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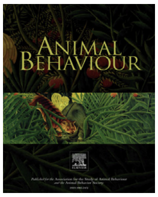

Impact of risk on animal behaviour and habitat transition probabilities

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Lions, *Panthera leo*, and leopards, *Panthera pardus*, coexist in space and compete for resources. Although direct killing of leopards by lions has been recorded, avoidance behaviour is an important part of leopard ecology that is difficult to measure through direct observation. Using tracking data from simultaneously collared lions and leopards, we investigated the effect of lion proximity on the behavioural ecology of leopards. We show that proximity to lions influenced leopard habitat use, transition probability and behaviour. Within enclosed habitats, lions were allowed to get closer to leopards before leopards engaged in a flight response. Visual observation data suggest that lions and leopards infrequently come into direct contact. However, tracking data indicate that avoidance was based on relative habitat cover and detectability, and as a result the two species were often located within close proximity. Finding new signals of interaction and avoidance within two well-studied predators with relatively small sample sizes suggests that this approach may have value to other systems, such as predator/prey interactions, or relationships between sympatric species, and at a scale hitherto not possible. This could be used to investigate the costs and benefits of animal foraging where competitive exclusion may occur, and is relevant for the large number of animals that are difficult to observe.

Predators can influence the ecology and population dynamics of other species not only through direct killing, but also indirectly by eliciting behavioural changes in response to risk (Creel, Winnie, & Christianson, 2013; Laundre, Hernandez, & Altendorf, 2001; Valeix, Loveridge, et al., 2009). The impacts of predators are typically measured in terms of total individuals killed (Lima, 1998) or biomass consumed (e.g. Bodendorfer, Hoppe-Dominik, Fischer, & Linsenmair, 2006; Hayward, O'Brien, Hofmeyr, & Kerley, 2007; Karanth & Sunquist, 2000). However, the indirect effects of predation, including behavioural modifications that result in ecological niche shifts, can affect the fitness, demographics and population density of a species (Creel et al., 2013; Valeix et al., 2010). Ungulate distribution and habitat selection are influenced by the risk of predation, and ungulates avoid areas of high predation risk and habitats that reduce their ability to escape (Laundre et al., 2001; Valeix et al., 2010), even though this behaviour negatively affects their rate of food ingestion and nutrient quality (e.g. Creel et al., 2013; Hernandez & Laundre, 2005). If predation risk is high, it can lead to ecological niche shifts that negatively affect the population dynamics of the subordinate species (Brown, Laundre, & Gurung, 1999; Spitz, Rousseau, & Ridoux, 2006).

Aggressive intraguild interactions between terrestrial carnivores have been well documented (e.g. Creel et al., 2013; Harihar, Pandav, & Goyal, 2011; Kamler, Davies-Mostert, Hunter, & Macdonald, 2007; Kamler, Stenkewitz, & Macdonald, 2013; Karanth & Sunquist, 2000; McDougal, 1988; Palomares & Caro, 1999), and as with herbivores, dominant carnivore species may also indirectly affect subordinate carnivore species by inducing behavioural adjustments associated with risk (e.g. Brown et al., 1999; Laundre et al., 2001). It is therefore conceivable that subordinate carnivores incur significant costs as a result of increased vigilance, avoidance behaviour, kleptoparasitism and restricted use of shared habitats (e.g. Creel et al., 2013; Lima, 1998; Valeix et al., 2010). These costs have been less well researched, but understanding the effects that predation and competition for resources have on the behaviour and distribution of key species is fundamental to informed management (e.g. Funston, Groom, & Lindsey, 2013), especially as protected areas, which are limited in size, become increasingly isolated (Lindsey, Romanach, Tambling, Chartier, & Groom, 2011).

Interpreting the indirect impacts of predation on an animal's behavioural ecology requires insight into the circumstantial decisions that an individual faces, which may be reflected in its activity and habitat use (Basille, Calenge, Marboutin, Andersen, &

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Gaillard, 2008; Jessopp, Cronin, & Hart, 2013), because where an animal is and what it is doing are influenced by its need for both short- and long-term risk avoidance (Lima, 1998; Valeix, Fritz, et al., 2009; Whitehead & Jonsen, 2013). Variation in risk between habitats, and the effect this has on behaviour, therefore requires serious consideration (Lind and Cresswell, 2005; Lone et al., 2014). Spatial heterogeneity of habitat and vegetation density influences the distribution of risk within the landscape (Laundre et al., 2001; Valeix, Loveridge, et al., 2009), and because predation risk influences habitat selection (Creel and Winnie, 2005; Valeix, Fritz, et al., 2009; Valeix et al., 2010) it is thus important to take into account different habitat types when investigating interspecies interactions. Determining habitat use and transition rates between habitat types with regard to predator proximity is therefore informative regarding the impact of risk on behavioural ecology.

However, unbiased observation of wild animals, and in particular nocturnal predators, is difficult (e.g. Broekhuis, Cozzi, Valeix, McNutt, & Macdonald, 2013; Funston, Mills, & Biggs, 2001; Hart, Mann, Coulson, Pettorelli, & Trathan, 2010; Jessopp, Cronin, & Hart et al., 2013), and attempts to do so may affect their behaviour or expose their position to potential predators or prey. At the landscape level, quantification of the behavioural response to predator proximity via direct observations is virtually impossible (Valeix et al., 2010); however, biologgers are commonly and increasingly used in ecological studies. These biologgers are able to record large time-referenced data sets on location, body orientation and temperature (among other parameters), from which utilization distributions, habitat selection, speed of movement and distances between individuals can be determined.

Inferring patterns of animal behaviour indirectly is limited insofar as it precludes highly detailed description of activity. However, even broad behavioural classification is insightful when related to the environment and distance from predators (e.g. Broekhuis et al., 2013; Milinski & Heller, 1978), and investigating the transitions between behavioural states, rather than focusing on them individually, may allow identification of the environmental factors that induce changes in behaviour (Bagniewska, Hart, Harrington, & Macdonald, 2013; Hart et al., 2010; Krebs & Davies, 1991). For example, consider the transition of Adelie penguins, *Pygoscelis adeliae*, between water, where they forage but are also at risk of predation by leopard seals, *Hydrurga leptonyx*, and ice, on which they are generally safe from predation (Ainley, Ballard, Karl, & Dugger, 2005); although movements between environments occur frequently, the probability of transition from water to land may be directly related to the presence and proximity of seals, i.e. the behavioural change points are coincident with a predator.

Using biotelemetry track data from both species, we aimed to investigate the effect of lion, *Panthera leo*, predation risk on the behavioural ecology of leopards, *Panthera pardus*, specifically, how the presence and proximity of lions influenced leopard behaviour and habitat transition probability. Lions and leopards are morphologically similar intraguild competitors that have extensive range and habitat overlap in Africa (Bauer, Nowell, & Packer, 2013; Henschel et al., 2008), as well as overlap in prey species utilization (Bodendorfer et al., 2006; Ogara et al., 2010). Leopards are solitary in nature, and smaller than lions (leopards: females 35–50 kg, males 50–75 kg; lions: females 140–160 kg, males 180–240 kg; Kock, Meltzer, & Burroughs, 2006), and leopards are consequently at risk of aggressive persecution by the physically and numerically dominant carnivore (e.g. Bonesi & Macdonald, 2004; Kamler et al., 2007, 2013; McDougal, 1988; see Fig. A1 in Appendix 1).

Studies of diving animals have used hidden Markov models (HMMs) to calculate the probability of transiting between as few as two dive states to accurately determine environmental predictors of behaviour (Bagniewska et al., 2013; Hart et al., 2010; Jessopp et al., 2013). Specifically, Hart et al. (2010) linked dive depth and duration to hidden behavioural states that were classified as either foraging or not foraging, and investigated the transitions between these states and the environmental conditions that triggered them. HMMs assume that the system is Markovian, with distinct states where the transition from time step t to $t+1$ is conditional on the state at t rather than previous states, and estimate the unknown states and the transition probabilities between them (Bagniewska et al., 2013). As Markov chain analyses consider state persistence and transitions between states, this makes them ideal for analysis of nonindependent temporal data such as movement trajectories (Hart et al., 2010; Patterson, Basson, Bravington, & Gunn, 2009). Markov chain analyses control for variables such as different amounts of habitat and density of predators, prey and competitors, and allow direct comparison of behaviour between habitat types and different areas.

Here we employed a Markov chain analysis of relatively high-resolution track (i.e. the same GPS fix rate used for detecting dynamic interactions between big cats; e.g. Benhamou, Valeix, Chamaillé-Jammes, Macdonald, & Loveridge, 2014) and environmental data to investigate behavioural changes in two terrestrial predators. This study was inspired by the pioneering work of Brown et al. (1999) and Laundre et al. (2001) regarding the ecological concept of fear, but is novel in that we had access to leopard populations both with and without lions present, as well as before and after the introduction of lions. A Markov chain analysis of this system is appropriate as it measures and removes the confounding effects of spatial autocorrelation, habitat variability and prey density, and focuses on the behavioural changes that occur when leopards come into close proximity to lions.

In the field of large-mammal ecology, properly controlled, large-scale in situ experimental manipulations are rare, and notoriously difficult to carry out (Bonesi & Macdonald, 2004; Creel et al., 2013). We took advantage of a unique opportunity to experimentally test the impact of lions on leopard behavioural ecology when an electrified fence that had historically excluded lions from a section of our study site (hereafter ‘Kwalusi’) was removed (see Fig. 1). Lions were present and abundant in the area adjacent to Kwalusi (hereafter ‘Mazunga’), and the fenced exclosure effectively created a sharp contrast in competition and predation by lions on an otherwise contiguous population of leopards. The fence was removed 18 months after the study began, allowing lions to move into and colonize the Kwalusi area, rapidly balancing their density between the two sites (du Preez, Loveridge, & Macdonald, 2014a). We thus compared, at the individual level, the behaviour of the leopard subpopulations with and without the risk of predation by lions, as well as the effect of the removal of the fence and rapid introduction of lions on the leopard population. Where lions were present, we also assessed the variation in predator proximity and resultant level of leopard response, so as not to simply dichotomize risk into only predator present/absent classes (e.g. Creel, Christianson, Liley, & Winnie, 2007; Creel et al., 2013).

Lions represent a significant source of mortality for leopards (Bailey, 1993; and see Fig. A1), and leopards are likely to actively avoid lions so as to reduce risk. However, avoidance behaviour may be a trade-off between running away, thereby alerting lions to their presence, and hiding, thereby risking close-quarter detection. Leopard behaviour and habitat use are thus likely to reflect both the real and perceived risk associated with lions (e.g. Brown et al., 1999; Laundre et al., 2001). We therefore expected to find changes in the transition rate from open to closed habitat and a change in behaviour within each habitat when lions were present compared to when they were absent. Moreover, as this behaviour is lion-moderated and based on detection of lions, we expected leopard behaviour to change based on the proximity of the nearest tracked lion.