



Food acquisition and predator avoidance in a Neotropical rodent



Lennart Suselbeek^{a,b,*}, Willem-Jan Emsens^{a,b,c}, Ben T. Hirsch^{b,d}, Roland Kays^{b,e,f},
J. Marcus Rowcliffe^g, Veronica Zamora-Gutierrez^{a,b,h}, Patrick A. Jansen^{a,b,i}

^a Department of Environmental Sciences, Wageningen University, Wageningen, The Netherlands

^b Smithsonian Tropical Research Institute (STRI), Balboa, Ancón, Panama

^c Department of Biology, University of Antwerp, Wilrijk, Belgium

^d School of Environment and Natural Resources, Ohio State University, Columbus, U.S.A.

^e Nature Research Center, North Carolina Museum of Natural Sciences, Raleigh, U.S.A.

^f Fisheries, Wildlife & Conservation Program, North Carolina State University, Raleigh, U.S.A.

^g Institute of Zoology, Zoological Society of London, London, U.K.

^h Department of Zoology, University of Cambridge, Cambridge, U.K.

ⁱ Centre for Ecological and Evolutionary Studies, University of Groningen, Groningen, The Netherlands

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Foraging activity in animals reflects a compromise between acquiring food and avoiding predation. The risk allocation hypothesis predicts that prey animals optimize this balance by concentrating their foraging activity at times of relatively low predation risk, as much as their energy status permits, but empirical evidence is scarce. We used a unique combination of automated telemetry, manual radiotelemetry and camera trapping to test whether activity at high risk times declined with food availability as predicted in a Neotropical forest rodent, the Central American agouti, *Dasyprocta punctata*. We found that the relative risk of predation by the main predator, the ocelot, *Leopardus pardalis*, estimated as the ratio of ocelot to agouti activity on camera trap photographs, was up to four orders of magnitude higher between sunset and sunrise than during the rest of the day. Kills of radiotracked agoutis by ocelots during this high-risk period far exceeded expectations given agouti activity. Both telemetric monitoring of radiotagged agoutis and camera monitoring of burrow entrances indicated that agoutis exited their burrows later at dawn, entered their burrows earlier at dusk and had lower overall activity levels when they lived in areas with higher food abundance. Thus, agoutis avoided activity during the high-risk period more strongly when access to food was higher. Our study provides quantitative empirical evidence of prey animals concentrating their activity at times of relatively low predation risk.

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Foraging success is a key determinant of fitness in animals; therefore most animal activity is dedicated to food acquisition. In prey species, however, foraging activity is predicted to increase the likelihood of encountering a predator (Abrams, Leimar, Nylin, & Wiklund, 1996; Houston, McNamara, & Hutchinson, 1993; Lima, 1998). Activity levels of prey species thus largely reflect a compromise between acquiring energy and avoiding predation (Bednekoff, 2007; Houston et al., 1993; Lima & Dill, 1990). In general, animals reduce their foraging activity levels as predation pressure increases, and as starvation risk decreases. For example, Kotler, Brown, and Bouskila (2004) showed that Allenby's gerbils, *Gerbillus andersoni allenbyi*, had lower activity levels when owls

were present (i.e. when predation risk was higher), and were more vigilant when additional food was supplied.

However, the level of predation pressure often varies widely over the day (Daly, Behrends, Wilson, & Jacobs, 1992; Kotler, Ayal, & Subach, 1994; Sih, 1992). The risk allocation hypothesis (RAH) predicts that prey animals should preferentially allocate their daily activity to times with relatively low predation pressure, thus minimizing their exposure to predators (Higginson, Fawcett, Trimmer, McNamara, & Houston, 2012; Lima & Bednekoff, 1999; Van Buskirk, Müller, Portmann, & Surbeck, 2002; Whitham & Mathis, 2000). The degree to which they do so should depend on local food availability, which determines the total amount of foraging time that prey need to acquire sufficient food (e.g. Berger-Tal, Mukherjee, Kotler, & Brown, 2009; Kotler, 1997; Lima, 1988).

Many studies have experimentally tested the prediction that prey animals vary their activity level in response to a change in predation pressure and/or food abundance (e.g. Anholt, Werner, &

* Correspondence: L. Suselbeek, Department of Environmental Sciences, Wageningen University, PO Box 47, 6700 AA Wageningen, The Netherlands.

E-mail address: lennart.suselbeek@wur.nl (L. Suselbeek).

Skelly, 2000; Kotler et al., 2004; Lenski, 1984; Lima, 1998). For example, resource-deprived tadpoles were shown to maintain higher levels of activity than satiated tadpoles, and consequently suffered higher rates of predation by larval dragonflies (Anholt & Werner, 1995); and gerbils respond to increased risk of predation by reducing their total time spent foraging (Kotler, 1997). Similarly, several studies have investigated whether prey animals respond to this trade-off by concentrating foraging activity at times of relatively low predation risk, (e.g. Creel, Winnie, Christianson, & Liley, 2008; Heithaus & Dill, 2002; Kotler, Brown, Mukherjee, Berger-Tal, & Bouskila, 2010; Metcalfe, Fraser, & Burns, 1998; Mukherjee, Zelcer, & Kotler, 2009). For example, red foxes, *Vulpes vulpes*, and gerbils (*G. andersoni allenbyi* and *Gerbillus pyramidum*) reduce their activity levels during full moon nights, when their main predators are most active (Kotler et al., 2010; Mukherjee et al., 2009).

Although many studies have investigated the trade-off between predator avoidance and food acquisition in systems in which predation pressure varies temporally, we know of no empirical studies in which both the temporal pattern of predation pressure and long-term food availability for prey are quantified. Although experimental studies have shown that prey respond differently to temporal variation in predation pressure, depending on their energetic state, these have largely been tests of short-term responses to a change in food availability (food augmentation or food deprivation; e.g., Kotler, 1997; Kotler et al., 2004; Lima, 1988; Metcalfe et al., 1998), whereas long-term responses to local food availability may be different. Therefore, in this study, we used a natural study system in which we quantified predation risk by looking at the timing of actual predation events and related these to the actual temporal distribution of prey and predator activity, while at the same time incorporating the effects of local food availability on the trade-off between foraging and avoiding predation.

We used a unique combination of automated telemetry, manual radiotelemetry and camera trapping to test whether activity at high-risk times declined with food availability as predicted in a Neotropical forest rodent, the Central American agouti, *Dasyprocta punctata*, in relation to the temporal pattern of predation risk by its principal predator, the ocelot, *Leopardus pardalis*. We identified the period of elevated predation risk by quantifying the daily pattern of predation risk as the ratio of ocelot to agouti activity estimated with camera traps, and assessed whether deaths of radiocollared agoutis occurred disproportionately during the period of elevated predation risk. We then tested the prediction that agoutis avoid activity during high-risk periods, and do so more when they have access to more food resources.

METHODS

Site and Species

Fieldwork was conducted between October 2008 and May 2010 on Barro Colorado Island (BCI) in Panama (9°10'N, 79°51'W). BCI is a 16 km² island located in the Gatun Lake of the Panama Canal, covered with a diverse semideciduous lowland moist tropical forest in different successional stages. Annual rainfall averages 2600 mm, with a marked dry period between December and April (Leigh, 1999). BCI has been protected from poaching since 1960 and has an almost complete mammal fauna (Wright, Gompper, & Deleon, 1994).

Central American agoutis (henceforth agoutis) are medium-sized (2–4 kg) scatter-hoarding rodents that range from southern Mexico to northern Colombia. Agoutis forage over a 2–4 ha home range and sleep or seek refuge in burrows, logs or dense vine tangles, where they are safe from predators (Aliaga-Rossel, Kays, & Fragoso, 2008; Emsens et al., 2013; Smythe, 1978). Agoutis are

primarily diurnal, but their activity period can include twilight and occasionally some night-time activity (Lambert, Kays, Jansen, Aliaga-Rossel, & Wikelski, 2009). Agoutis on BCI feed on large fruits and seeds, in particular those of the palm species *Astrocaryum standleyanum* (henceforth *Astrocaryum*; Emsens et al., 2013; Hirsch, Kays, Pereira, & Jansen, 2012; Jansen et al., 2012; Smythe, 1978, 1989). Seeds are cached as food reserves, and agoutis depend on these caches to survive during the low-fruit season (Aliaga-Rossel et al., 2008; Smythe, 1978). This seed dispersal behaviour by agoutis is considered to be crucially important for large-seeded trees in the Neotropics (Hirsch et al., 2012; Jansen et al., 2012). Agoutis on BCI have a high mortality rate (69% per year), most of which is caused by ocelots (Aliaga-Rossel, Moreno, Kays, & Giacalone, 2006). In turn, agoutis are a principal prey for ocelots, which are primarily nocturnal but also opportunistically hunt during the day (Aliaga-Rossel et al., 2006; Emsens, Hirsch, Kays, & Jansen, in press; Moreno et al., 2012; Moreno, Kays, & Samudio, 2006).

Agouti Capturing and Radiotracking

Agoutis were captured using live traps (106 × 30 cm and 30 cm high; Tomahawk Live Trap, WI, U.S.A.) that were run during October 2008–March 2009 and December 2009–April 2010, coinciding with periods of low food abundance and little breeding (Smythe, 1978). This way, we minimized the chance of capturing pregnant or lactating individuals. Traps were secured to the ground with stakes and logs to minimize the potential for harassment of trapped animals by predators. Large palm leaves were placed in the traps for a more natural look and to serve as bedding material. Traps were baited with fresh coconut or banana, which served also as food and a water source. Traps were checked twice daily following peak agouti activity times to minimize the amount of time animals were trapped. The maximum amount of time that an agouti could be in a trap was 6 h. Captured animals were anaesthetized with 0.8 mg/kg Telazol (tiletamine hydrochloride + zolazepam), injected intramuscularly by a qualified person, while the animal was still in the trap. After the anaesthetic was administered, the animal was left alone for a few minutes while we observed it from a distance (approximately 15 m away). Adult and large juveniles (>2.3 kg; Smythe, 1978) were fitted with a 41 g VHF radiocollar (Advanced Telemetry Systems Inc., Isanti, MN, U.S.A.), whereas others were released without marking. The smallest individual collared was 2.3 kg, which meant that the radiocollar weight constituted about 1.8% of the animal's weight. On average, the collar constituted 1.3% of the agouti's weight (mean collared agouti weight = 3.1 kg). Radiocollars had no notable effects on animal locomotion or range of movement, based on personal observations and numerous videos obtained by camera traps throughout the agouti home ranges (Hirsch, Kays, & Jansen, 2013). After handling, animals were placed back in the traps on a dry and clean piece of fabric until they recovered, which took about 45 min to 1 h. While the animal was recovering, we always kept the trap closed and covered it with a tarpaulin to ensure dry and safe recovery while we remained in the vicinity to prevent predation of the sedated animal. After it had fully recovered, we quietly opened the trap and walked away to let the animal walk out from the trap by itself. If possible, the radiocollar was removed after it stopped transmitting a signal; however, this was only possible when there was a new trapping session, so collars were not always removed. We found no evidence of any long-term effects and we have recorded agoutis living more than 3 years while wearing a collar, which is longer than the average life span of agoutis on BCI. All trapping and marking procedures were approved by the Institutional Animal Care and Use Committee of the Smithsonian Tropical Research Institute (STRI IACUC 2008-06-

8–24–08) and conducted under research permits authorized by the Barro Colorado Nature Monument.

A total of 51 agoutis were radiocollared and captured at sites within 3 km of each other. Some agoutis had limited data collected because they died early on ($N = 1$), had premature radiocollar failure ($N = 5$) or were living outside our main study area ($N = 9$). In total, 36 radiocollared agoutis were used in this study. Using an automated radiotelemetry system (ARTS), we obtained the exact time of death for 19 individuals and we obtained high-quality activity data for 10 individuals. We located the burrows of an additional nine individuals and placed camera traps at the entrance of these burrows to record activity there. Although most individuals that entered/exited the agouti burrows were radiocollared, we did use data from any noncollared animal that used the burrow (see Emsens et al., 2013 for further details). For two of the 10 individuals for which we obtained high-quality activity data, we also obtained the exact time of death. Accordingly, the total number of individuals used in this study was at least 36.

During late October 2008–March 2009, we measured the home ranges of 10 radiocollared agoutis by manually collecting bearings multiple times per week using a hand-held receiver (AOR 8000; AOR Ltd, Japan) and a Yagi directional antenna. We used LOAS 4.0 (Ecological Software Solutions LLC, FL, U.S.A.) to calculate location fixes from the bearings and obtained 100% minimum convex polygons (MCP) from these locations using ArcGIS 9.3 (ESRI, CA, U.S.A.).

During February–May 2010, we pinpointed the exact location of nine agouti burrows by manually radiotracking nine radiocollared agoutis during the night, when they normally reside in their refuges (Emsens et al., 2013). All burrow locations were recorded with a global positioning system (GPS) receiver (Garmin CSx60; Garmin Ltd, KS, U.S.A.).

Temporal Pattern of Predation Risk

To determine which time periods had elevated predation risk for agoutis, we quantified the ratio of ocelot to agouti activity over time, a measure of the relative per-agouti threat of predation at a given time of day. We used this ratio as a proxy for predation pressure, reasoning that predation pressure is relative and therefore should be determined by total prey numbers, or in other words, the availability of other agoutis that can be preyed upon. Given that ocelots have large home ranges (6–14 km²; Di Bitetti, Paviolo, & De Angelo, 2006; Moreno et al., 2012), each overlapping with hundreds of agouti home ranges, we assumed that all radiocollared agoutis were effectively hunted by the same predator population.

We measured daily activity patterns for agoutis and ocelots at the population level using unbaited motion-triggered camera traps (RC55; Reconyx Inc., WI, U.S.A.) that were deployed at 1371 different locations across BCI, during 2008–2010 (for details on camera trapping procedures, see Kays, Tilak, Kranstauber, et al., 2011). Each camera deployment averaged 8.1 days ($SD = 1.6$, range 1.1–16.9), and total sampling effort was 11 123 camera trapping days (ca. 30.5 years). Photographs were processed and identified to species in a custom database (Kays, Tilak, Kranstauber, et al., 2011). We created activity plots for agoutis and ocelots using the timestamp on each photograph, and fitted multimodal distributions of activity times with Von Mises mixture distributions in R (R Development Core Team, 2011). We then estimated the temporal pattern of predation pressure by dividing the fitted distribution for ocelot activity by that of agouti activity to obtain the ratio of ocelot to agouti activity.

To determine how much of agouti mortality was due to ocelots and fell during the high-risk period of the day, we used ARTS to track the activity continuously and record the exact time of death for radiocollared agoutis. The ARTS included a wireless network to the laboratory on BCI, making these data available to us in real time

via a web-accessible database (for a detailed description of the ARTS on BCI, see Kays, Tilak, Crofoot, et al., 2011). As radio signal strength varies when an animal is active owing to the changing orientation of the collar towards the ARTS antennas (Cochran & Lord, 1963), we were able to obtain accurate death times of individual agoutis. Predation events were detected as a short period of fluctuations in the radio signal strength (the actual predation), followed by a constant signal strength (the carcass lying motionless). As soon as we detected a mortality event, we located the carcass to check for bite marks and then deployed a camera trap at the carcass to record any predators returning to their meal. This allowed us to record the exact time of death for 19 agoutis, and to identify the predator for 18 agoutis.

Responses to Food Abundance

To determine how food abundance affected individual agouti activity patterns, we compared activity patterns between agoutis that lived in areas of contrasting abundance of *Astrocaryum* fruits. We assumed that individuals living in food-poor areas were more food limited than were individuals living in food-rich areas. We followed two approaches to test our predictions. The first approach was to monitor activity of 10 radiocollared agoutis over time. During 2008–2009, we recorded the signal strength of radiocollared agoutis every 5 min using the ARTS system. We took a 3-week (ca. 6000 readings per individual) subsample of all ARTS activity measurements in January–February 2009, during which the ARTS system was working optimally and the largest number of radiocollared agoutis was simultaneously monitored. We followed the protocol of Lambert et al. (2009) for establishing a threshold signal strength change, which indicated a change in the position or orientation of a radiotransmitter as happens during movement (Cochran & Lord, 1963), to distinguish agouti activity from inactivity. Daily activity levels were then obtained by calculating the proportion of 5 min intervals that showed activity while an individual was outside its refuge (i.e. between the average daily start and end of activity, for each individual agouti). In addition, we derived the times at which the agoutis entered and exited their refuges ($N = 83$ days per agouti, $SD = 12$, range 60–100) from sudden declines or increases in radio signal strength, respectively. This worked only when agoutis spent the night in a burrow, because if they slept ‘outside’ in, for example, dense vine tangles, the change in signal strength was minimal. For each individual, we averaged refuge exit and entry times and the duration between them over all days, and then subtracted these times from the exact times of sunrise and sunset, providing us with an estimate of the start and end of daily activity expressed in minutes before sunrise and sunset, respectively. We defined a period of morning and evening twilight as being the periods between civil dawn and sunrise and between sunset and civil dusk, respectively. Daily times of sunrise, sunset, dawn and dusk were obtained from Thorsen (2008).

The second approach was to monitor the entrance of nine agouti burrows with camera traps and record the times at which agoutis entered and exited. This could be any local individual, tagged or untagged. At each of the nine burrows, we placed a camera trap at 1.5–3 m from the entrance. Burrows were typically used as shelter by different individuals, but never simultaneously (Emsens et al., 2013). For each night that a burrow was used, we recorded the exact entry and exit time of the individual. These exit and entry times were taken as the start and end times of daily activity, which is a safe assumption as camera traps recorded that agoutis, once they entered a burrow, never emerged before dawn. We focused on burrows, because these, unlike other types of refuges used by agoutis (Emsens et al., 2013), have a single entrance and can thus be effectively monitored with one camera trap.

Food Abundance

We quantified local food abundance as the local number of *Astrocaryum* fruits. These fruits are a staple food for agoutis on BCI during the season of our study (e.g. Aliaga-Rossel et al., 2008; Emsens et al., 2013; Smythe, 1978, 1989). To estimate the number of fruits, we mapped all reproductive individuals of *Astrocaryum* throughout the study area by walking parallel transects with a GPS receiver, and counted the fruits on each palm using a pair of binoculars (see Jansen et al., 2008). For agoutis that were radiotracked during 2008–2009, we used the total number of *Astrocaryum* fruits produced in the home range as the measure of food abundance; for agouti burrows monitored in 2010 we used the total number of *Astrocaryum* fruits in a 100 m (3.14 ha) radius around the burrow, an area that approximates the average home range size known for agoutis (Aliaga-Rossel et al., 2008; Emsens et al., 2013; Smythe, 1978).

Statistical Analysis

We used a chi-square test to determine whether the occurrence of agouti deaths during the period of high predation pressure was disproportionate to agouti activity during that period. We used least squares regression, weighted for sample size, to describe the relationship between food abundance and agouti activity. In all analyses, food abundance was log-transformed to avoid high leverage problems, and because relative (rather than absolute) differences in fruit abundance were important in our study. All analyses were performed in R 2.12.2 (R Development Core Team, 2011).

RESULTS

Temporal Pattern of Predation Risk

Agouti activity ($N = 29\,390$ camera trap observations, 2.6 per day) was almost exclusively during daytime, with 94.9% occurring between sunrise and sunset (Fig. 1a). By contrast, ocelot activity ($N = 490$ observations; 0.044 per day) was heavily biased but not limited to night-time and twilight, with 77.8% of observations occurring between sunset and sunrise (Fig. 1a). Activity overlap between the two species was largest around sunrise and sunset. The ratio of ocelot to agouti observations was 1:60 overall but varied over the day by four orders of magnitude, from around 1:500 during the day, increasing steeply immediately after sunset to as much as 30:1 around midnight, and dropping sharply just before sunrise (Fig. 1b). The change of the ratio was largely driven by variation in agouti activity, not ocelot activity. Thus the time between sunset and sunrise was identified as the period of elevated risk of agouti predation by ocelots.

Observations on agouti kills confirmed that risk was elevated during this period. The ARTS gave us the exact date and time of 19 deaths of radiocollared agoutis. Camera traps and observations of traces and dental marks at 18 of the 19 carcasses showed that 16 mortalities (89%) were the result of ocelot predation, whereas two were from other causes (no wounds or external marks on the animals). Ten of these 16 ocelot kills (62.5%) occurred between sunset and sunrise, whereas just 5.1% of agouti activity occurred during this period (Fig. 1a). Thus, ocelot predation on agoutis during this period was disproportionate to agouti activity levels ($\chi^2_1 = 109$, $P < 0.001$).

Responses to Food Abundance

We found substantial variation in food abundance inside agouti home ranges, as well as in the behavioural responses to this food availability. Home range size (100% MCP) of the 10 radiocollared individuals monitored with ARTS ranged between 1.29 and 3.5 ha.

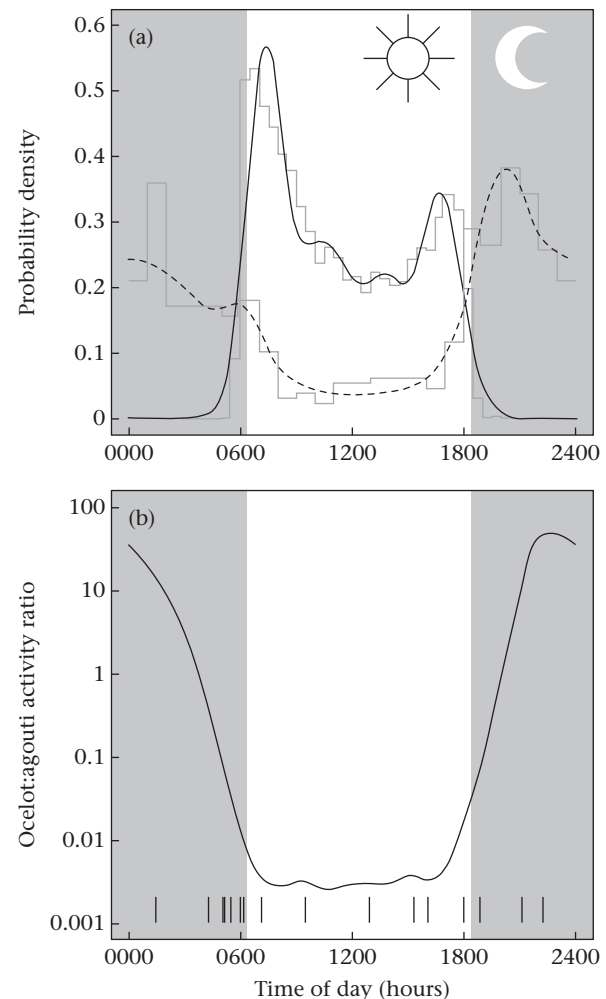


Figure 1. (a) Daily activity patterns of Central American agouti (solid curve) and ocelot (dashed curve), and (b) the daily pattern of the ratio of ocelot:agouti activity, on Barro Colorado Island, Panama. Patterns were derived from the distribution of camera trap photographs over the day (histograms) fitted with mixed von Mises distributions (smooth curves). The activity ratio in (b) measures the risk of agouti predation by ocelot. Ticks in (b) mark the exact times at which radiocollared agoutis were killed by ocelots. Night-time (the period between average sunset and sunrise) is coloured grey.

The number of *Astrocaryum* fruits inside the home ranges ranged 12-fold (1192–14 521), and fruit density within a 100 m radius around the nine camera-monitored agouti burrows ranged eight-fold (809–6169 per ha).

We found that agouti activity during the period of elevated predation risk declined with food abundance. Agoutis started their activity significantly later in the morning when they had access to more food. This pattern was evident both for estimates based on ARTS tracking (weighted linear regression: $R^2 = 0.72$, $F_{1,8} = 20.42$, $P = 0.002$; Fig. 2a) and for estimates based on camera traps at burrow entrances ($R^2 = 0.79$, $F_{1,6} = 22.05$, $P = 0.003$; Fig. 2c). Similarly, agoutis ended their activity significantly earlier in the evening when they had access to more food. This was apparent from time estimates based on ARTS ($R^2 = 0.66$, $F_{1,8} = 15.46$, $P = 0.004$; Fig. 2b) and from times recorded by camera traps at burrow entrances ($R^2 = 0.60$, $F_{1,7} = 10.71$, $P = 0.014$; Fig. 2d). Consequently, the duration of daily activity declined significantly with food abundance, both for agoutis monitored with ARTS ($R^2 = 0.73$, $F_{1,8} = 21.38$, $P = 0.002$) and for agoutis monitored with camera traps at burrows ($R^2 = 0.71$, $F_{1,6} = 14.95$, $P = 0.008$).

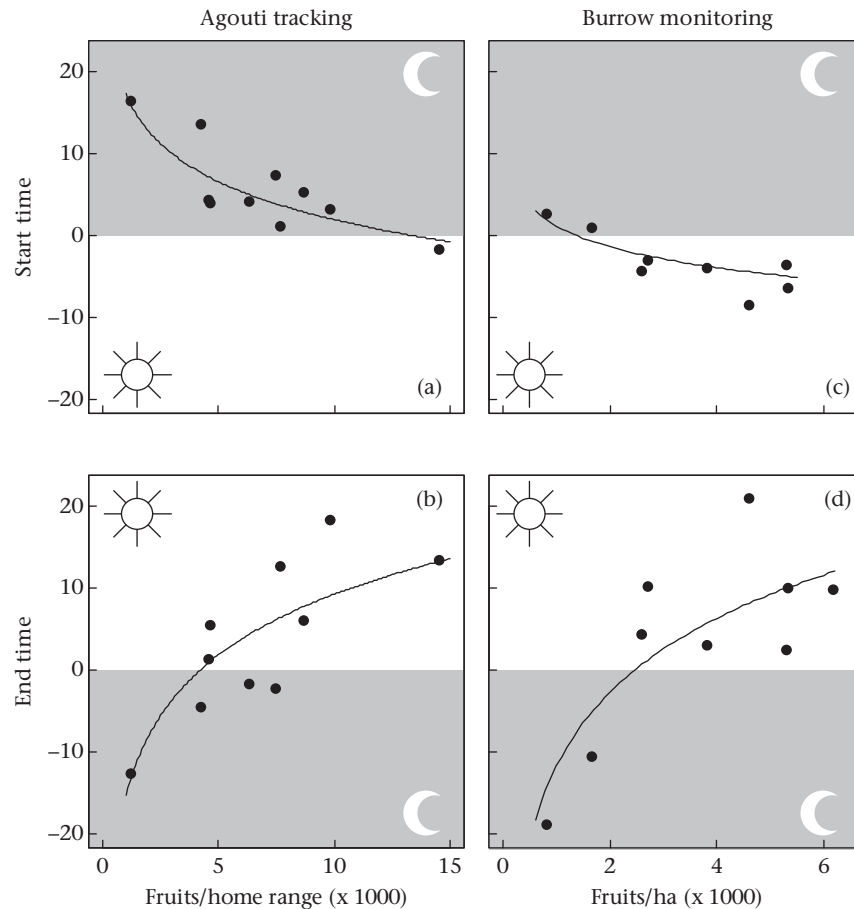


Figure 2. Start and end times of daily activity of Central American agoutis across a gradient of food abundance on Barro Colorado Island, Panama, obtained using two different methods and two sets of individuals. (a, b) Average refuge (a) exit and (b) entry times, expressed in minutes before sunrise and minutes before sunset, respectively, for 10 agoutis radiotracked with an automated radiotelemetry system, and derived from signal disappearance and reappearance. (c, d) Average times at which agoutis (c) exited and (d) entered burrows, based on monitoring of agouti burrow entrances with camera traps. Food abundance was quantified as the total number of *Astrocaryum* fruits in an agouti home range (a, b) or as the average number of *Astrocaryum* fruits per ha in a 100 m radius around an agouti burrow (c, d).

Using the ARTS, we found that agoutis were actively moving for 37–62% of the time that they spent outside their refuges. The overall level of activity declined with food abundance (weighted linear regression: $R^2 = 0.51$, $F_{1,8} = 8.36$, $P = 0.020$; Fig. 3a), as well as the proportion of time spent active during high-risk periods (i.e. between sunset and sunrise; $R^2 = 0.77$, $F_{1,8} = 27.47$, $P = 0.001$; Fig. 3b), indicating that agoutis in more food-rich areas not only avoided activity during high-risk periods of morning and evening twilight, but were also less active while outside their refuges. However, activity patterns of all individuals showed a distinct lull during the early afternoon, regardless of their food status.

DISCUSSION

Theory predicts that prey animals optimize the balance between food acquisition and predator avoidance by concentrating their foraging activity at times of relatively low predation risk, as much as their energy status permits (e.g. McNamara & Houston, 1986; Whitham & Mathis, 2000), but empirical evidence is scarce (but see Creel et al., 2008; Kotler et al., 2004; Mukherjee et al., 2009). Our study provides quantitative empirical evidence for avoidance of periods of high predation risk by a prey species. Using a combination of automated telemetry, manual telemetry and camera trapping, we quantified the period of elevated predation risk for Central American agoutis on Barro Colorado Island, Panama. We found that agoutis avoided activity during these high-risk periods

more strongly when they had access to more food. Our study provides quantitative evidence of prey animals concentrating their foraging activity at times of relatively low predation risk.

Monitoring with telemetry and remote cameras showed that predation by ocelots was by far the primary cause of death of agoutis. Relative predation risk, estimated as the ratio of ocelot to agouti detections by camera traps, varied dramatically over the course of the day, increasing steeply at sunset, remaining high during the night and dropping sharply towards sunrise. This temporal change in risk was both predictable and relatively long lasting, in contrast to situations in which an animal changes its behaviour in the presence of a predator (see further discussion in Higginson et al., 2012). Actual agouti predation by ocelots occurred disproportionately during this risky time period, confirming the high danger of night-time activity. The variation in predation risk was driven by variation in the number of agoutis that were active (i.e. risk dilution), rather than by variation in ocelot activity, which was less concentrated at particular times of the day. Previous studies of predation risk also report that twilight is a period of elevated predation risk for many prey species owing to low light levels and potential overlap in activity of predator species during this period (e.g. Lima, 1988; Lima & Dill, 1990), but whether mortality during these periods is disproportionate to prey activity levels is usually unknown.

We found that agoutis initiated activity later in the morning, and entered their refuges earlier in the evening when they lived in areas with more food. Consequently, better-provisioned agoutis were less

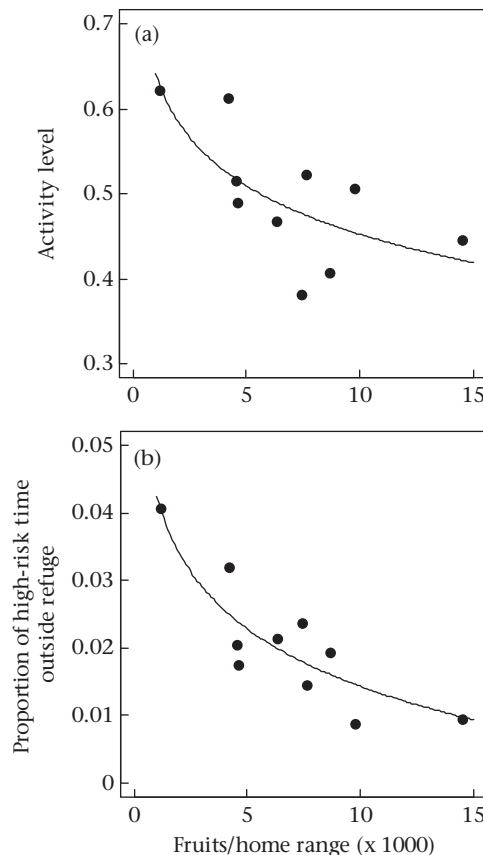


Figure 3. Activity levels of 10 radiocollared agoutis across a gradient of food abundance on Barro Colorado Island, Panama, as estimated with automated telemetry (6048 data points per individual). (a) The proportion of time individuals were active while outside their refuges. (b) The proportion of time spent active during high-risk periods (i.e. between sunset and sunrise). Food abundance was quantified as the total number of *Astrocaryum* fruits within the agoutis' home range.

active during periods of increased predator activity, thereby avoiding predation risk. In addition, agoutis in areas with more food were less active while outside their refuges compared with agoutis living in areas with less food. Decreased activity by agoutis living in food-rich areas may be at least partly explained by the fact that they tend to have smaller home ranges and can encounter food more readily than agoutis living in areas with low food density (Emsens et al., 2013). Because predation pressure is unequal throughout the day, the relationship between the amount of time agoutis were active and their overall risk of predation was nonlinear. A relatively modest increase in time spent foraging during early morning hours can result in a substantial increase in predation pressure. This finding is in line with the generally reported tendency for hungry animals to take greater risks (e.g. Berger-Tal, Mukherjee, Kotler, & Brown, 2010; Horat & Semlitsch, 1994; Kotler, 1997; Pettersson & Brönmark, 1993; Whitham & Mathis, 2000). For instance, energy-deprived dark-eyed juncos, *Junco hyemalis*, initiate activity earlier in high-risk dim light conditions than well-fed individuals (Lima, 1988). Similarly, when red foxes are hungrier they spend more time foraging in high-risk patches, thereby increasing their risk of injury (Berger-Tal et al., 2009).

The risk avoidance patterns that we found were robust and corroborated with different methods. The relationship between telemetry-derived activity patterns and fruit counts in agouti home ranges was similar to the relationship between camera-derived activity patterns and fruit counts in a 100 m radius around agouti burrows. The only discrepancy was that radiotracking yielded

consistently earlier (10–15 min) agouti emergence from the burrows than camera trapping. A plausible explanation is that agoutis first move towards the entrance of their burrow and sit there for a short period of time to check whether everything is safe before they emerge. At this time, they had emerged far enough for the radio-telemetry signal to have increased significantly in strength, whereas the camera trap only detected the agouti when it physically left the burrow. This also explains why we did not find this discrepancy in the timing of burrow entrance in the evening, when agoutis apparently run straight down into the safety of their burrow. If true, this may be evidence not only that agoutis are aware of the hypothesized increased levels of predation near burrow entrances (e.g. Emsens et al., 2013; Emsens et al., in press), but also that they behave in a manner that should reduce their susceptibility to predation during burrow emergence.

Agouti activity peaked in the early morning (0600–0900 hours) and late afternoon (1600–1800 hours), and showed a pronounced lull during the early afternoon. A logical question is why agoutis in areas with less food do not noticeably increase their activity during that lull to avoid the high-risk times. The activity patterns documented here may be driven by factors other than predation risk. Bimodal daily activity patterns are common in diurnal mammals (e.g. Aschoff, 1966) and are likely to be related to energy intake and expenditure (e.g. Daan, 1981; Wauters, Swinnen, & Dhondt, 1992). Energy reserves are low after resting periods (e.g. Lima, 1986) and need to be quickly replenished by intense foraging activity. Low activity in the early afternoon may also be linked to heat stress (e.g. Cuesta, Clesse, Pevet, & Challet, 2009), satiation and gut capacity (e.g. Wauters et al., 1992), or energy expenditure (e.g. Daan, 1981). The exact reasons that agoutis avoid midday activity deserve further study. Temporal differences in energy levels may partially explain why agoutis living in areas with different amounts of food availability exhibit different activity patterns. Agoutis living in food-poor areas may have lower energy reserves and thus have greater energetic requirements for waking up early and foraging for food. Alternatively, agoutis in food-rich areas may have more energy reserves, and can thus afford to wake up late, avoid the early morning predation risk, and then quickly encounter food after leaving the burrow.

Previous studies of ocelot scat samples had already shown that agoutis comprise a substantial part of the ocelot's diet (Aliaga-Rossel et al., 2006; Moreno et al., 2006). Our results show that ocelots are also the principal predator of agoutis on BCI. Ocelots were identified as predators through a unique combination of automated telemetry to detect kills and camera traps and observations of visual traces and dental marks on the carcasses to identify the killer. The results also showed that ocelot kills of agoutis occurred disproportionately during twilight.

Where previous studies investigating the trade-off between food acquisition and predation avoidance in relation to temporal variation in predation risk focused either on responses to temporal variation in predation pressure or on responses to short-term changes in prey food availability (e.g. Heithaus & Dill, 2002; Kotler et al., 2010; Lima, 1988; Mukherjee et al., 2009), our study combined both aspects by empirically defining the most risky periods of the day, based on simultaneous measurements of daily prey and predator activity, and confirmed these high-risk periods with precise timings of actual predation events, while at the same time measuring the local food availability for prey. This provided us with a quantitative estimate of prey food availability and of the temporal variation in predation pressure for agoutis on BCI. The ratio of agoutis to ocelots varied from around 30 ocelots per agouti during the night to around 500 agoutis per ocelot during the day. Although this 10 000-fold difference in ocelot to agouti ratio is already dramatic, the true risk imposed on agoutis that are active during the

night is likely to be even larger as a result of the superior night vision of ocelots compared with agoutis.

To summarize, our findings indicate that agoutis balance finding food and avoiding predators in the long term, depending on local food resources. Agoutis reduce their activity levels in a way that disproportionately reduces predation risk, but they can do so only when they have access to more food, which is in full agreement with theory (e.g. Houston et al., 1993; Lima, 1998; Lima & Dill, 1990) and empirical studies (e.g. Heithaus & Dill, 2002; Kotler et al., 2004, 2010; Mukherjee et al., 2009). We predict that other animal species that live in areas of varying food abundance and temporal changes in predation risk will also show similar behavioural shifts in temporal activity levels. Although this study was able to investigate the activity of both predator and prey simultaneously, we were not able to assess whether these animals varied their space use in accordance with theory. We predict that ocelots would preferentially hunt in areas with lower agouti food availability during the late morning and early evening periods as, based on our findings, the probability of encountering an agouti during these periods would be highest in food-poor areas. We also predict that agoutis would preferentially forage in 'safer' areas during these same times, although we are unclear about which exact habitat features are 'safer'.

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