



Living in a landscape of fear: the impact of predation, resource availability and habitat structure on primate range use



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ARTICLE INFO

Article history:

Received 30 August 2013
Initial acceptance 27 September 2013
Final acceptance 6 November 2013
Available online 31 December 2013
MS. number: 13-00717

Keywords:

blue monkey
Cercopithecus aethiops
Cercopithecus albogularis
fruit availability
geographical information system (GIS)
intergroup competition
local convex hulls (LoCoH) analysis
spatial regression
Sykes monkey

Spatial variation in predation risk generates a 'landscape of fear', with prey animals modifying their distribution and behaviour in response to this variable predation risk. In systems comprising multiple predators and prey species, a key challenge is distinguishing the independent effects of different predator guilds on prey responses. We exploited the acoustically distinct alarm calls of samango monkeys, *Cercopithecus mitis erythrarchus*, to create a predator-specific landscape of fear from eagles to assess its impact on space use within mixed regressive–spatial regressive models incorporating data on resource distribution and structural characteristics of the environment. The landscape of fear from eagles was the most significant determinant of samango range use, with no effect of resource availability. The monkeys also selected areas of their range with higher canopies and higher understory visibility, behaviour consistent with further minimizing risk of predation. These results contrast with those of vervet monkeys, *Chlorocebus aethiops pygerythrus*, at the same site for which the landscapes of fear from leopards and baboons were the most significant determinants of space use. While highlighting that predation risk is a key driver of primate behaviour in this population, the landscapes of fear experienced by samango monkeys and vervet monkeys appear to differ despite exposure to identical predator guilds. This emphasizes the importance of distinguishing between the risk effects of different predators in understanding prey ecology, but also that closely related prey species may respond to these predator-specific risks in different ways.

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Predation is a major selective force driving animal evolution (Dawkins & Krebs, 1979) with almost all animal species engaged in some form of predator–prey interaction (Abrams, 2000). Understanding how animals manage the risk of predation is thus a central issue in behavioural ecology (Quinn & Cresswell, 2004). Predation imposes two costs on prey individuals: the direct fitness costs of mortality resulting from successful predation and the indirect costs of employing behaviours to reduce mortality risks. These nonlethal effects of predators appear to affect almost every aspect of prey behaviour and ecology (Caro, 2005; Lima, 1998; Werner & Peacor, 2006). Nevertheless, these risk effects are among the most difficult to quantify (Creel & Christianson, 2008; Creel, Winnie, Christianson, & Liley, 2008; Hill & Dunbar, 1998).

Spatial variation in risk is a key driver of nonlethal predation effects (Cresswell & Quinn, 2013), primarily because of the constraints this places on foraging behaviour and the subsequent impact this has on competitive and trophic interactions (Creel,

Christianson, Liley, & Winnie, 2007; Minderman, Lind, & Cresswell, 2006; Peckarsky & McIntosh, 1998; Willems & Hill, 2009). Spatial variation in perceived predation risk has often been conceptualized as a 'landscape of fear' (Brown & Kotler, 2004; Brown, Laundre, & Gurung, 1999; Laundré, Hernandez, & Altendorf, 2001), with approaches such as giving-up densities quantifying the trade-offs animals make between nutrient acquisition and the costs of predation (Brown, 1988). One of the challenges though is that these methods do not strictly measure perceived predation risk (Searle, Stokes, & Gordon, 2008) and in multipredator environments they do not convey information on the impact of different predators on the behavioural responses of prey species. This latter issue is critical, since when prey are subject to attack from several predators that present different types of risk, the appropriate antipredator responses differ between predator guilds (Cresswell & Quinn, 2013; Preisser, Orrock, & Schmitz, 2007; Shultz, Noe, McGraw, & Dunbar, 2004; Willems & Hill, 2009). As a consequence, to understand how prey manage the risk of predation within their environment, the risk of predation from each predator guild must be quantified independently. Nevertheless, there is a significant body of evidence to suggest that animals trade food availability against predation risk in habitat choice (Cowlshaw,

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1997; Fortin & Fortin, 2009; Willems & Hill, 2009). The landscape of fear is thus a powerful concept in animal ecology and has been suggested to be the key landscape within an animal's environment (Brown & Kotler, 2004). To test this assertion, however, methods are required that exclusively reflect perceived predation risk and distinguish between predator-specific predation risks in determining prey behaviour.

In a novel approach, Willems and Hill (2009) showed that predator-specific landscapes of fear could be constructed on the basis of vervet monkey, *Chlorocebus aethiops pygerythrus*, alarm calls. Vervet monkeys' predators at their South African field site included leopard, *Panthera pardus*, African crowned eagle, *Stephanoaetus coronatus*, chacma baboon, *Papio ursinus*, and African rock python, *Python sebae*. When predator-specific landscapes of fear were combined with data on resource distribution in a spatially explicit model, the ranging behaviour of the study group could be interpreted as an adaptive response to the spatial availability of resources and the perceived risk of predation by some, but not all, predators (Willems & Hill, 2009). The landscapes of fear for baboon and leopard were negatively associated with the group's utilization distribution indicating that the monkeys avoided areas of high perceived predation risk by these two predators. Furthermore, the effects of fear exceeded those of local resource availability in determining range use. In contrast, the spatial distribution and local frequency of alarm responses to eagles and snakes did not significantly affect range use. This highlighted the value of their framework in distinguishing between the effects of different predators in studies of predator–prey ecology in multipredator environments. Willems and Hill (2009) also noted the potential for integrating additional variables such as the structural characteristics of a habitat and the utilization distributions of predators and neighbouring groups into their modelling approach and advocated these as an avenue for future research.

In this study we applied the framework of Willems and Hill (2009) to a population of samango monkeys, *Cercopithecus mitis erythrarchus*, inhabiting the same multipredator environment as in the original vervet study. Initially we directly replicated the modelling approach and variable selection of Willems and Hill (2009) to facilitate a direct comparison of our results with the previous models on vervet monkeys. In doing so, we assessed the impact that substrate preferences (arboreal versus semiterrestrial) have on the exposure to different predator guilds and the implications of this for predator-specific landscapes of fear and range use. Samango monkeys, as an arboreal species, may experience different predation threats to more terrestrial species such as vervet monkeys (Lawes, 1991; McGraw, 2002), so influencing the relative importance of different predators in driving ranging behaviour.

We then extended the modelling framework of Willems and Hill (2009) in two ways. First, we replaced categorical habitat types with continuous spatial measures of resource availability and structural characteristics of habitats (e.g. canopy height, habitat visibility) to investigate the key drivers of habitat choice within the landscape of fear. Samango monkeys have been observed to spend most of their time high in the canopy (Thomas, 1991), with the ground perceived as higher risk (Emerson, Brown, & Linden, 2011), suggesting that areas of tall canopy will be preferred. Similarly, habitats with dense understory vegetation may provide cover for terrestrial ambush predators (du Bothma & Le Riche, 1986) while areas of high visibility may increase an individual's ability to monitor threats from predators or competitors (Cowlshaw, 1994; Hill & Weingrill, 2007; Jaffe & Isbell, 2009). For example, vervet monkeys have been shown to decrease vigilance in high-visibility areas (Chapman, 1985; Enstam & Isbell, 2002). Samango monkeys are thus predicted to prefer higher visibility habitats. Since canopy height and visibility will vary independently between habitat

types, consideration of the spatial variation in these parameters should be more informative than broad habitat classifications. Second, we explored the impact of competition with neighbouring groups. Intraspecific competition and the active avoidance of neighbouring groups have long been recognized as significant factors shaping space use strategies and movement decisions in many species (Gibson & Koenig, 2012; Markham, Guttal, Alberts, & Altmann, 2013), and yet how intraspecific competition, predation risk and resource availability interact in determining spatial range use is largely unknown.

METHODS

Study Species and Field Site

Samango monkeys are medium-sized (adult females about 4.4 kg, adult males about 7.6 kg; Harvey, Martin, & Clutton-Brock, 1987) arboreal, diurnal guenons. They form single-male, multi-female groups (Henzi & Lawes, 1987; Rudran, 1978), with group sizes ranging from four to 65 (Beeson, Tame, Keeming, & Lea, 1996; Butynski, 1990; Houle, Chapman, & Vickery, 2010; Lawes, Cords, & Lehn, 2013; Smith, Link, & Cords, 2008). Samango monkeys are primarily frugivorous but supplement their diets with leaves, insects and flowers (Coleman, 2013; Lawes, 1991; Lawes, Henzi, & Perrin, 1990). Like vervet monkeys, samango monkeys have acoustically distinct alarm calls for different predator guilds which can be differentiated by human observers (Brown, 1989; Papworth, Bose, Barker, Schel, & Zuberbuhler, 2008).

Research was conducted at the Lajuma Research Centre, located in the Soutpansberg Mountains, Limpopo Province, South Africa (23°02'23"S, 29°26'05"E). Substantial local variation in abiotic factors such as elevation and water availability results in a variety of microclimates which are able to support a substantial diversity of both flora and fauna (Brock, Nortje, & Gaigher, 2003; Willems, 2007). The study area has natural fragments of tall forest (10–20 m height) occurring among areas of natural short forest (5–10 m height). Local climate is classified as temperate/mesothermal, with cool dry winters from April to September and warm to hot wet summers from October to March (Willems, 2007). Mean annual temperature on site averages 17.1 °C, with a mean annual rainfall of 724 mm (Willems, Barton, & Hill, 2009). On site, samango monkeys are sympatric with vervet monkeys, chacma baboon, thick-tailed galago, *Otolemur crassicaudatus*, and southern lesser bushbaby, *Galago moholi*. Potential predators include leopard, crowned eagle, African black eagle, *Aquila verreauxii*, and African rock python. Venomous snakes, including black mamba, *Dendroaspis polylepis*, puff adder, *Bitis arietans*, and Mozambique spitting cobra, *Naja mossambica*, while not actively preying on samango monkeys, still pose potential mortality threats and may affect range use.

Permission to conduct research in South Africa was provided by the Limpopo Province Department of Economic Development and Tourism, with the research receiving ethical approval from the Durham University's Life Sciences Ethical Review Process Committee.

Behavioural Data

A well-habituated group of approximately 40 samango monkeys was observed over a 16-month period (September 2009–December 2010). We restrict the data presented here to that collected during the final 12 months (January–December 2010) to confine the analyses to a single annual cycle. Behavioural data were collected over 8 full follow days per month (totalling 96 days), with a successful day defined as following the group from dawn to dusk without losing audiovisual contact for more than a total of 60 min. Study days ranged from approximately 11.5 to 14 h depending upon

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