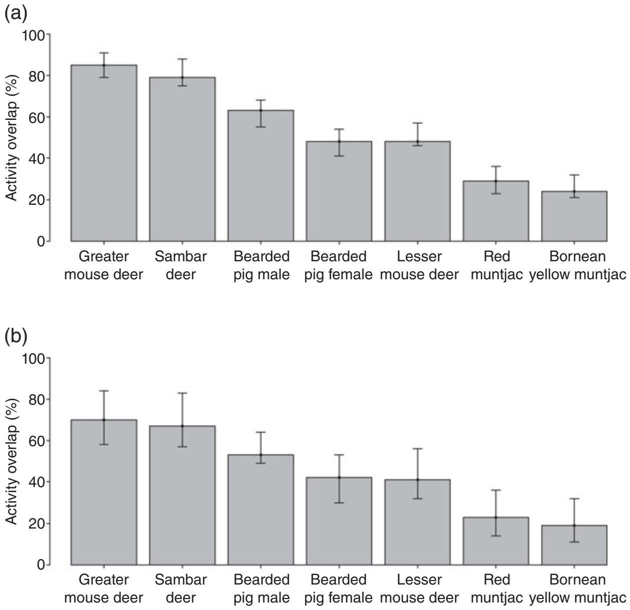

Figure 4 The overlap between each ungulate species and (a) male clouded leopards and (b) female clouded leopards. Error bars show 95% bootstrap confidence intervals.

While there may be other contributory factors shaping the pigs' activity patterns that we are not accounting for, this activity shift for bearded pigs suggests that they may be prey species for clouded leopards, as it was only in Sepilok where the pigs were active nocturnally. The apparent behavioural plasticity of the bearded pig, allowing increased diurnality in the presence of clouded leopards, may be a tactic to avoid predation. Similarity in activity patterns between predator and prey is, by itself, not compelling evidence that a predator relies on any prey species. Felids such as jaguars and pumas may have activity patterns in phase with their main prey (Harmsen *et al.*, 2011) or, as with lions, have cycles that oppose those of their prey (Mills & Shenk, 1992). Predator–prey size relationships are also known to be important in shaping trophic links (Owen-Smith & Mills, 2008). Bearded pigs fall with the mass range that clouded leopards are likely to take based on prey mass to predator mass allometries (e.g. Carbone *et al.*, 1999; Macdonald, Mosser & Gittleman, 2010). Although adult pigs are at the greater end of this mass range, clouded leopards might target juvenile animals.

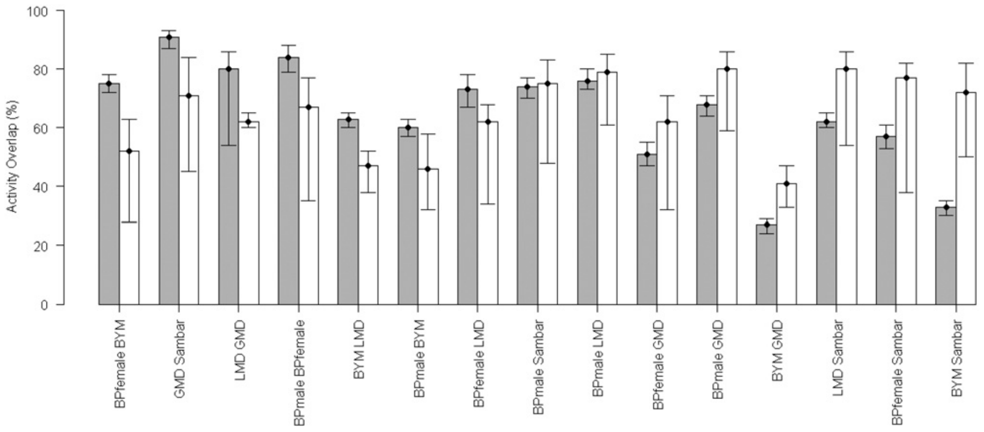

Figure 5 The difference in overlap between each pair of ungulates in areas with clouded leopards (grey bars) and without (white bars). Error bars show 95% bootstrap confidence intervals. BP = bearded pig *Sus barbatus*, BYM = Bornean yellow muntjac *Muntiacus atherodes*, LMD = lesser mouse deer *Tragulus kanchil*, GMD = greater mouse deer *Tragulus napu*. The dyads are ordered with greater shifts in overlap to the right.

The weak evidence for activity shifts for the other ungulates between areas of different predation threat raises questions about their capacity to respond to contours in the landscape of fear. In Borneo, opportunistic observations of clouded leopards with kills (Rabinowitz *et al.*, 1987) or the discovery of dead animals, presumed to have been killed by clouded leopards (Mohamed *et al.*, 2009), indicate that sambar deer, mouse deer species and muntjac species are also preyed on by clouded leopards, although we do not know their relative importance in its diet. Threat of predation by clouded leopards may be a weaker force in shaping their activity patterns than that of other predators, or avoiding contest competition for instance. Yellow and red muntjacs were diurnal as both Payne & Francis (1998) and Kawanishi & Sunquist (2004) have observed. For the yellow muntjac, this pattern held regardless of predation pressures (we could not assess this effect for the red muntjac due to small sample sizes). This presumed adaptation for diurnality may prevent a shift in the activity of yellow muntjacs, perhaps due to poor vision at night. A primarily nocturnal activity pattern for muntjacs in Lao People's Democratic Republic was, however, described by Kamler *et al.* (2012) who speculated that this was due to predation by the diurnal dhole *Cuon alpinus*. We also found high overlap between the two muntjacs' activity cycles. Both muntjacs have largely frugivorous diets, but red muntjacs are thought to browse more than do yellow (Barrette, 1977), which may explain the lack of temporal segregation. The low overlap between the muntjacs and the greater mouse deer may also be partly explained by diet; the greater mouse deer also eats fruit (Payne & Francis, 1998) and so this may be a strategy on the part of the mouse deer to avoid contest competition with the larger species. We describe a crepuscular activity cycle for the lesser mouse deer, a pattern also found by Matsubayashi *et al.* (2003), and this was not affected by the presence of clouded leopards. It is likely that to avoid contest competition with the larger nocturnal greater mouse deer, the activity of the lesser mouse deer, which is also frugivorous (Payne & Francis, 1998), is restricted to a crepuscular cycle. Consequently, temporal overlap between the two mouse deer species was relatively low. We found sambar deer to be strongly nocturnal corroborating Schaller (1967) and Kawanishi & Sunquist (2004). In this latter study, the activity pattern of the sambar deer may have been shaped by avoidance of the diurnal tiger. The highest coefficient of activity overlap was found between the sambar deer and the greater mouse deer. These species have dissimilar diets; the sambar deer is a mixed feeder, but predominantly a grazer and browser (Payne & Francis, 1998), and so competition for food is minimal.

In the absence of clouded leopards, the overlaps between species' activity patterns clearly differed (Fig. 5). The dyads including sambar occur mainly on the right of the x-axis where overlaps increased in the absence of clouded leopards. Increased contest competition between sambar deer and other ungulates (with the exception of the greater mouse deer) due to increased overlap in activity cycles, however, is unlikely for these very dispersed resources.

Temporal interactions are only one facet of the predator–prey relationship; spatial shifts of predator and prey populations relative to each other will play a role. The ecology of fear concept (Brown, Laundré & Gurung, 1999) codifies the naturalistic observation that prey species are likely to avoid areas (even those good for foraging) where they are particularly vulnerable to predators. We have presented data consistent with the possibility of temporal avoidance of clouded leopards by bearded pigs, and perhaps by greater mouse deer. The next priority is to find out whether they, or indeed any of the species that did not exhibit a temporal shift, adapt their use of space to the risk of predation by clouded leopards.

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