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ORIGINAL PAPER

Prey refuges as predator hotspots: ocelot (*Leopardus pardalis*) attraction to agouti (*Dasyprocta punctata*) dens

Willem-Jan Emsens · Ben T. Hirsch · Roland Kays · Patrick A. Jansen

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Abstract We tested the hypothesis that prey refuges attract predators, leading to elevated predator activity in the vicinity of refuges. We used camera traps to determine whether the spatial activity of a predator, the ocelot (*Leopardus pardalis*), was biased toward refuge locations of its principal prey, the agouti (*Dasyprocta punctata*). We radio-tracked agoutis at night to locate active refuges and compared the activity of ocelots between these refuges and surrounding control grid locations. We found that ocelots visited the area near agouti refuges significantly more often and for longer periods of time than control locations, and that they actively investigated the refuge entrances. Both occupied and unoccupied refuges were visited, but the duration of inspection was longer at occupied refuges. As the ocelots could probably not see the agoutis within the refuges, olfaction likely cued foraging ocelots. Two refuges were repeatedly visited by the same ocelots on different days, suggesting spatial memory. Overall, our results suggest that predators can be attracted to prey refuges or refuging prey. The benefits to prey of staying nearby a refuge would thus be counterbalanced by higher likelihoods of predator encounter. This should stimulate prey to use multiple refuges alternatingly and to not enter or exit refuges at times of high predator activity.

Keywords Agouti · Behavior · Movement · Ocelot · Predation · Refuge

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W.-J. Emsens · B. T. Hirsch · R. Kays · P. A. Jansen
Smithsonian Tropical Research Institute (STRI), Apartado, 0843-03092 Balboa, Panama

W.-J. Emsens · P. A. Jansen
Department of Environmental Sciences, Wageningen University, PO Box 47, 6700 AA Wageningen, The Netherlands

W.-J. Emsens
Department of Biology, Ecosystem Management Research Group, University of Antwerp, Universiteitsplein 1, 2610 Wilrijk, Belgium

B. T. Hirsch
School of Environment and Natural Resources, Ohio State University, 2021 Coffey Rd, Columbus, OH 43210, USA

R. Kays
North Carolina Museum of Natural Sciences, 11 W. Jones Street, Raleigh, NC 27601, USA

R. Kays
Program of Fisheries, Wildlife and Conservation Biology, North Carolina State University, Raleigh, NC 27695, USA

W.-J. Emsens (✉)
Antwerp University, Universiteitsplein 1, 2610 Wilrijk Antwerp, Belgium
e-mail: w.emsens@gmail.com

Introduction

Prey species often attempt to minimize their spatial and temporal overlap with predators. They may, for example, avoid activity in relatively dangerous habitats or particular times of the day (Craig and Freeman 1991; Harmsen et al. 2011). Moreover, many prey species use refuges to minimize exposure to predators while resting or to retreat to safety while active. It is generally assumed that staying close to a refuge is an effective antipredator strategy (Kramer and Bonenfant 1997; Camp et al. 2012). By staying near a refuge, prey need less time to reach protection when a predator is encountered (Blumstein 1998; Camp et al. 2012) and thus only stray from the vicinity of refuges for critical activities such as foraging or mating (Kramer and Bonenfant 1997).

Predators, on the other hand, aim to maximize prey encounter rates, concentrating their search in areas where prey are expected to be more common or more easily captured (Sih 1984; Stephens and Krebs 1986). It has been suggested that predators therefore cue in to refuges of their prey and obtain information about how

and when they are used (Day and Elwood 1999; Heymann 1995). Reports of snakes (*Epicrates inornatus*) gathering near bat-cave exits (Rodriguez-Duran 1996), weasels (*Mustela nivalis*) cueing in to vole scent marks left at vole refuges (Ylonen et al. 2003), or leopards (*Panthera pardus*) hunting baboons near baboon sleep sites (Cowlishaw 1994) indicate that such predator attraction to refuges exists. In this context, prey refuges that are used frequently would be locations of elevated predator activity. Little is known about "prey tracking" responses on small scales, for example within a predator's home range. This can be related to the difficulty of tracking small-scale movements of freely-moving predators, particularly elusive and nocturnal felids, in relation to their prey (Maffei et al. 2005; Hammond et al. 2007; Roth and Lima 2007).

In this paper, we test the hypothesis that prey refuges and refuging prey attract predators, elevating predator abundance in the vicinity of refuges. We used camera traps to determine whether active refuges of Central American agoutis (*Dasyprocta punctata*) are locations of elevated visitation rate and activity of the agoutis' principal predator, the ocelot (*Leopardus pardalis*).

Materials and methods

Study site and species

Field work was conducted from February through May 2010 on Barro Colorado Island (BCI), Panama (9°10′N, 79°51′W). BCI is a 1,560-ha island covered with tropical moist forest of different successional stages (Leigh 1999) and is administered by the Smithsonian Tropical Research Institute. The climate is seasonal, with a 4-month dry season from December–March. Our study area consisted of 30 ha of dense late-secondary forest in the center of BCI.

The Central American agouti is a 2–4-kg caviomorph solitary scatter-hoarding rodent that ranges from Mexico to Argentina. Agoutis shelter in multiple burrows, hollow logs, or woody debris throughout the home range (Emsens et al. 2013; Smythe 1978). Agoutis are primarily diurnal, with occasional bouts of nocturnal activity (Lambert et al. 2009; Smythe 1978). The ocelot is a largely nocturnal and inconspicuous felid, occurring from the southern USA to Argentina. Home-range size of one individual ocelot may cover many square kilometers (Dillon and Kelly 2008). On BCI, agoutis are an important component of the ocelot's diet (Moreno et al. 2006), and ocelots in turn are the principal predator of agoutis (Aliaga-Rossel et al. 2006).

Camera trapping

We used motion-triggered camera traps (RC55, Reconyx Inc., Holmen WI, USA) to monitor ocelot activity at refuges used by agoutis and at 144 control points in the surrounding area, using standard procedures for unbaited camera trapping (Kays et al. 2011). If ocelots indeed cue in to agouti refuges, then this should be reflected in a disproportionate number of ocelot counts at the refuges in comparison with these control points.

The agouti refuges were located by manually radio-tracking radio-collared agoutis during the night (AOR 8000, AOR Ltd., Japan), when agoutis were most likely to reside in their refuge (Emsens et al. 2013). Agoutis were captured using live traps (Tomahawk Live Trap Co., Hazelhurst, Wisconsin, USA) baited with banana or coconut. Traps were checked twice daily shortly after peak agouti activity times. Adult individuals (>2.3 kg; Smythe 1978) were anesthetized with 0.8 mg/kg Telazol (Tilamine hydrocholoride + Zolazepam) and fitted with a VHF radio collar (Advanced Telemetry Systems Inc., Isanti MN, USA). The trapping and radio-collaring procedures were approved by the Institutional Animal Care and Use Committee of the Smithsonian Tropical Research Institute and conducted under research permits authorized by the Barro Colorado Nature Monument. Individuals were tracked once every 2–4 nights during February through May 2010 to locate active refuges that they used for resting. As agoutis frequently switch between multiple refuges (Emsens et al. 2013), these "active" refuges were not constantly used. Refuge locations were recorded with a GPS receiver (Garmin 60CSx).

We monitored refuges with a visible entrance, i.e., burrows and hollow logs. Refuges that consisted of large piles of woody debris (up to many square meters), or dense vine tangles, were excluded as it was impossible to aim the camera at a distinct entrance. In total, we monitored 11 different refuges that were scattered across the 30-ha study site. At each refuge, a camera facing the entrance was attached to a tree trunk at 1.5–3-m distance and 20–30-cm height. The 144 control deployments were arranged in a randomly generated grid surrounding the refuge deployments. The grid points had 50 m interspacing and covered the entire 30-ha study area (Fig. 1). The control deployments only visually differed from the refuge deployments in that they had no refuge; all other (possible) variation was considered random. Control deployments were divided over four consecutive 1-week batches. We respected a 100 m minimum distance between simultaneous deployments to avoid spatiotemporal correlation of ocelot observations. For the control deployments, camera traps were attached to a tree trunk at 20 cm above the ground facing the most open direction to maximize animal detection distance. All cameras were programmed to take a continuous series of photographs at 1 s intervals whenever animals triggered the sensor.

We collected an average of 45.9 days of footage per refuge (SD=27.14) and an average of 7.33 days (SD=0.66) per control point. For each deployment, we measured the maximum detection distance by hand-waving 15 cm above

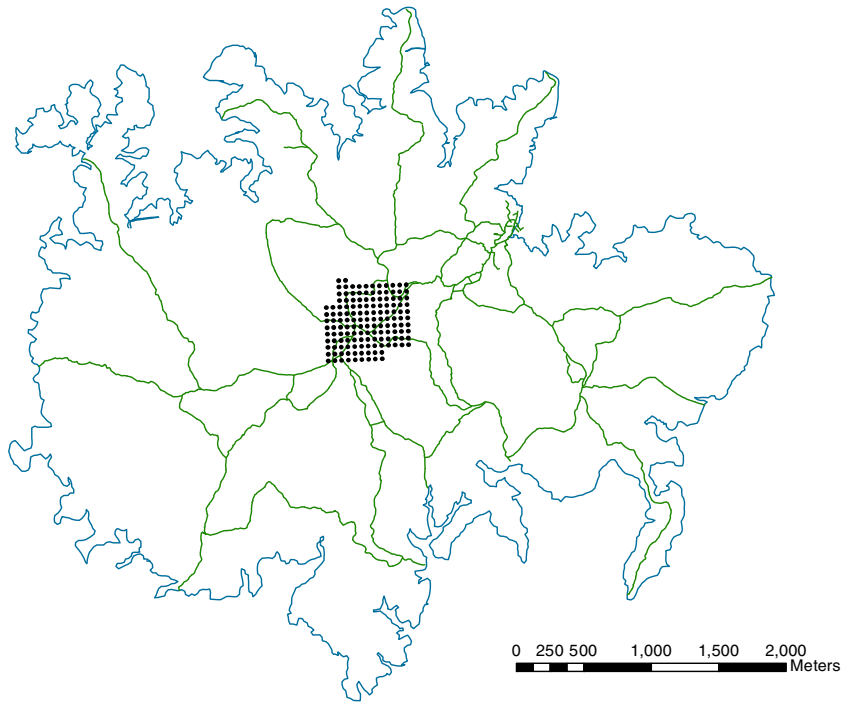

Fig. 1 Grid camera deployments (*black dots*) in the 30-ha study area at the center of Barro Colorado Island, Panama

the ground at different distances from the camera in walk test mode (Kays et al. 2011). Detection distances were significantly shorter for the refuge deployments (Wilcoxon rank-sum test; W=299.5, P<0.001), as the latter were set to face the refuge entrance rather than to maximize detection distance. All footage was analyzed post hoc for ocelot visits, with exact date, time, ocelot residence time, and ocelot ID (based on each individual's unique spotted pattern) in a custom-made database (Kays et al. 2011). Additionally, we combined our camera-trapping with manual agouti radio-tracking to determine if a refuge was actually occupied by an agouti during nighttime.

Statistical analyses

Analyses were conducted in R 2.15.2 (R Development Core Team 2013). We used Poisson regression for count data (Generalized Linear Model with Poisson error) to test whether ocelots visited refuge locations more frequently than surrounding grid points. Because the number of events recorded increases linearly with deployment duration and detection distance, the logarithms of both variables were included in the model as offsets (Crawley 2007). There was no overdispersion in the model. In the results section, the visit rate is expressed as the number of visits per day (deployment duration) and meter (detection distance). We used a Wilcoxon rank-sum test to compare the duration of ocelot visits between refuges and control points and between occupied and non-occupied refuges.

Results

We accumulated a total of 1,055 days of camera trapping at the 144 control points and 505 days at the 11 agouti refuges. At least five different ocelots were photographed across the 30-ha study area at the time of our study, suggesting a high degree of home-range overlap. The average rate at which cameras recorded ocelots was 2.3 times higher for refuges (0.0151 d^{-1} m^{-1}; 15 detections in total) than for control points (0.0067 d^{-1} m^{-1}; 20 detections). This difference was significant (GLM with Poisson errors, β=0.78 (±0.34 SE); W_1=5.31; P=0.02), suggesting that the higher rate of refuge visits is not attributed to chance alone. All but one of the ocelot refuge visits occurred between 19:00 h–07:30 h. Ocelot residence time was generally brief (<3 min), but significantly longer than the residence times at the control points (Wilcoxon rank-sum test, W=34.5; P<0.001; Fig. 2a).

Out of the 15 refuge visits by ocelots, 5 visits occurred when the refuge was actually occupied by an agouti. Ocelots spent significantly more time near occupied refuges than near vacant refuges (Wilcoxon rank-sum test, W=50; P=0.002; Fig 2b). The majority of ocelots (73 %) showed behavior that indicated interest in the refuge, such as leaping on top of the refuge or sticking their heads inside the entrance (Fig. 3, Movie S1). No distinct behavior was observed at control locations. Some ocelots visited the same refuge repeatedly: one refuge was visited five times in 1 month by two different ocelots, while another refuge was visited twice in 2 weeks by the same ocelot. As ocelots were not able to actually enter any of the refuges, no agoutis were observed to

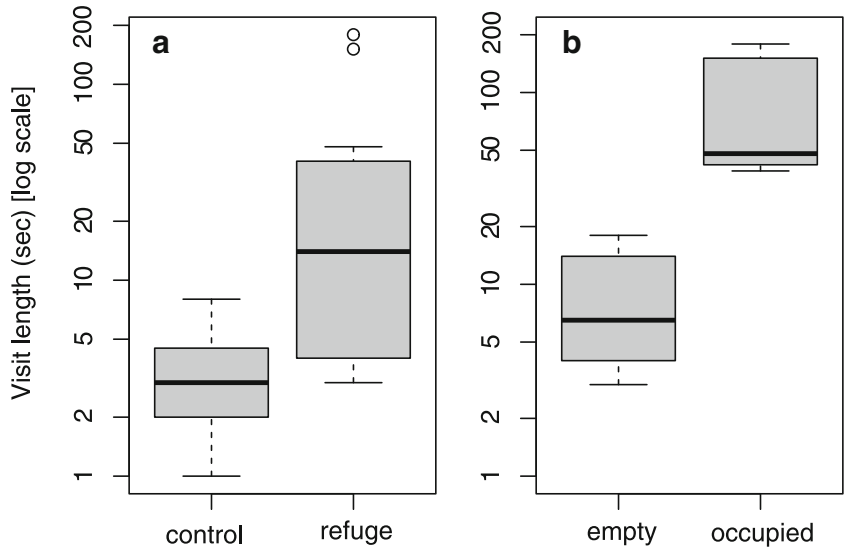

Fig. 2 Length of visits by ocelots (*Leopardus pardalis*) for **a** refuges (n=15, the *two circles* indicate outliers) versus control grid points (n=20) and **b** unoccupied (n=10) versus occupied refuges (n=5), on Barro Colorado Island, Panama

be harmed when inside the refuges, indicating that refuges did provide adequate protection against ocelots.

Agoutis did not show any peculiar behavior at their refuges, apart from a single occasion where a male agouti was seen spraying urine at its refuge entrance (scent-marking) and another occasion where an agouti was blocking the entrance with woody debris and litter. Generally, agoutis tended not to stick around at the refuge entrance, and entries and exits were swift. Once agoutis had entered their refuge, typically around dusk, they did not exit until dawn.

Discussion

Our results show that agouti refuges were more frequently visited by ocelots than were surrounding control locations, and the majority of ocelots clearly showed interest in the refuge entrances. Although higher predator visit rates at prey refuges are not surprising per se, empirical proof of such behavior in wild predators is scarce.

We posit that ocelots track agouti scent marks at the refuges, as they were unlikely to actually see the agoutis that were hidden within the refuges. Although tracking scent marks is a common strategy in mammalian predators (Banks et al. 2000; Ylonen et al. 2003; Hughes et al. 2010), evidence for such behavior in felids is scarce and considered of less importance (Turner et al. 2000; Sunquist and Sunquist 2002) but see Hughes et al.(2010). Emmons (1988) previously hypothesized that olfaction is an important cue to foraging ocelots. Because agouti refuges are generally used repeatedly (Emsens et al. 2013), they may emit odors regardless of whether the agouti is inside at the time of predator inspection. Moreover, agouti scent-marking as observed in our study, meant as a signal to other agoutis, should provide an olfactory cue to predators (Banks et al. 2000; Hughes et al. 2010). The fact that ocelots tended to stay longer near a refuge if it was occupied by an agouti also indicates that olfactory cues are important. This result also reveals a limitation of this study as it cannot be exactly determined whether ocelots are seeking out agouti refuge locations per se, or if they smell the agoutis inside the refuges. However, most refuges were unoccupied at the time of ocelot inspection, suggesting that ocelots are attracted to the refuges at least to some extent. Moreover, two refuges were repeatedly visited by the same two ocelots, suggesting spatial memory. Although our observations on these revisitation events are too sparse to draw firm conclusions, it is in general not uncommon for predators to memorize and revisit locations of potentially profitable patches and thus learn about prey refuge use (Day and Elwood 1999; Heymann 1995). For example, spatial memory has been linked to egg-predating crows revisiting nest sites where they had prior predation success (Sonerud and Fjeld 1987) and for red foxes that quickly move between different (previously visited) profitable patches to increase their foraging efficiency (Phillips et al. 2004).

No agoutis were seen to be harmed while inside the refuges, suggesting that refuges provide adequate protection once inside. However, our findings suggest that areas nearby refuges can host elevated predator activity. This could imply that staying close to a refuge while active is not necessarily an effective antipredator strategy. Although the presence of a refuge may diminish predation risk by offering a quick escape route (Kramer and Bonenfant 1997; Camp et al. 2012), this advantage holds only if prey can timely detect the predator and flee. The careful stalking behavior of the ocelot (Emmons 1988; Sunquist and Sunquist 2002), in combination with the typical dense cover provided by its forest habitat (Sunquist and Sunquist 2002; WJ Emsens personal observation), suggests

Fig. 3 Radio-tagged agouti leaving its refuge at dawn (**a**) and ocelot inspecting the refuge in which the agouti was spending the night (**b**)

that agouti predation risk is affected by the probability of an ocelot encounter more than by the distance to the nearest refuge.

Agoutis at our study site predictably enter and exit their refuges at sunset, which overlaps with the main activity of ocelots. We propose that the high predation pressure on agoutis by ocelots (Aliaga-Rossel et al. 2006; Moreno et al. 2006) can be partly explained by these felids scanning refuge locations. Such visits may be most dangerous to the agouti at dusk and dawn, when agoutis are expected to be in the vicinity of their refuge. This finding is in agreement with Aliaga-Rossel et al. (2006) who reported that two out of four agoutis killed during their study were found significantly closer to their nearest refuge than to random locations within their home range. Frequent switching between multiple refuges, which has been observed in agoutis (Emsens et al. 2013) as well as in other species, e.g., golden-handed tamarins, *Saguinus midas* (Day and Elwood 1999) or springhares, *Pedetes capensis* (Peinke and Brown 2005), could be an antipredator strategy to diminish refuge use predictability (Day and Elwood 1999).

We have shown that predators actively cue into prey refuges and refuging prey, possibly making refuges locations of elevated predation risk. We propose that prey animals should minimize predation mortality by avoiding activity overlap with their predators (e.g., by seeking refuge before

any high-risk period), or by minimizing their predictability (e.g., through frequent refuge switching).

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