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Food acquisition and predator avoidance in a Neotropical rodent

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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 radio-tagged 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.

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, &

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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 km^2 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-