

Being the underdog: an elusive small carnivore uses space with prey and time without enemies

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Abstract

Rare and elusive species are seldom the first choice of model for the study of ecological questions, yet rarity and elusiveness often emerge from ecological processes. One of these processes is interspecific killing, the most extreme form of interference competition among carnivores. Subdominant species can avoid falling victim to other carnivores through spatial and/or temporal separation. The smallest carnivore species, including members of the Mustelidae, are typically the most threatened by other predators but are also exceedingly challenging to study in the wild. As a consequence, we have only limited knowledge of how the most at-risk members of carnivore communities deal with being both hunters and hunted. We explored whether activity and space use of a little-known small carnivore, the Altai mountain weasel *Mustela altaica*, reflect the activity and distribution of its main prey, pika *Ochotona* sp., and two sympatric predators, the stone marten *Martes foina* and the red fox *Vulpes vulpes*. Spatial and temporal patterns of photographic captures in Pakistan's northern mountains suggest that weasels may cope with being both predator and prey by frequenting areas used by pikas while exhibiting diurnal activity that contrasts with that of the mostly nocturnal/crepuscular stone marten and red fox. Camera trap studies are now common and are staged in many different ecosystems. The data yielded offer an opportunity not only to fill knowledge gaps concerning less-studied species but also to non-invasively test ecological hypotheses linked with rarity and elusiveness.

Introduction

Interspecific killing, the most extreme form of interference competition, is a common phenomenon in ecological communities with multiple carnivore species (Polis, Myers & Holt, 1989; Palomares & Caro, 1999; Donadio & Buskirk, 2006). Like their prey, many predators find themselves in a landscape of fear (Laundre, Hernandez & Altendorf, 2001; Ritchie & Johnson, 2009). Having to look over its shoulder for more dominant predators (including humans; Ordiz, Bischof & Swenson, 2013) forces a carnivore to trade-off other activities with predator avoidance, and the main dimensions for such adjustments are time and space. Subdominant species may reduce the risk of aggressive interaction or other forms of interference by inhabiting different areas, using different habitats or habitat strata, or through temporal segregation of activity (Palomares & Caro, 1999; Hunter & Caro, 2008).

Interference competition seems to have shaped many aspects of carnivore biology, including patterns of distribution, morphology and behaviour (Donadio & Buskirk, 2006).

Smaller species are more likely to fall victim to predation by other carnivores and are under the greatest competitive pressure (Hunter & Caro, 2008). Yet, most studies on spatio-temporal partitioning among mammalian carnivores have focused on large- and medium-sized species, and comparatively little is known about how the very small (<0.5 kg) and presumably most at-risk carnivores deal with being both hunter and hunted. Weasels *Mustela* sp., although having played a prominent role in the development of concepts in guild ecology (Dayan & Simberloff, 1994; McDonald, 2002), are notoriously difficult to study in the wild and remain elusive in the literature on spatial and temporal niche separation (St-Pierre, Ouellet & Crete, 2006; Chiang *et al.*, 2012).

Here we evaluate spatial and temporal patterns in camera trap captures of the Altai mountain weasel *Mustela altaica* in the mountains of northern Pakistan in relation to its main prey and two larger, potentially threatening predators. Little was known about this small weasel half a century ago (Heptner & Naumov, 1967), and the situation remains nearly unchanged today (Wilson & Mittermeier, 2009; Hornskov &

Foggin, 2012). Scientific papers dedicated to the species are few and often limited to descriptive notes (Blumstein, 1993; Hornskov & Foggin, 2012). Therefore, one of our objectives is to share new information about this sparsely studied inhabitant of Asia's alpine meadows, steppes and forests (Roberts, 1997). Despite its wide geographic range (Fig. 1), the Altai mountain weasel is listed as near threatened by the International Union for Conservation of Nature (IUCN), attributable mainly to habitat conversion/loss and control of its main prey, pika *Ochotona* sp. (Abramov, Wozencraft & Ying-xiang, 2008; Wilson & Mittermeier, 2009; IUCN, 2012). In our study region, pikas are represented by large-eared pika *O. macrotis* and Royle's pika *O. roylei* because of their similarity in appearance and ecology (e.g. treated as conspecific by Roberts, 1997); we refer to both as 'pika' from here on. Pikas are associated mainly with rocky slopes and talus and feed on a wide variety of plant species (Flux & Angermann, 1990; Roberts, 1997). Because of their medium size and because they

are active throughout the winter, pikas are important prey for avian and mammalian predators (Flux & Angermann, 1990; Roberts, 1997).

The Altai mountain weasel is among the smallest members of a diverse carnivore guild in our study region, ranging from the least weasel *Mustela nivalis* to the brown bear *Ursus arctos*. Although several other sympatric carnivore species are potential competitors, we expect stone marten *Martes foina* and red fox *Vulpes vulpes* to be particularly threatening to the smaller Altai mountain weasel. Pikas are an important prey also for stone marten (Flux & Angermann, 1990), and diet overlap has been identified as a likely factor motivating interspecific killing (Donadio & Buskirk, 2006). Stone martens are known to kill other mustelids (e.g. Padial, Avila & Gil-Sanchez, 2002; Lanszki, Sárdi & Széles, 2009), suggesting that they may also be a threat to Altai mountain weasels. The red fox is the most widespread wild carnivore in our study region. Red foxes, although often themselves the victims of interspecific killings by larger species (Palomares & Caro, 1999), have a reputation for interference competition with other smaller carnivores (e.g. Frafjord, Becker & Angerbjorn, 1989; Ralls & White, 1995; Lindstrom *et al.*, 1995). Foxes can be a significant predator on small mustelids (Mulder, 1990; Dell'Arte *et al.*, 2007) and may compete directly not only with the Altai mountain weasel but also with the stone marten (Padial *et al.*, 2002; Weber *et al.*, 2002). Red foxes prey on pikas (Blumstein & Robertson, 1995; Roberts, 1997) but remain generalist predators.

How does the Altai mountain weasel cope with the threat posed by two sympatric larger predators, both capable of killing or otherwise interfering with weasels? Expecting spatio-temporal strategies that ensure access to prey and limit encounters with predators, we make the following predictions:

P1 Spatial association with prey. We predict that weasel site occupancy is positively affected by occupancy of pika. Temporal association is likely less important because Altai mountain weasels, like other small mustelids, are able to pursue their prey underground.

P2 Spatial or temporal avoidance of predators. We predict that weasel site occupancy is negatively affected by occupancy of fox/marten. Alternatively, we predict that weasel circadian activity patterns show less overlap with fox/marten activity than would be expected by chance.

We test these predictions using camera trap data collected in the mountains of northern Pakistan. More specifically, we evaluate co-occupancy among species and compare circadian activity patterns. Research on rare and elusive species generally produces small sample sizes, which discourages attempts to answer questions about ecological patterns and usually results in descriptive treatment instead. This can have consequences for our understanding of general ecological princi-

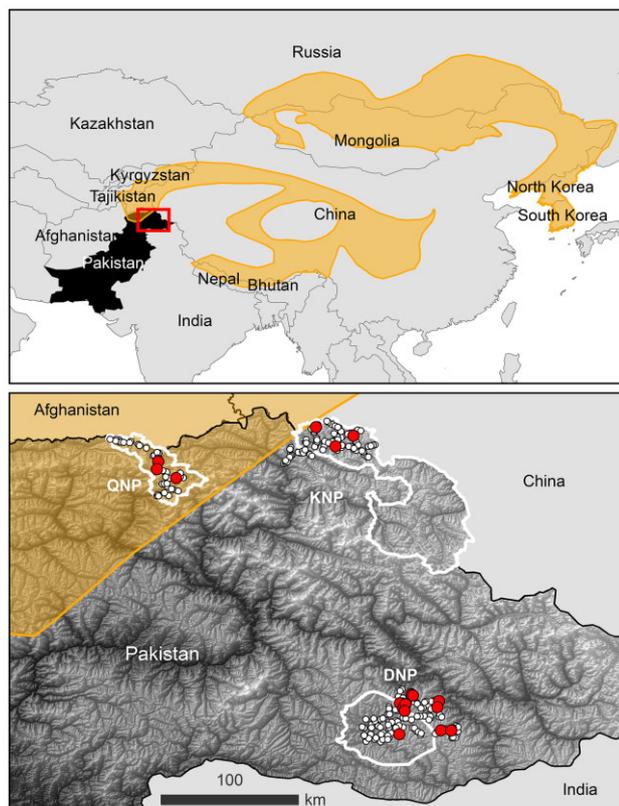


Figure 1 Locations of camera trap stations (white dots) in and around three national parks (white outlines; Qurumber National Park, QNP; Khunjerab National Park, KNP; and Deosai National Park, DNP) in northern Pakistan. The semi-transparent orange polygon represents the Altai mountain weasel *Mustela altaica* range reported by the International Union for Conservation of Nature (Abramov *et al.*, 2008). Red dots indicate camera trap locations where Altai mountain weasels were photo-captured during this study.



Figure 2 Examples of camera trap photos captured of Altai mountain weasels *Mustela altaica* during camera trapping in northern Pakistan. Photos (a) and (b) were taken in Deosai National Park, (c) and (d) in Khunjerab National Park.

pals, as most species are inherently rare (Gaston, 1994). Here we illustrate how we may be able to obtain both information about a species' status and a better understanding of ecological context.

Material and methods

Study areas and camera trapping

Data analysed here originate from a larger project studying carnivore guild ecology using non-invasive methods. Altai mountain weasels were photo-captured in three study areas, situated in and around three national parks in northern Pakistan (Figs 1 and 2). Qurumber National Park (QNP; 36.71° N, 73.98° E; 2500–5900 m a.s.l.) is located in the Pamir Mountains, Khunjerab National Park (KNP; 36.86° N, 75.11° E; 2700–5700 m a.s.l.) in the Karakoram Mountains and Deosai National Park (DNP; 35.07° N, 75.64° E; 3400–5300 m a.s.l.) is a large alpine plateau positioned between the Karakoram and the Himalaya. The landscape in QNP and KNP is rugged, dominated by narrow valleys, ravines, cliffs and ridges, and mostly glaciated mountain crests. Four vegetation zones can be distinguished along the elevation gradient: alpine dry steppe, subalpine scrub zone, alpine meadows and permanent snowfields. The central part of DNP is comparatively flat, whereas the peripheral areas have steeper terrain more similar to that in QNP and KNP. The study areas are described in more detail in Bellemain *et al.* (2007; DNP) and Bischof *et al.* (2013; KNP and QNP).

Camera traps were deployed 25 September to 16 November 2011 in KNP (85 stations), 18 June to 30 July 2012 in QNP (45 stations) and 23 September to 9 November 2012 in DNP

(112 stations). Camera trap locations were selected based on terrain features favoured by mammalian carnivores (ridges, cliff bases, draws) and preferably the presence of carnivore and/or prey sign. Camera traps were separated by at least 1 km with some exceptions because of constraints posed by terrain. At each site, a single motion-triggered digital camera with infrared flash (HC500/PC900, Reconyx, Holmen, WI, USA) was installed by affixing it at a height of *c.* 50–60 cm to a steel pole driven into the ground. Camera traps were set to take consecutive images (1-s picture interval) when triggered and were typically kept active at a given location between 10 and 15 days.

Camera trap studies targeting carnivores sometimes utilize bait or olfactory lures to attract animals, thereby increasing detectability and consequently survey efficiency (Bischof *et al.*, 2013). During the surveys in QNP and KNP (the earlier surveys), camera traps were randomly assigned to one of three treatments: (1) castor-based scent lure (containing beaver *Castor canadensis* castoreum); (2) skunk-based scent lure (skunk *Mephitis mephitis* anal scent gland); (3) no lures/attractants (control). In DNP we used castor-based trapping lure throughout. We describe how we analytically dealt with this inconsistency between surveys in the following subsection. Camera trapping procedure and lure application are described in detail in Bischof *et al.* (2013).

Occupancy

We used hierarchical analysis to jointly model detection and presence/absence and to evaluate the effect of site covariates on occupancy. We fitted multi-species occupancy models in a Bayesian estimation framework following the approach

by Waddle *et al.* (2010), which simultaneously estimates occupancy and detection parameters for multiple species, meanwhile allowing one species' occupancy or detection to be influenced by the occupancy of another. The Bayesian approach (for an accessible introduction aimed at ecologists, see Kéry, 2011) also provided the flexibility needed to address irregularities associated with data obtained from multiple study areas and different sampling bouts. We considered the following species interactions: pika occupancy affecting (a) fox, (b) weasel and (c) marten occupancy; fox affecting (d) weasel occupancy; marten affecting (e) weasel occupancy; fox affecting (f) marten occupancy. Detection occasions were pooled into 5-day periods. Based on preliminary findings from species-specific occupancy models, we included the following additional site covariates for red fox: lure treatment (none, castor, skunk; on detection), study area (DNP, KNP, QNP; on detection and occupancy) and habitat (forest/scrub, pasture/grassland, barren; on occupancy); for stone marten: area (on detection) and habitat (on detection and occupancy). The effect of lure on fox detection probability was modelled only using data from KNP and QNP where all three lure treatments had been applied; for DNP (castor-based lures throughout), the effects of area and lure were not separately estimated, thereby accounting for confounding. Our goal in this study was not to produce estimates of these site covariate effects; they were included solely to control for their effects. See Bischof *et al.* (2013) for a more detailed treatment of covariate effects in occupancy models for our study system. We fitted models using the R2jags package in R (R Development Core Team, 2012; Su & Yajima, 2012) and JAGS (Plummer, 2003). Given the small number of photo-captures of weasels and pikas, our data were inadequate for precise estimation of parameters associated with these species. Specifically, preliminary analyses showed that posterior estimates of occupancy interaction effects involving pikas were pushed against the boundaries of flat priors. Therefore, rather than evaluating the absolute magnitude of the various species interaction effects, we used relatively narrow normally distributed priors (mean = 0, precision = 0.1) for all species interaction effects and compared the extent and direction of the posterior distribution's deviation from 0 to assess the level of support for avoidance or association. We used flat priors for all other parameters. We ran three chains with 30 000 iterations (+10 000 iterations burn-in), thinned by 30. Model convergence was assessed with the R-hat statistic and trace plots. The model definition and the data used in the analysis are provided in the electronic Supporting Information Appendices S1 and S2.

Circadian activity

We estimated circadian activity patterns for each of the four species using generalized additive mixed-effect models (GAMMs) with a Poisson link (gamm function in the R package mgcv; Wood, 2011). We used the total number of visits (photographic captures at least 30 min apart) associated with each hour of the day (0–23) at each station as a response, hour of the day as the predictor variable and station ID

as a random effect on the intercept to account for non-independence of multiple visits at the same station. Activity patterns were compared using plots of GAMM-predicted relative activity for each species.

Results

Occupancy

We set a total of 242 operational camera trap stations and photo-captured nine species of carnivore in this study, including the three species used in the analysis. In order of size (largest to smallest) these species were brown bear (8 camera trap stations), grey wolf *Canis lupus* (15 stations), snow leopard *Panthera uncia* (17 stations), Eurasian lynx *Lynx lynx* (3 stations), red fox (146 stations), Pallas's cat *Otocolobus manul* (1 station), stone marten (52 stations), Altai mountain weasel (18 stations) and least weasel (1 station). Pikas were photo-captured at 22 stations. Multi-species occupancy models revealed that both weasels and martens were more likely to use sites at which pikas were present (P1; Fig. 3b,c), whereas pika presence did not appear to influence fox occupancy (Fig. 3a). Instead of spatial separation, weasels were more likely to occupy sites at which martens were also present (P2; Fig. 3e). This interaction, because of its masking effect in the model, was excluded when estimating the effect of pika occupancy on weasel occupancy. We found little support for weasel and marten occupancy being influenced by fox presence, although the coefficients for occupancy interaction effects tended to be negative (P2; Fig. 3d,f).

Circadian activity

GAMMs for all four species showed a significant effect of time of day on the number of visits at a camera trap station (Fig. 4). Weasels exhibited mostly diurnal activity at camera trap stations, with 80% of photo-captures during daylight hours and a peak in activity around midday (Fig. 4a). By contrast, stone martens were strictly nocturnal, without a single photo-capture during daylight hours (P2; Fig. 4b). Foxes and pikas were mainly nocturnal/crepuscular, but with captures also during daytime (Fig. 4c,d).

Discussion

Small predators in a landscape of fear

Predators live, as their prey, in a landscape of fear, where size matters and typically the smaller the species the greater the risk of being killed by other carnivores. The smallest carnivores, such as weasels, are difficult to study in their natural communities, but camera traps allowed us to non-invasively evaluate spatio-temporal activity patterns of an elusive small mustelid in a remote region. The Altai mountain weasel appears to deal with being both hunter and hunted by frequenting areas used by its main prey (P1; Fig. 3) and exhibiting a mostly diurnal activity pattern contrasting with two

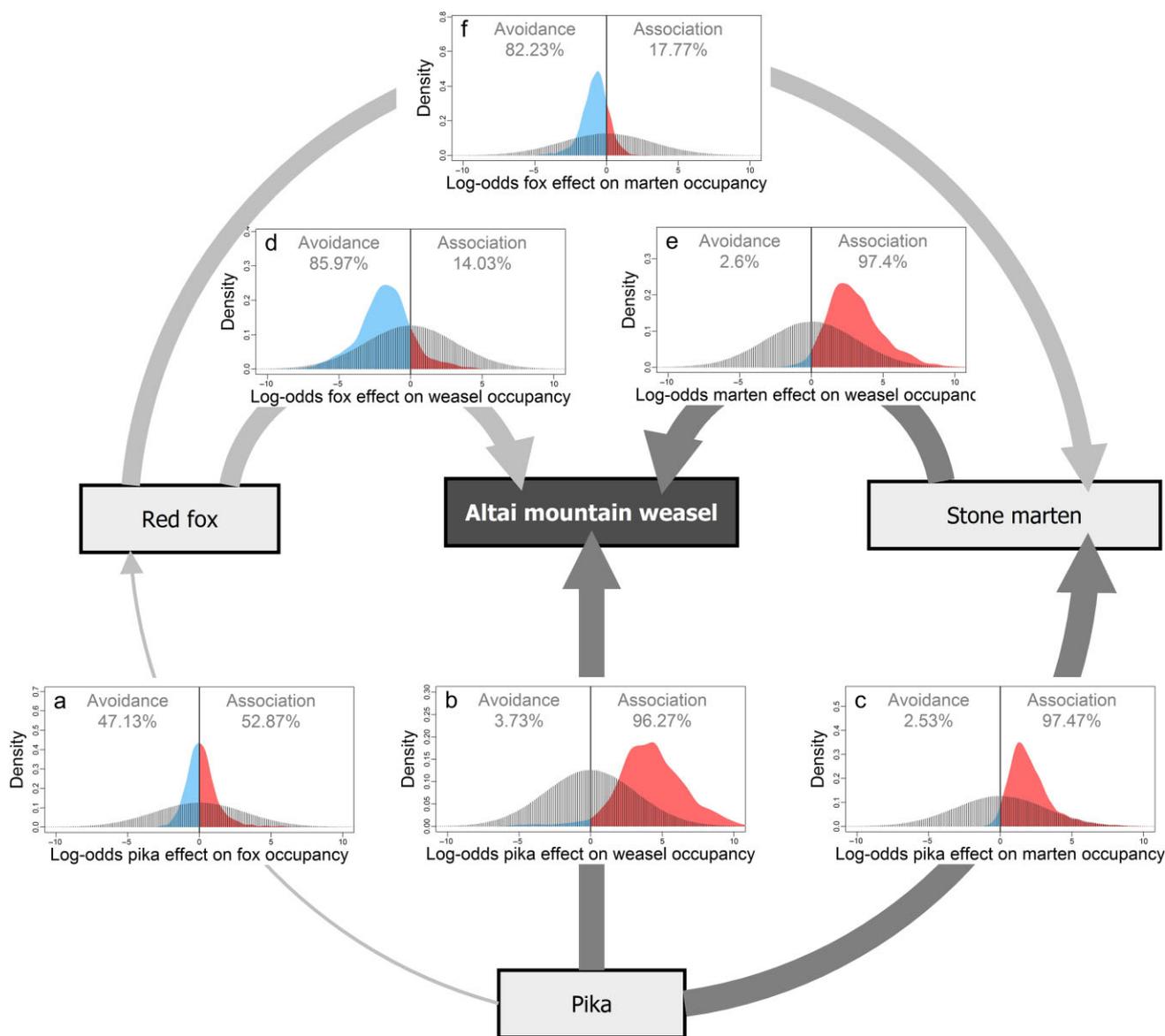


Figure 3 (a–f) Results from Bayesian multi-species occupancy models evaluating spatial relationships between Altai mountain weasel *Mustela altaica*, stone marten *Martes foina*, red fox *Vulpes vulpes* and pika *Ochotona* sp. Plots associated with a given interaction (indicated by arrows) show the distribution of the prior (grey) and posterior probability of the estimated influence of one species' occupancy on that of another (red part: probability of positive association, blue part: probability of negative association/avoidance). The strength of the evidence (positive or negative) for an effect of one species' occupancy on that of another is indicated by relative arrow thickness; darker arrows represent positive associations with a model-predicted probability >0.95.

nocturnal/crepuscular predators: the stone marten and the red fox (P2; Fig. 4). Strict spatial avoidance of the generalist red fox at the scale measured here is not a viable option for smaller carnivores because foxes are ubiquitous across our study areas. Furthermore, weasels seem to use, rather than avoid, areas occupied by martens, presumably a result of similarities in habitat selection and diet. This makes the weasel's diurnal activity an effective strategy for avoiding both enemies. Although circadian activity of the marten was more similar

to that of the red fox, we also detected what could be temporal avoidance of foxes by martens: foxes were at times active during daytime and had their peak in activity before midnight (Fig. 4c), whereas martens were never detected during daylight and showed a peak in activity after midnight (Fig. 4b).

Larger carnivores can alter the role that smaller subdominant species play in ecological communities not only by reducing their numbers but also by forcing behavioural adjustments

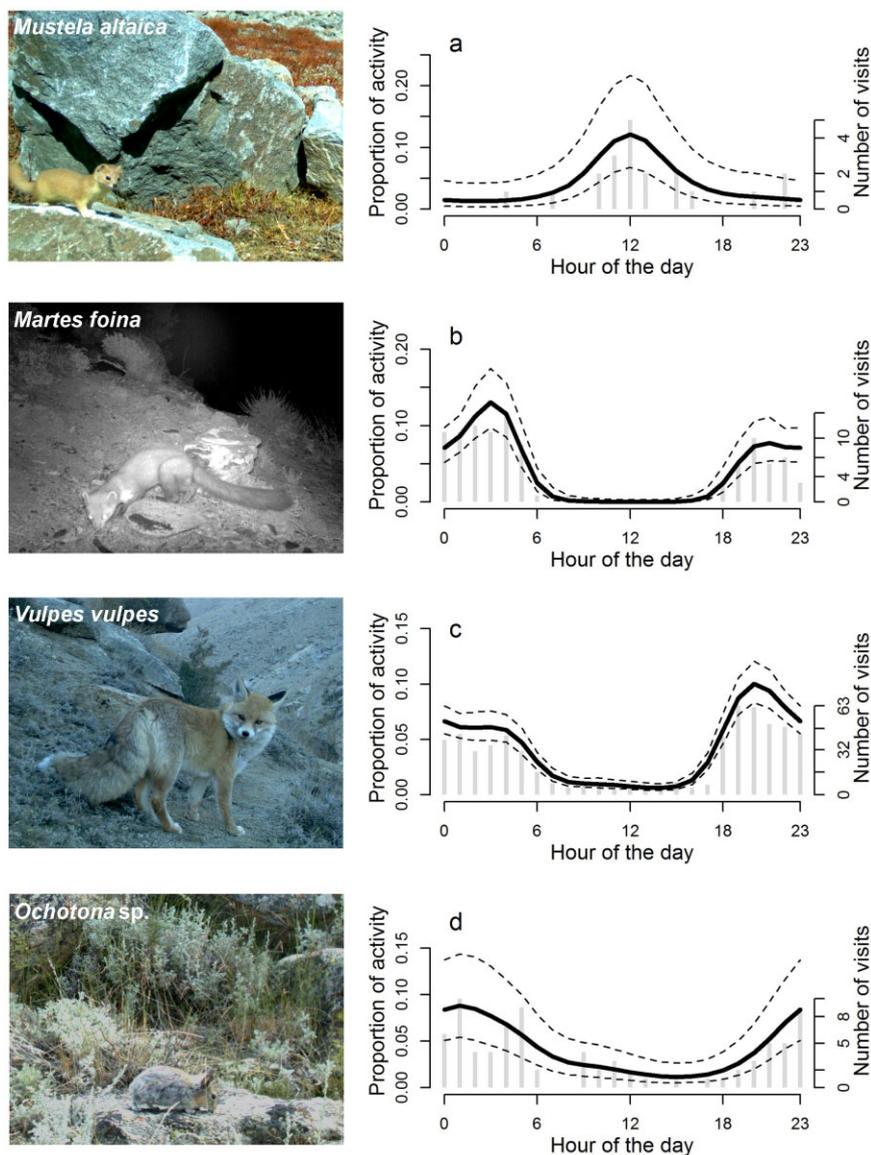


Figure 4 (a–d) Circadian activity of Altai mountain weasel *Mustela altaica*, stone marten *Martes foina*, red fox *Vulpes vulpes* and pika *Ochotona* sp. based on visits recorded at camera traps. Predictions from generalized additive mixed-effect models (scaled to sum to 1) are shown as bold lines, together with 95% confidence interval limits (dashed). Vertical grey bars represent the number of recorded visits at a given hour of the day. An example photograph, captured during camera trapping, is shown for each species on the left.

that reduce their effectiveness as predators – mechanisms that are captured also by the mesopredator release hypothesis (Prugh *et al.*, 2009). Living in a carnivore community where almost all other species are larger, the Altai mountain weasel faces the very real possibility of aggressive and ultimately lethal attention from other predators unless it incorporates predator avoidance during its activities. Small mustelids are well equipped for life in a competitive community, in part because their size and agility gives them access to a diversity of habitat strata. In addition to temporal avoidance, Altai mountain weasels, and to lesser extent stone martens, can reduce the chance of encountering red foxes and other dominant predators by using crevices and burrows less accessible to larger and less agile competitors. Although the weasel’s circadian activity did not mirror that of pika (Fig. 4), being able to pursue prey both above and underground (Heptner & Naumov, 1967;

Wanhong, Wenyang & Naichang, 1996), may allow the weasel to prioritize predator avoidance when establishing activity patterns without becoming an inefficient predator (see also St-Pierre *et al.*, 2006).

Predator–prey relationships tend to be complex as they are influenced by individual attributes, environmental conditions, as well as the status and characteristics of the populations involved (Penteriani *et al.*, 2013). Complexity is increased if we consider the involvement of additional actors, such as multiple competing predators. We focused on a small subset of species from a larger ecological community and ignored that foxes and martens make foraging decisions while themselves under the risk of being killed by larger carnivores, whereas the weasel’s potential enemies include additional predators, such as raptors (Hoset *et al.*, 2009). A potential loss in realism because of our simplistic view of the Altai mountain

weasel's world is outweighed by the benefits of conceptual transparency. Because of our singular reliance on camera traps, we did not document direct predation on or aggressive encounters with weasels in this study. Nonetheless, the red fox was the most common carnivore, and the stone marten the most common mustelid detected during camera trapping; both species are known threats to smaller carnivores. The patterns we observed are themselves telling; temporal partitioning between carnivores has been suggested as a more likely result of interference than exclusion competition because it reduces the chance of physical interaction (Brook, Johnson & Ritchie, 2012).

Camera traps for assessing temporal and spatial partitioning

Camera trapping studies, like most surveys of fauna and flora, suffer from imperfect detection. Ignoring this and simply analysing rates will in most cases lead to biased and potentially erroneous conclusions. Camera traps have been used mainly for the study of large- and medium-sized animals and may be biased against small, fast-moving species (Glen *et al.*, 2013). This in itself is not a problem for estimating parameters related to presence/absence if species-specific differences in detection probability are accounted for in analytical models, for example, through the use of hierarchical methods. However, a relationship between detectability and time of day (potentially species specific) would bias circadian activity estimates based on rates. We cannot exclude the possibility of such a bias in our study; however, even if present, we think that it is unlikely to have caused a mislabelling of the weasel's circadian activity pattern as diurnal, because smaller species (mice, voles) were caught almost exclusively at night, as was the larger, but morphologically similar and fast-moving stone marten. Although not unbiased, camera trap data yield less biased estimates of circadian activity than opportunistic observations by humans (Bridges & Noss, 2011).

Both spatial and temporal partitioning within a guild can take place at various scales. For example, carnivores may avoid more dominant members of their guild through temporal partitioning not only by exhibiting contrasting circadian activity but also by concentrating their activity during moon phases that minimize encounters with threatening species and possibly increase encounters with prey (Mukherjee, Zelcer & Kotler, 2009; Penteriani *et al.*, 2013). Similarly, in the spatial dimension avoidance can be accomplished through the use of separate areas, different macro- and microhabitats, or habitat strata (Padiál *et al.*, 2002; Hunter & Caro, 2008; Viota *et al.*, 2012). Camera traps are well suited to determine patterns in presence/absence and activity (O'Connell, Nichols & Karanth, 2011), but future studies should evaluate the possibilities and limitations of detecting segregation at different scales within guilds using non-invasively collected data.

The main limitation of our study, shared with other camera trap studies and observational studies in general, is that we are drawing inferences from patterns. Experimentation could help determine causality, that is, whether it is truly the risk of

predation by nocturnal/crepuscular predators that motivates the observed circadian activity of Altai mountain weasels or whether other factors are responsible, for example, that activity coincides with the warmer part of the day or with the period when prey is most vulnerable (see also Hayward & Slotow, 2009).

Elusive species and the study of ecological patterns

Our selection of the Altai mountain weasel for this analysis was in part motivated by the relative dearth of information on many small carnivores, compared with large predators and species that are of commercial interest to fur harvesters and trophy hunters or play a significant role in human-wildlife conflict. As a rule, elusive or rare species do not make good models for exploring questions about general ecological phenomena. Yet, in some cases elusiveness and rarity could be expressions of the focal ecological mechanism at work. Despite the Altai mountain weasel's low detection probability, camera trapping revealed pronounced patterns that are indicative of spatio-temporal strategies related to predation and predator avoidance, something that remains difficult to show for small carnivores. As an additional benefit, we obtained new information about this little-known species. Some of our camera trap sites with Altai mountain weasel detections were more than 200 km from the current range boundary reported for the species (Abramov *et al.*, 2008; Fig. 1). Furthermore, with few exceptions (e.g. Wanhong, *et al.*, 1996), the Altai mountain weasel is portrayed as crepuscular/nocturnal (Wilson & Mittermeier, 2009), yet the majority of photos in all our study areas were captured during daytime (Fig. 4). Camera trap studies are now widespread, often extending into remote and unstudied areas. The data they produce on rare and elusive species – whether these are the focus of a particular survey or ancillary to it (McCarthy *et al.*, 2010) – offer an opportunity to both test ecological hypotheses linked with rarity and elusiveness and to fill knowledge gaps concerning less-studied species.

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Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Definition of the Bayesian multi-species occupancy model in the JAGS language.

Appendix S2. Data file (in .RData format) for use with the Bayesian multi-species occupancy model.