



# Influences of Predator Cues on the Incidence of Ungulates, Mesopredators and Top Predators in the Greater Khingan Mountains, Northeastern China

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## ABSTRACT

Top predators can affect the behaviour of prey species via lethal (direct kill) or non-lethal effects (*i.e.*, through predation risk). For example, prey species may move from areas perceived as risky to safer spaces where predation risk is lower, which can have important consequences for investment in foraging, movement, and mating, and for the behaviour and habitat use of other species, such as mesopredators. These changes in prey and mesopredator behaviours are likely mediated by the presence of predator cues in the environment. Here, we test how different predator cues (visual and odor) from familiar and novel predators (brown bear and Amur tiger, respectively) influence ungulate, mesopredator, and top predator visitation rates to camera trap sites in a national nature reserve in China. The comparison of these predator types is of particular interest in this region as Amur tigers may shortly be reintroduced here. We found that visual but not odour cues significantly affected ungulate visitation rates: ungulates showed reduced visitation to sites with either a novel or familiar visual predator cue. When combined, mesopredators and top predators also showed a small reduction in visitation rates to tiger cue sites compared to bear cue sites, suggesting a possible novel predator effect. The generalisation and contextual importance of predator cues for prey and mesopredators have been little studied. Understanding how species respond to novel cues may help to determine extinction probabilities and overall plasticity in the face of change. This study is, therefore, an important step forward in understanding predator cue responses at the community level. This is also the first study to test the ecological function of Amur tiger cues in the wild environment and may serve as essential information in the rewilding process of captive Amur tiger plans.

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## Authors' Contribution

GJ, HM and FY conceived and designed the study. HM, FY, DW and YL conducted field work and collected data. KM and HM analysed the data and revised the manuscript. HM wrote the manuscript.

## Key words

Predator cues, Ungulates, Mesopredators, *Panthera tigris altaica*, Camera trap, Fear ecology.

## INTRODUCTION

Top predators can affect the behaviour of prey species via lethal (direct kill) or non-lethal effects (*i.e.*, through predation risk) (Lima and Bednekoff, 1999; Tolon *et al.*, 2009; Farnworth *et al.*, 2016). Predation risk determines habitat use by prey species (Laundré *et al.*, 2001; Hernández and Laundré, 2005), as prey may change their activity patterns when confronted with risk (Lima and Bednekoff, 1999; Tolon *et al.*, 2009). Differential use

of habitats due to variation in predation risk is known as the landscape of fear phenomena (Laundré *et al.*, 2001; Hernández and Laundré, 2005; Brook *et al.*, 2012). Prey species such as ungulates tend to move from “risky” zones (*e.g.*, where predator density is higher, or refuge scarcer) to safer spaces (*e.g.*, reduced predator density, more refugia available) to reduce their predation risk (Tolon *et al.* (2009). Alterations in behavior can result in trade-offs between daily activities such as foraging, movement, and mating, and safety behaviours, especially in high risk habitats. For example, both ungulates and mesopredators adopt “safety” behaviours like vigilance, reduced foraging time, and shifting to safe habitats when under high predation risk (Creel *et al.*, 2005; Li *et al.*, 2011; Zheng *et al.*, 2013;

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Kuijper *et al.*, 2014). Thus, top predators can indirectly control the behavior and habitat use of mesopredators, as well as prey (Palacios *et al.*, 2016).

Changes in prey and mesopredator behaviours are likely mediated by the presence of predator cues in the environment (Apfelbach *et al.*, 2005; Caro, 2005). According to Creel *et al.* (2008) presence of cues indicating the availability of predators within the habitat can be sufficient enough for prey to assess the predation risk within the area. Top predator odour cues like feces, urine, and fur, are used by most mammalian prey species to detect the presence of danger during foraging; cues, therefore, help to recognize the extent of risk (Garvey *et al.*, 2016, 2017). The presence of predator odours can trigger prey species to respond by altering their behavior (Apfelbach *et al.*, 2005; Caro, 2005), such as decreasing visitation to specific areas (Nersesian *et al.*, 2012) and increased protection of young (Schulte *et al.*, 2013). In the presence of wolves, elk change behaviours like vigilance levels and movement (Creel *et al.*, 2005, 2008). The accuracy of risk perception based on predator cues may increase once different cues are combined, or used in different contexts; for example lizards and newts use predator cues in a habitat-dependent manner, relying more on visual cues in an open area, and odour cues in a dense vegetative habitat (Mathis and Vincent, 2000). Visual and odour cues have the potential to convey different information (Smith and Belk, 2001), and may also differ in intensity and longevity (Brown and Cowan, 2000; Kats and Dill, 2016), as well as detectability by different species (*e.g.*, some may have a greater ability to detect visual cues than others based on differences in visual acuity (González and Rodríguez-Gironés, 2013).

A number of studies have shown the effects of predator cues on ungulate and/or mesopredator behavior (*e.g.*, Hughes *et al.*, 2010; Cremona *et al.*, 2014; Kuijper *et al.*, 2014; Wikenros *et al.*, 2015; Natt *et al.*, 2017; Suárez-Tangil and Rodríguez, 2017; Wikenros *et al.*, 2017; Goullaud *et al.*, 2018). However, less has been done to identify specific cues used to assess the presence of risk at the community level (Winnie, 2012; Beschta and Ripple, 2013; Kuijper *et al.*, 2014). For example, although prey get information about the proximity of predators via some cue channels, for the most part in the type of visual and odour cues (Kelley and Magurran, 2003), most studies have considered only one cue. The relative importance of cue type for different species (of both predator and prey) is therefore relatively understudied. Further, the study on the effects of predator cues on prey species behavior vastly outweighs that on the effects on mesopredator species, though this is likely to be equally important in structuring communities, and some clear effects have been shown. For example, Palacios *et al.* (2016) showed that experimental

modification of apex predator cues (*e.g.*, predator odour and visual cues) reduced the distance swum, the area used and even foraging behaviours carried out by mesopredators. Mesopredators also respond especially quickly to predator species that have recently consumed conspecifics (Cremona *et al.*, 2014).

The Siberia Tiger Park in Heilongjiang, China has bred a reasonable Amur tiger number and is planning a program to train and reintroduce them in the wild (Wang *et al.*, 2018). Thus, comparison of these predator types is of particular interest in this region, as for how native prey and mesopredator species respond to these novel cues gives us insight into how predator-prey dynamics are likely to unfold in this region going forward. Currently, we are in a period of anthropogenic change; species are shifting ranges, and animals may be encountering novel predators that are moving into their range (Chen *et al.*, 2011; Van Dyck, 2012; Wong and Candolin, 2015). Knowing how species respond to novel cues might help to determine extinction probabilities and overall plasticity in the face of change. To our current understanding, this is the first study that involves captive Amur tiger ecological influence on prey site visitation rate in the wild, which as we have noted is likely to be important in the future as this species regains some of its prevalence in the region.

Here, we test how different predator cues (visual and odour) from familiar and novel predators (brown bear vs. Amur tiger) influence ungulate, mesopredator, and top predator visitation rates to camera trap sites in Hanma National Nature Reserve, China. Previous work has demonstrated reductions in visitation rate to sites where predator cues are prevalent in both ungulates (Kuijper *et al.*, 2014; Wikenros *et al.*, 2015; Venter *et al.*, 2017), and mesopredators (Palacios *et al.*, 2016; Wikenros *et al.*, 2017; Haswell *et al.*, 2018; Sivy *et al.*, 2018). We, therefore, predict that overall, ungulate and mesopredator visitation rates should be reduced at camera trap sites where predator cues are present, versus sites where control cues are present. We also predict that cue type might differentially influence prey and mesopredator visitation rates to camera trap sites. Different prey responds differently towards different predator cues, but also the intensity of predator cues determines the intensity of response (González and Rodríguez-Gironés, 2013). We predict that odour cues might induce a weaker response in terms of visitation rate because they are more affected by wind and are likely to be less long-lived than visual cues (Brown and Cowan, 2000; Kats and Dill, 2016). We also predict differences in prey and mesopredator response to predator cues based on predator type. Correct identification and response to predator cues are important for prey species fitness and often relies on experience (Carthey and Blumstein, 2017; Saxon-Mills

*et al.*, 2018). Due to this, prey species may show a very minimal or no response to cues from a novel predator or one that has not existed in a system for many generations (Saxon-Mills *et al.*, 2018). Amur tigers have been absent from this region for many decades with no reported sightings in our study area in recent history (Turvey *et al.*, 2017). We predict that prey and mesopredator response to familiar predator cues (brown bear visual odour cues) will be greater (a more significant drop in visitation rate) than the response to novel predator cues (tiger visual and odour cues).

## MATERIALS AND METHODS

### Study site

This study was conducted between July 2016 and June 2017 in the Greater Khingan Mountains of Hanma National Nature reserve (51°20'02"–51°49'48"N, 122°23'34"–122°52'46"E), close to the small city of Genhe, Inner Mongolia, North East China (Fig. 1). In total, Hanma comprises an area of 1073.48 km<sup>2</sup>. Habitats, including vegetation and species characteristics, are described elsewhere (Zhai-Penghui, 2015; Guo *et al.*, 2017). Predators and mesopredators present in this system include the Eurasian lynx (*Lynx lynx*), wolf (*Canis lupus*), wolverine (*Gulo gulo*), and brown bear (*Ursus arctos*). Naturally occurring ungulate species include roe deer (*Capreolus pygargus*), moose (*Alces alces*), musk deer (*Moschus sifanicus*), reindeer (*Rangifer tarandus*), and red deer (*Cervus elaphus*) (Zhai-Penghui, 2015).

### Experiment design

#### Design

First, we established treatment plots or grids, with one square plot for each treatment type: the visual cue experiment comprised three plots (Aa- tiger visual, Ab- bear visual, Ac- control), and the odour cue experiment comprised two plots (Ba- tiger, Bb- control; Fig. 1). Plot grids were determined randomly using the fishnet method in ArcGIS 9.3 (Krivoruchko, 2011), which laid grid cells of specified areas within the study area. Here, we set up camera traps, at least 1km from each other. At first, the odour group grids were designed to be the same as the visual cue experiment (*i.e.*, with one plot for the treatment and another plot for the control), but given unavoidable differences in environmental conditions across the designated grid sites (*i.e.*, mountains and swamp areas). We, therefore, redesigned the layout for this experiment so that each grid contained both treatment and control (*i.e.*, Ba and Bb, respectively; Fig. 1) to avoid confounding effects of habitat type. We installed a total of 113 camera traps (LTL ACORN scouting camera; Ltl 5210 5MP and

Ltl 5210A 12MP, and Nighthawk Bestguarder SG-990V infrared sensor trigger self-timer digital camera) in all over the Hanma national nature reserve. In our designed study grids there were a total of 86 cameras. We additionally set up 27 no treatment cameras to establish baseline visitation rates with no manipulation present; these were placed randomly within and outside the grids to the areas with high chances to capture mammals, *i.e.*, nearby water points, areas with numerous animal ways and droppings. Cameras were set to a video mode to record for 20s at each 5s interval when triggered by an animal passing across. The treatments and controls used were: photos of Amur tigers *Panthera tigris tigris* (Kitchener *et al.*, 2017) and brown bear *Ursus arctos* (Blanco *et al.*, 2011) as visual cues and a blank model (vegetation) as their control. Lastly, we used Amur tiger feces as odour cue and soil as its control (Fig. 2).

Visual cue plots were specified as grids of 3.2 km × 3.2 km; the odour cue experiment plots were specified as grids of 1.6 km × 1.6 km. The latter was smaller due to the topography of this area having lower accessibility. Each visual cue plot had 18 camera traps, and the smaller odour cue plots had 8 camera traps each. In total we established seven plots; two for treatments (*i.e.*, Fig. 1A, C) and one as control (Fig. 1C) for the visual cue experiment. The two other plots for odour experiment were divided each into treatment and its control due to the reasons stated above; making it four as previously stated. We chose to have separate plots for each treatment type as opposed to dispersing predator cue and control sites randomly due to the small size of the reserve which might have resulted in treatments influencing the visitation rates of nearby camera trap sites. The separation of treatment types ensured that this was not the case. We are confident that there was no effect of grid placement on visitation rates, again due to the small size of the reserve, and because all grids were similar in habitat and vegetation density.

### Study 1: Visual cue experiment

In tiger visual grid (Fig. 1Aa), tiger visual cues (a life-size photo of a standing tiger printed on a canvas; Figure 2 following studies by Li *et al.* (2011) and Fischer *et al.* (2017)) were placed at pre-designated plot points by tying the print to two trees located adjacent to each other. Then, cameras were tied about 50cm height from the ground to one of the trees to record incidence of visitation and ungulate/mesopredator behaviours. The bear visual grid (Fig. 1Ac) was set up in the same way, with brown bear visual cues (life-size photo of a standing bear printed on a canvas). A control grid (Fig. 1Ab), contained canvases printed with a photo of vegetation/habitat-like environment. Each visual cue grid contained 18 camera trap plots (18 x tiger, 18 x bear, 18 x controls).

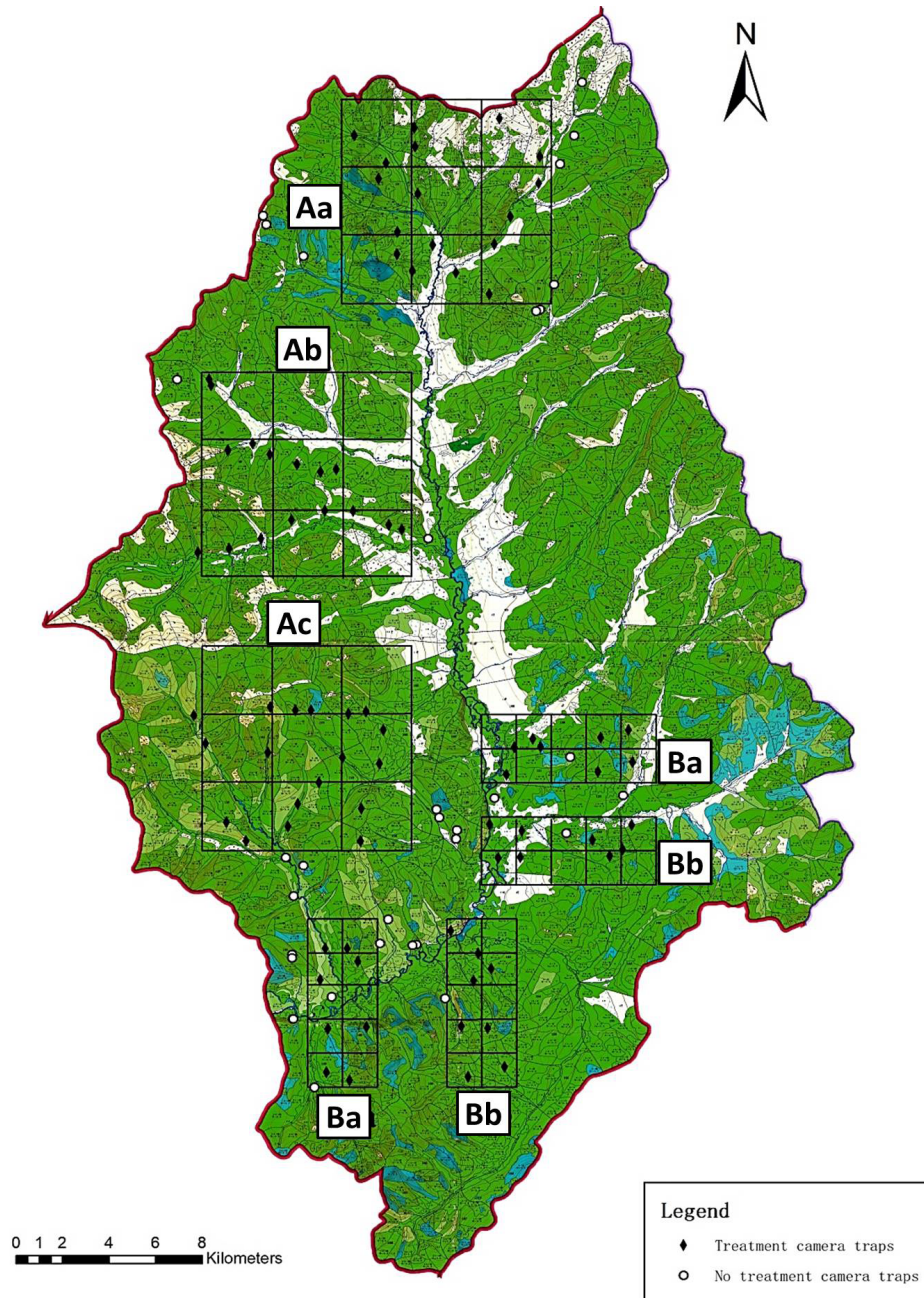


Fig. 1. Experimental sites and camera trap distribution in Hanma National Nature Reserve. Black boxes indicate reserve areas selected for experimental treatment group sites as determined by the fishnet method in ArcGIS 9.3. Then A- visual cue experiment (Aa- tiger, Ab- bear, Ac- control), and the odour cue experiment comprises of (Ba- tiger, Bb- control). Tiger visual (Aa) includes a life-size photo of a standing tiger printed on a canvas which is tied to two trees that are side by side, with a camera tied to one of the trees; the same size and settings were for the bear visual (Ab). For the control visual (Ac), a canvas with the same size as tiger and bear visual cues was printed with vegetation colour to mimic the habitat and then tied side by side to two trees with a camera tied to one of the trees to record visitation incidences. For the tiger odour cue experiment (Ba, b), a plastic bottle with tiger feces (*i.e.*, Ba groups) was tied to a tree, and then a camera is tied to the opposite tree to record the visitation rate; the same was done to odour cue control (Bb) groups, but here the bottle was filled with soil. Finally, there were cameras at no treatment sites indicated as white round spots with neither treatment nor control. Red circles indicate individual camera trap sites each of which includes one motion-triggered camera.

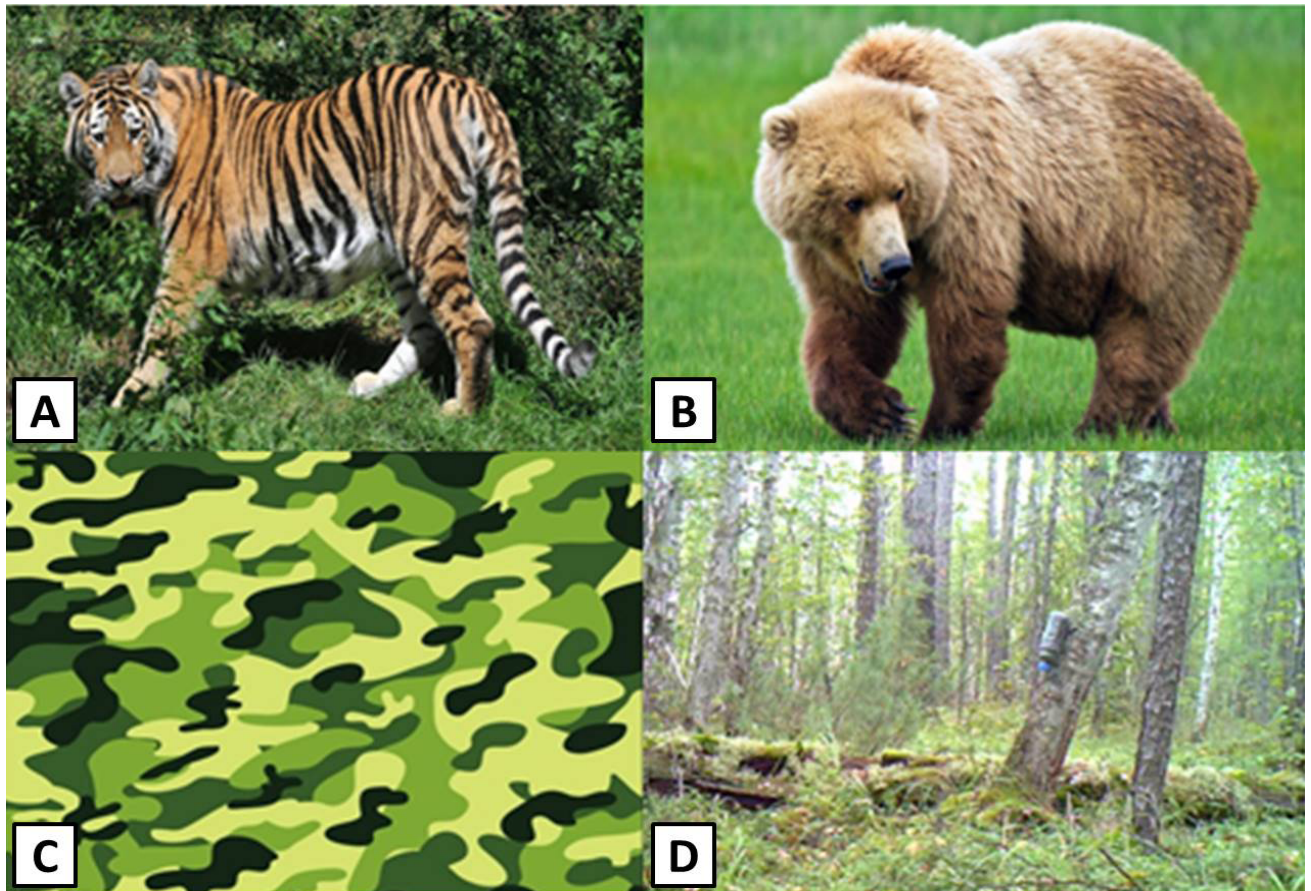


Fig. 2. Experiment, and control visual and odour cues. From top left to bottom right is a tiger, bear, and control visual cues; and tiger odour cue, respectively. Tiger odour control cue looks similar to tiger control cue with the differences in their content (tiger feces vs. soil).

#### Study 2: Odour cue experiment

The Amur tiger feces from Harbin Siberian Tiger Park were collected by hand and refrigerated (maximum of 6 days in storage) before being transferred to 150 ml plastic bottles, pierced with small holes in order to let the tiger feces odour escape. Plastic bottles (150 ml) with the same volume of soil were used as controls. In both treatment and control plots, the plastic bottle containing either soil or feces was tied at a tree bark (Fig. 2D) at the height that is equivalent to the camera trap height (located at opposite tree) so that the camera could record animal incidences of visitation at the station and behaviours expressed. Each odour cue experiment grid contained 8 camera trap sites (*i.e.*, 8 x tiger feces, and 8 x controls at Figure 1Ba; and 8 x tiger feces, and 8 x controls at Figure 1Bb).

#### Data collection

After one year of recording, we collected the memory cards (SD) from the cameras and brought them back to

the laboratory for analysis. Using focal animal sampling and all-occurrence methodology (Altmann, 1974; Lehner, 1992; Martin *et al.*, 1993; Margulis, 2016) we extracted the required data (namely – incidences in which an ungulate or mesopredator triggered the camera to record). Triggered recordings that were within 30 min of each other and contained the same animal were counted as one visit. Ungulate species detected were roe deer, moose, musk deer, red deer, and wild boar. Mesopredators were defined as predators or population of predators that are classified to be in the mid-size of the available predators within the given ecosystem (Groom *et al.*, 2006; Prugh *et al.*, 2009; Wallach *et al.*, 2015); under this definition, we detected sable *Martes zibellina* and weasels *Mustela nivalis* in this system. Top predators (apex predators, alpha predators or mega-predators) were defined as large predators with no natural predators to feed on them within the food chain (Groom *et al.*, 2006; Prugh *et al.*, 2009; Sukhdeo, 2012; Wallach *et al.*, 2015); we detected bear, lynx, and

wolverine as top predators in this system.

For the visual cue experiment, data were collected from a total of 83 deployed cameras. Some cameras stopped functioning soon after deployment (within 30 days) and were not included in data analysis ( $n = 3$  tiger photo cameras,  $n = 2$  bear photo cameras,  $n = 6$  control cameras) resulting in a sample of 69 cameras. In this sample, the mean length of camera activity was  $280.0 \text{ days} \pm 11.1$ , and the total number of mammals captured on camera was 997.

For the odour cue experiment, data were collected from a total of 61 deployed cameras. Again, we excluded cameras that were active for fewer than 30 days ( $n = 1$  control cameras, no predator odour cameras excluded), resulting in a sample of 57 cameras. In this sample, the mean length of camera activity was  $251.6 \text{ days} \pm 14.5$ , and the total number of mammals captured on camera was 837.

We also collected data from 27 no treatment cameras, again excluding cameras that were active for fewer than 30 days ( $n = 3$  cameras), resulting in a total of 24 cameras.

#### Statistical analysis

For analysis of both experiments, the number of a) ungulates, b) mesopredators, and c) top predators was set as the dependent variable in three separate generalized linear models (GLMs), with treatment, and number of days of camera activity as independent variables. For the photo cue experiment, treatment was a four-level factor: no treatment, tiger cue, bear cue, and control cue. For the odour cue experiment, treatment was a three-level factor: no treatment, tiger odour cue, control cue. Given the skew towards 0s and low numbers in mammal incidence data in both experiments, we used a negative binomial error structure to account for overdispersion, with a log link. All models were constructed using the *glm.nb* function (MASS package; Venables and Ripley, 2002) in the statistical software, R version 3.2.3 (R Core Team, 2015). We compared models (the full model, single-term models, a null model) using AIC, and report the best model (lowest AIC value). Significance values in models were determined using likelihood ratio tests. Where treatment was significant, we used post-hoc tests (Tukey tests) to determine whether some treatment types had stronger effects than others, as predicted.

For analysis of the photo experiment, we initially constructed models containing either all four treatments, or the two predator cue treatments grouped (*i.e.*, a predator cue treatment level), and tested which better fit the data using AIC comparison (Akaike, 2011). If the model containing the four-level treatment variable (including both predator cue types) was within 2AICc of the model containing the three-level treatment variables (predator

cue types grouped), we maintained the separate cue types, as we were interested in potential differences in responses to different predators.

In models analysing the odour cue experiment, we additionally included cue ID as an independent variable to account for potentially varying effects of different individual cues, as two different tiger odour cues and two different control cues were used. In all three models, cue ID was not a significant predictor variable, so we do not report results for this here.

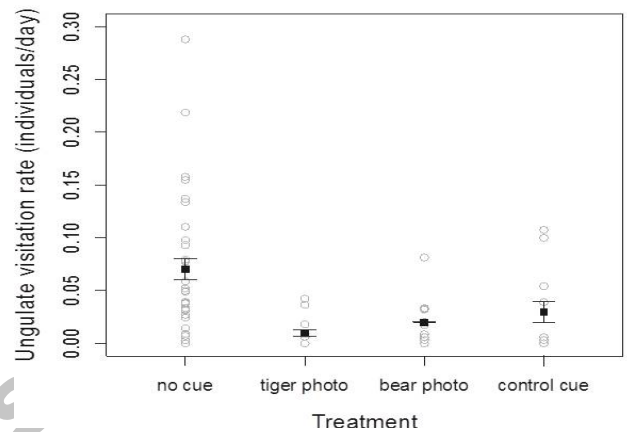


Fig. 3. Ungulate visitation rates (individuals/day) at camera trap sites under four different treatments: no cue, predator photo cues (amur tiger/brown bear), and a control cue. Treatment significantly predicted ungulate visitation rate ( $\chi^2_3 = 18.53$ ,  $P < 0.001$ ; Table I). Visitation to sites with the tiger cue and the bear cue differed significantly from visitation to sites where no cue was present (tiger photo  $Z = -4.51$ ,  $P < 0.0001$ ; bear photo  $Z = -2.97$ ,  $P = 0.015$ , respectively). Visitation to no cue and control cue sites did not differ ( $Z = -1.65$ ,  $P = 0.35$ ). Visitation responses to tiger and bear cues were not statistically different ( $Z = -1.46$ ,  $P = 0.46$ ).

## RESULTS

#### Photo cue experiment

Treatment significantly predicted ungulate visitation to camera trap sites ( $\chi^2_3 = 18.53$ ,  $P < 0.001$ ; Table I; Fig. 3). Post-hoc tests revealed that visitation to sites with the tiger cue and the bear cue was significantly lower than visitation to sites where no cue was present (tiger photo  $Z = -4.51$ ,  $P < 0.0001$ ; bear photo  $Z = -2.97$ ,  $P = 0.015$ , respectively). Visitation to no cue and control cue sites did not differ, as expected ( $Z = -1.65$ ,  $P = 0.35$ ). Interestingly, visitation responses to tiger and bear cues were not statistically different ( $Z = -1.46$ ,  $P = 0.46$ ). The length of camera activity (days) was positively correlated with ungulate visitation ( $\chi^2_1 = 4.38$ ,  $P < 0.05$ ).

**Table I.- Results from best model (GLM) of ungulate visitation to camera traps.**

|                         | Estimate | S.E.  | Z     | P      |
|-------------------------|----------|-------|-------|--------|
| Intercept               | 1.82     | 0.44  | 4.10  |        |
| Treatment               |          |       |       | 0.0003 |
| No cue                  | 0.00     |       |       |        |
| Tiger photo cue         | -1.61    | 0.36  | -4.51 |        |
| Bear photo cue          | -1.01    | 0.34  | -2.97 |        |
| Control cue             | -0.66    | 0.40  | -1.65 |        |
| Days of camera activity | 0.003    | 0.001 | 2.18  | 0.004  |

**Table II.- Results from best model (GLM) of all predator (mesopredator + top predator) visitation to camera traps.**

|                 | Estimate | S.E. | Z     | P    |
|-----------------|----------|------|-------|------|
| Intercept       | 0.68     | 0.31 | 2.22  |      |
| Treatment       |          |      |       | 0.06 |
| No cue          | 0.00     |      |       |      |
| Tiger photo cue | -0.83    | 0.59 | -1.41 |      |
| Bear photo cue  | 0.88     | 0.52 | -1.70 |      |
| Control cue     | -0.39    | 0.66 | -0.59 |      |

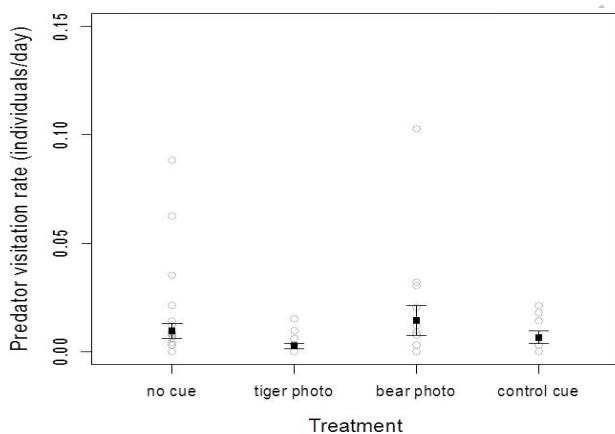


Fig. 4. Predator (mesopredators and top predators combined) visitation rates (individuals/day) at camera trap sites under four different treatments: no cue, predator photo cues (amur tiger/brown bear), and a control cue. Combined mesopredators and top predators showed a small effect of treatment on visitation rates ( $X^2_3 = 7.43$ ,  $P = 0.06$ ; Table II); post-hoc testing showed that the only significant difference between cue types was that visitation to bear cue sites was slightly higher than visitation to tiger cue sites ( $Z = -2.62$ ,  $P < 0.05$ ).

Treatment did not significantly predict mesopredator visitation ( $X^2_1 = 1.14$ ,  $P = 0.77$ ); the null model best described this data. Treatment also did not significantly

predict top predator visitation ( $X^2_1 = 2.81$ ,  $P = 0.24$ ); the null model best described this data. Combining mesopredators and top predators showed a small effect of treatment on visitation rates ( $X^2_3 = 7.43$ ,  $P = 0.06$ ; Fig. 4): post-hoc testing showed that the only significant difference between cue types was that visitation to bear cue sites was slightly higher than visitation to tiger cue sites ( $Z = -2.62$ ,  $P < 0.05$ ).

#### Odour cue experiment

Odour cue treatment did not significantly predict ungulate visitation ( $X^2_1 = 0.71$ ,  $P = 0.70$ ); mesopredator visitation ( $X^2_1 = 1.14$ ,  $P = 0.77$ ); or, top predator visitation ( $X^2_1 = 2.81$ ,  $P = 0.24$ ) to camera trap sites. The null model best described these data in all three cases. The null model also best described visitation rates of all predators combined; treatment was not significant ( $X^2_2 = 2.12$ ,  $P = 0.35$ ).

## DISCUSSION

In this study, we tested how visual and odour cues from familiar and novel predators (brown bear vs. Amur tiger) influenced ungulate, mesopredator, and top predator visitation rates to camera trap sites in Hanma National Nature Reserve. We show that visual cues predicted ungulate visitation rates and ungulates responded equally to the novel and familiar predators. Odour cue, on the other hand, did not influence ungulate visitation rates. Mesopredator visitation was not influenced by either cue type, contrary to predictions, though mesopredators and top predators combined showed a weakly stronger negative response to tiger versus bear cues, suggesting a small novel predator effect on visitation rates. Predator avoidance has vital biological and transformative outcomes on communities and trophic cascades (Peacor and Werner, 2001; González and Rodríguez-Gironés, 2013); nevertheless, the generalisation and contextual importance of predator cues have also been little studied. This study is, therefore, an essential and exciting step forward in understanding predator cue responses at the community level, which may have implications for conservation in this region. There has been a study by Wang *et al.* (2018) on the captive Amur tiger responses towards its natural prey cues; here we test the response of prey towards the Amur tiger, providing insight into its ecological functioning in the wild environment to which it may soon be reintroduced.

#### Photo cue experiment

There has been work by various authors on studying the influence of predation risk to ungulates, but less has

been done to identify the cue used by ungulates to assess presence of risk (Winnie, 2012; Beschta and Ripple, 2013; Kuijper *et al.*, 2014), and equally little to understand whether mesopredators use the same cues within a community. Our results confirm that predation risk as assessed using predator visual cues (both Amur tiger and brown bear photos) significantly influences ungulate visitation rate at predator cues sites. There was a difference in visitation rate of ungulates (roe deer, moose and musk deer) to the camera sites with tiger and bear visual cues compared to camera sites at the control sites as well as at no treatment sites: more ungulates visited no treatment and control sites as opposed to sites where there were predator visual cues. This result is in line with a study on tammar wallabies (*Macropus eugenii*), showing that they respond to visual predator cues; tammar wallabies increased vigilance behaviours and reduced feeding rate after confronting fox visual cues (Blumstein *et al.*, 2000). Our results are contrary to a study by Venter *et al.* (2017), which reported that large grazing herbivores (such as zebra, red hartebeest, and eland) do not appear to rely on visual cues while on foraging activities. How ungulate species respond to visual predator cues may have a size-dependent component. For example, small prey species such as impala, warthog, waterbuck, and kudu minimize their chances of encountering predators by evading the use of same space with all predators, while larger ungulate species like wildebeest, giraffe, and zebra only avoided sharing space with lion and leopards (Thaker *et al.*, 2011). Our ungulate group contained moose, roe deer, and musk deer, with roe deer a majority. Moose are relatively large and comparable to zebra, red hartebeest, and eland, whereas roe deer and musk deer are much smaller. This may explain the difference in our results from those of Venter *et al.* (2017), indicating that visual cues inhibit visitation rate to the predator visual cue camera sites. Unfortunately, our small sample size of moose mean that we cannot further interpret our results based on ungulate size classes, but this would be a fruitful area of further study in this system.

We show that responses of ungulates to Amur tiger and brown bear cues in terms of site visitation are not statistically different, though tiger cues are relatively novel given their long absence in this region, contrary to our prediction that ungulates should show a stronger response to the cue with which they were more familiar (Wiles *et al.*, 2003; Carthey and Blumstein, 2017; Saxon-Mills *et al.*, 2018). This indicates a degree of generalization of predator visual cues that do not appear to rely strongly on previous experience. This is similar to Dunlop-Hayden and Rehage (2011) results which indicated no differences in prey reaction towards native vs. non-native predators. Alternatively, ungulates may have been responding to

novelty *per se*, which in itself can elicit fear responses (Sneddon *et al.*, 2003). An appropriate way to test this further might be to repeat the experiment using an additional novel cue such as a photograph of a train or other novel object, to determine whether the equal response to tiger cues as bear cues is because tiger cues are inherently novel, or because they are recognised as a predatory threat. It is worth to note that there are no any literature which show existence of tiger in the study area, even local people suggest that tiger has never lived in this ecosystem.

Mesopredator release theory suggests that an increase in apex predators also suppresses mesopredators in the area (Haswell *et al.*, 2018). Mesopredators are likely to also use predator cues, for example, Switalski (2003) suggested that when wolves are within the area of study, coyotes use a visual cue to detect their predator (wolves) availability. Additionally, Palacios *et al.* (2016) proposed that that presence of any kind of apex predator cue (coral whether visual, chemical or even combined (coral trout *Plectropomus leopardus*) limits the distance its mesopredator prey (dottyback *Pseudochromis fuscus*) would swim or engage in other activities like foraging. Interestingly our study contradicts the above studies because both Amur tiger and brown bear cues showed no significant influence on visitation rates of mesopredators alone (though in combination with top predators, mesopredators showed slightly lower visitation to tiger cue sites). This may be because brown bear are few in our study area compared to the incidence of top predators in the coral trout and wolf systems, hence lessening the chance that bears interact directly with mesopredators, implying that mesopredators might not use bear visual cues (but may still respond to a novel cue, such as the tiger).

#### *Odour cue experiment*

Wikenros *et al.* (2015) studied the response of red deer and roe deer to Eurasian lynx olfactory cues, concluding that both red deer and roe deer decreased their visitation duration at the treatment sites. Also, Noell (2013) states that ungulates have a strong ability to detect the smell, but their response to predator cues vary (Apfelbach *et al.*, 2005). We predicted that odour cue would predict ungulate visitation rates significantly in the wild, but this was not the case in our study. Nevertheless, our data support other previous findings that indicate that predator cues do not affect deer visitation rate to the chemical cue environment (Kimball *et al.*, 2009; Elmeros *et al.*, 2011). We believe that wetness and wind have a role in determining the effectiveness and longevity of odour cues. The odour cue experimental sites were located in the mountain that faces a large swamp area that contains water in summer and autumn. This might have influenced our result too due to

the wet wind that blows towards the side of the camera trap experiment site. The current study acts as a foundational base for another ecologist to carry out further experiments on the ecological functioning role of captive Amur tiger odour in the wild.

Our result is in line with numerous other studies which reported that there is a weaker response of mammalian mesopredators (Garvey *et al.*, 2016) towards the risk posed by their top predator. Tiger odour cue did not predict mesopredator visitation to the camera trap sites. Sih *et al.* (2010) suggested that prey species may need to have preceding experience toward the predator chemical cue before an experiment can be done. We agree with this idea; and we think that mesopredators of our study area might have evolved a lack of fear of tigers due to unfamiliarity (Suraci *et al.*, 2017). This is because as discussed in the visual cue experiment that there is no clear record evidence that tiger ever existed in the area recently; but some archives indicate that there are signs for the tiger to have existed in the area in the distant past (Turvey *et al.*, 2017). The same reasons (wetness and windward side) discussed in the above paragraph for ungulates applies here too. It would be informative to repeat the experiment using the familiar predator odour cue (brown bear), as the lack of response by both ungulates and mesopredators toward the tiger odour cue may have been due to lack of familiarity, rather than a lack of response generally to chemical cues. Unfortunately, we did not have access to suitable brown bear cues for this study.

#### *Visual vs odour cues influence on visitation rate*

Normally visual cue indicates the predator is present and prey/mesopredator will be in immediate danger if they come face to face with the cue, this means they have to minimize unnecessary movements or opting to flee from the area. However, feces may mean that there is a tiger in the area but investigating the cue could provide information on the sex of the donor, what it has eaten, etc. Tigers are territorial and the feces were fresh, it could mean that the donor is not likely to be back to this spot for a while and therefore the area is safe in the immediate future. Hence less fear, similar to our results. Apfelbach *et al.* (2005) indicate that body odour is a better test for antipredator responses than feces or urine, and studies of antipredator responses are moving towards using body odour if possible rather than feces as it is a less confusing cue of immediate predator presence.

## CONCLUSION

To our understanding, this is the first study to test the ecological function of Amur tiger cues in China

and possibly worldwide in the wild environment. We demonstrate that captive Amur tiger visual and odour cues do not predict mesopredators and top predator visitation rates significantly, but both captive Amur tiger and brown bear visual cues predict the visitation rate of ungulates significantly to predator treatment sites. Our results have laid down foundations on the understanding of the ecological functioning of captive Amur tiger visual and odour cues. Therefore our study together with that of Wang *et al.* (2018) may save as key in the rewilding process of captive Amur tiger plans.

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#### *Statement of conflict of interest*

The authors declare that they have no conflict of interests regarding the publication of this article.

## REFERENCES

- Altmann, J., 1974. Observational study of behavior: Sampling methods. *Behaviour*, **49**: 227-266. <https://doi.org/10.1163/156853974X00534>
- Apfelbach, R., Blanchard, C.D., Blanchard, R.J., Hayes, R.A. and McGregor, I.S., 2005. The effects of predator odors in mammalian prey species: A review of field and laboratory studies. *Neurosci. Biobehav. Rev.*, **29**: 1123-1144. <https://doi.org/10.1016/j.neubiorev.2005.05.005>
- Beschta, R.L. and Ripple, W.J., 2013. Are wolves saving yellowstone's aspen? A landscape-level test of a behaviorally mediated trophic cascade: Comment. *Ecology*, **94**: 1420-1425. <https://doi.org/10.1890/11-0063.1>
- Blanco, J.C., Ballesteros, F., García-Serrano, A., Herrero, J., Nores, C. and Palomero, G., 2011. Behaviour of brown bears killing wild ungulates in the cantabrian mountains, southwestern europe. *Eur. J. Wildl. Res.*, **57**: 669-673. <https://doi.org/10.1007/s00436-011-0700-0>

- [org/10.1007/s10344-010-0464-z](https://doi.org/10.1007/s10344-010-0464-z)
- Blumstein, D.T., Daniel, J.C., Griffin, A.S. and Evans, C.S., 2000. Insular tammar wallabies (*Macropus eugenii*) respond to visual but not acoustic cues from predators. *Behav. Ecol.*, **11**: 528-535. <https://doi.org/10.1093/beheco/11.5.528>
- Brook, L.A., Johnson, C.N. and Ritchie, E.G., 2012. Effects of predator control on behaviour of an apex predator and indirect consequences for mesopredator suppression. *J. appl. Ecol.*, **49**: 1278-1286. <https://doi.org/10.1111/j.1365-2664.2012.02207.x>
- Brown, G.E. and Cowan, J., 2000. Foraging trade-offs and predator inspection in an ostariophysan fish: Switching from chemical to visual cues. *Behaviour*, **137**: 181-195. <https://doi.org/10.1163/156853900502015>
- Caro, T., 2005. *Antipredator defenses in birds and mammals*. University of Chicago Press, Chicago, Illinois, United States.
- Carthey, A.J.R. and Blumstein, D.T., 2017. Predicting predator recognition in a changing world. *Trends Ecol. Evol.*, **33**: 106-115. <https://doi.org/10.1016/j.tree.2017.10.009>
- Chen, I.C., Hill, J.K., Ohlemüller, R., Roy, D.B. and Thomas, C.D., 2011. Rapid range shifts of species associated with high levels of climate warming. *Science*, **333**: 1024-1026. <https://doi.org/10.1126/science.1206432>
- Creel, S., Winnie, J., Maxwell, B., Hamlin, K. and Creel, M., 2005. Elk alter habitat selection as an antipredator response to wolves. *Ecology*, **86**: 3387-3397. <https://doi.org/10.1890/05-0032>
- Creel, S., Winnie, J.A., Christianson, D. and Liley, S., 2008. Time and space in general models of antipredator response: Tests with wolves and elk. *Anim. Behav.*, **76**: 1139-1146. <https://doi.org/10.1016/j.anbehav.2008.07.006>
- Cremona, T., Crowther, M.S. and Webb, J.K., 2014. Variation of prey responses to cues from a mesopredator and an apex predator. *Austral. Ecol.*, **39**: 749-754. <https://doi.org/10.1111/aec.12138>
- Dunlop-Hayden, K. and Rehage, J.S., 2011. Antipredator behavior and cue recognition by multiple everglades prey to a novel cichlid predator. *Behaviour*, **148**: 795-823. <https://doi.org/10.1163/000579511X577256>
- Elmeros, M., Winblad, J.K., Andersen, P.N., Madsen, A.B. and Christensen, J.T., 2011. Effectiveness of odour repellents on red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*): A field test. *Eur. J. Wildl. Res.*, **57**: 1223-1226. <https://doi.org/10.1007/s10344-011-0517-y>
- Farnworth, B., Innes, J. and Waas, J.R., 2016. Converting predation cues into conservation tools: The effect of light on mouse foraging behaviour. *PLoS One*, **11**: e0145432. <https://doi.org/10.1371/journal.pone.0145432>
- Fischer, S., Oberhammer, E., Cunha-Saraiva, F., Gerber, N. and Taborsky, B., 2017. Smell or vision? The use of different sensory modalities in predator discrimination. *Behav. Ecol. Sociobiol.*, **71**: 143. <https://doi.org/10.1007/s00265-017-2371-8>
- Garvey, P.M., Glen, A.S., Clout, M.N., Wyse, S.V., Nichols, M. and Pech, R.P., 2017. Exploiting interspecific olfactory communication to monitor predators. *Ecol. Appl.*, **27**: 389-402. <https://doi.org/10.1002/eap.1483>
- Garvey, P.M., Glen, A.S. and Pech, R.P., 2016. Dominant predator odour triggers caution and eavesdropping behaviour in a mammalian mesopredator. *Behav. Ecol. Sociobiol.*, **70**: 481-492. <https://doi.org/10.1007/s00265-016-2063-9>
- González, F.G. and Rodríguez-Gironés, M.A., 2013. Seeing is believing: Information content and behavioural response to visual and chemical cues. *Proc. R. Soc. London B: Biol. Sci.*, **280**: 886. <https://doi.org/10.1098/rspb.2013.0886>
- Goullaoud, E.L., de Zwaan, D.R. and Martin, K., 2018. Predation risk-induced adjustments in provisioning behavior for horned lark (*Eremophila alpestris*) in british columbia. *Wilson J. Ornithol.*, **130**: 180-190. <https://doi.org/10.1676/16-150.1>
- Groom, M.J., Meffe, G.K. and Carroll, C.R., 2006. *Principles of conservation biology*. Sinauer Associates, Sunderland.
- Guo, K., Liu, H., Bao, H., Hu, J., Wang, S., Zhang, W., Zhao, Y. and Jiang, G., 2017. Habitat selection and their interspecific interactions for mammal assemblage in the Greater Khingan Mountains, northeastern China. *Wildl. Biol.*, **2017**: 00261. <https://doi.org/10.2981/wlb.00261>
- Haswell, P.M., Jones, K.A., Kusak, J. and Hayward, M.W., 2018. Fear, foraging and olfaction: How mesopredators avoid costly interactions with apex predators. *Oecologia*, **187**: 573-583. <https://doi.org/10.1007/s00442-018-4133-3>
- Hernández, L. and Landré, J.W., 2005. Foraging in the landscape of fear and its implications for habitat use and diet quality of elk *cervus elaphus* and bison *bison bison*. *Wildl. Biol.*, **11**: 215-220. [https://doi.org/10.2981/0909-6396\(2005\)11\[215:FITLOF\]2.0.CO;2](https://doi.org/10.2981/0909-6396(2005)11[215:FITLOF]2.0.CO;2)
- Hughes, N.K., Price, C.J. and Banks, P.B., 2010. Predators are attracted to the olfactory signals of

- prey. *PLoS One*, **5**: e13114. <https://doi.org/10.1371/journal.pone.0013114>
- Kats, L.B. and Dill, L.M., 2016. The scent of death: Chemosensory assessment of predation risk by prey animals. *Ecoscience*, **5**: 361-394. <https://doi.org/10.1080/11956860.1998.11682468>
- Kelley, J.L. and Magurran, A.E., 2003. Learned predator recognition and antipredator responses in fishes. *Fish Fish.*, **4**: 216-226. <https://doi.org/10.1046/j.1467-2979.2003.00126.x>
- Kimball, B.A., Taylor, J., Perry, K.R. and Capelli, C., 2009. Deer responses to repellent stimuli. *J. chem. Ecol.*, **35**: 1461-1470. <https://doi.org/10.1007/s10886-009-9721-6>
- Kitchener, A.C., Breitenmoser-Würsten, C., Eizirik, E., Gentry, A., Werdelin, L., Wilting, A., Yamaguchi, N. and Johnson, W.E., 2017. A revised taxonomy of the felidae: The final report of the cat classification task force of the iucn cat specialist group. Cat News, NZP Staff Publications.
- Krivoruchko, K., 2011. *Spatial statistical data analysis for gis users*. Esri Press, Redlands.
- Kuijper, D.P., Verwijmeren, M., Churski, M., Zbyryt, A., Schmidt, K., Jędrzejewska, B. and Smit, C., 2014. What cues do ungulates use to assess predation risk in dense temperate forests? *PLoS One*, **9**: e84607. <https://doi.org/10.1371/journal.pone.0084607>
- Laundré, J.W., Hernández, L. and Altendorf, K.B., 2001. Wolves, elk, and bison: Reestablishing the landscape of fear in Yellowstone National Park, USA. *Can. J. Zool.*, **79**: 1401-1409. <https://doi.org/10.1139/z01-094>
- Lehner, P.N., 1992. Sampling methods in behavior research. *Poult. Sci.*, **71**: 643-649. <https://doi.org/10.3382/ps.0710643>
- Li, C., Yang, X., Ding, Y., Zhang, L., Fang, H., Tang, S. and Jiang, Z., 2011. Do pere david's deer lose memories of their ancestral predators? *PLoS One*, **6**: e23623. <https://doi.org/10.1371/journal.pone.0023623>
- Lima, S.L. and Bednekoff, P.A., 1999. Temporal variation in danger drives antipredator behavior: The predation risk allocation hypothesis. *Am. Natural.*, **153**: 649-659. <https://doi.org/10.1086/303202>
- Margulis, S., 2016. *Sampling animal behavior*. Animal Behavior Society Workshop, July 30, 2016.
- Martin, P., Bateson, P.P.G. and Bateson, P., 1993. *Measuring behaviour: An introductory guide*. Cambridge University Press. <https://doi.org/10.1017/CBO9781139168342>
- Mathis, A. and Vincent, F., 2000. Differential use of visual and chemical cues in predator recognition and threat-sensitive predator-avoidance responses by larval newts (*Notophthalmus viridescens*). *Can. J. Zool.*, **78**: 1646-1652. <https://doi.org/10.1139/cjz-78-9-1646>
- Natt, M., Lönnstedt, O.M. and McCormick, M.I., 2017. Coral reef fish predator maintains olfactory acuity in degraded coral habitats. *PLoS One*, **12**: e0179300. <https://doi.org/10.1371/journal.pone.0179300>
- Nersesian, C.L., Banks, P.B. and McArthur, C., 2012. Behavioural responses to indirect and direct predator cues by a mammalian herbivore, the common brushtail possum. *Behav. Ecol. Sociobiol.*, **66**: 47-55. <https://doi.org/10.1007/s00265-011-1250-y>
- Noell, S., 2013. *Effects of brown bear (Ursus arctos) odour on the patch choice and behaviour of different ungulate species*. Dept. of Wildlife, Fish and Environmental Studies, SLU, Umeå. Available at: <https://stud.epsilon.slu.se/6003/> (Accessed on August 31, 2019).
- Palacios, M., Warren, D.T. and McCormick, M.I., 2016. Sensory cues of a top-predator indirectly control a reef fish mesopredator. *Oikos*, **125**: 201-209. <https://doi.org/10.1111/oik.02116>
- Peacor, S.D. and Werner, E.E., 2001. The contribution of trait-mediated indirect effects to the net effects of a predator. *Proc. natl. Acad. Sci.*, **98**: 3904-3908. <https://doi.org/10.1073/pnas.071061998>
- Prugh, L.R., Stoner, C.J., Epps, C.W., Bean, W.T., Ripple, W.J., Laliberte, A.S. and Brashares, J.S., 2009. The rise of the mesopredator. *Bioscience*, **59**: 779-791. <https://doi.org/10.1525/bio.2009.59.9.9>
- Saxon-Mills, E.C., Moseby, K., Blumstein, D.T. and Letnic, M., 2018. Prey naïveté and the anti-predator responses of a vulnerable marsupial prey to known and novel predators. *Behav. Ecol. Sociobiol.*, **72**: 151. <https://doi.org/10.1007/s00265-018-2568-5>
- Schulte, L.M., Schulte, R. and Lötters, S., 2013. Avoiding predation: The importance of chemical and visual cues in poison frog reproductive behaviour. In: *Chemical signals in vertebrates*. Springer, pp. 309-321. [https://doi.org/10.1007/978-1-4614-5927-9\\_25](https://doi.org/10.1007/978-1-4614-5927-9_25)
- Sih, A., Bolnick, D.I., Luttbeg, B., Orrock, J.L., Peacor, S.D., Pintor, L.M., Preisser, E., Rehage, J.S. and Vonesh, J.R., 2010. Predator-prey naïveté, antipredator behavior, and the ecology of predator invasions. *Oikos*, **119**: 610-621. <https://doi.org/10.1111/j.1600-0706.2009.18039.x>
- Sivy, K.J., Pozzanghera, C.B., Colson, K.E., Mumma, M.A. and Prugh, L.R., 2018. Apex predators and the facilitation of resource partitioning among

- mesopredators. *Oikos*, **127**: 607-621. <https://doi.org/10.1111/oik.04647>
- Smith, M.E. and Belk, M.C., 2001. Risk assessment in western mosquitofish (*Gambusia affinis*): Do multiple cues have additive effects? *Behav. Ecol. Sociobiol.*, **51**: 101-107. <https://doi.org/10.1007/s002650100415>
- Sneddon, L.U., Braithwaite, V.A. and Gentle, M.J., 2003. Novel object test: Examining nociception and fear in the rainbow trout. *J. Pain*, **4**: 431-440. [https://doi.org/10.1067/S1526-5900\(03\)00717-X](https://doi.org/10.1067/S1526-5900(03)00717-X)
- Suárez-Tangil, B.D. and Rodríguez, A., 2017. Detection of iberian terrestrial mammals employing olfactory, visual and auditory attractants. *Eur. J. Wildl. Res.*, **63**: 93. <https://doi.org/10.1007/s10344-017-1150-1>
- Sukhdeo, M.V., 2012. Where are the parasites in food webs? *Parasites Vectors*, **5**: 239. <https://doi.org/10.1186/1756-3305-5-239>
- Suraci, J.P., Roberts, D.J., Clinchy, M. and Zanette, L.Y., 2017. Fearlessness towards extirpated large carnivores may exacerbate the impacts of naïve mesocarnivores. *Behav. Ecol.*, **28**: 439-447. <https://doi.org/10.1093/beheco/arw178>
- Switalski, T.A., 2003. Coyote foraging ecology and vigilance in response to gray wolf reintroduction in yellowstone national park. *Can. J. Zool.*, **81**: 985-993. <https://doi.org/10.1139/z03-080>
- Thaker, M., Vanak, A.T., Owen, C.R., Ogden, M.B., Niemann, S.M. and Slotow, R., 2011. Minimizing predation risk in a landscape of multiple predators: Effects on the spatial distribution of african ungulates. *Ecology*, **92**: 398-407. <https://doi.org/10.1890/10-0126.1>
- Tolon, V., Dray, S., Loison, A., Zeileis, A., Fischer, C. and Baubet, E., 2009. Responding to spatial and temporal variations in predation risk: Space use of a game species in a changing landscape of fear. *Can. J. Zool.*, **87**: 1129-1137. <https://doi.org/10.1139/Z09-101>
- Turvey, S.T., Crees, J.J., Li, Z., Bielby, J. and Yuan, J., 2017. Long-term archives reveal shifting extinction selectivity in china's postglacial mammal fauna. *Proc. R. Soc. B*, **284**: 20171979. <https://doi.org/10.1098/rspb.2017.1979>
- Van Dyck, H., 2012. Changing organisms in rapidly changing anthropogenic landscapes: The significance of the umwelt-concept and functional habitat for animal conservation. *Evolut. Applic.*, **5**: 144-153. <https://doi.org/10.1111/j.1752-4571.2011.00230.x>
- Venter, J.A., Prins, H.H., Mashanova, A. and Slotow, R., 2017. Ungulates rely less on visual cues, but more on adapting movement behaviour, when searching for forage. *PeerJ*, **5**: e3178. <https://doi.org/10.7717/peerj.3178>
- Wallach, A.D., Izhaki, I., Toms, J.D., Ripple, W.J. and Shanas, U., 2015. What is an apex predator? *Oikos*, **124**: 1453-1461. <https://doi.org/10.1111/oik.01977>
- Wang, Q., Liu, D., Holyoak, M., Jia, T., Yang, S., Liu, X., Kong, X. and Jiang, G., 2018. Innate preference for native prey and personality implications in captive amur tigers. *Appl. Anim. Behav. Sci.*, **210**: 95-102. <https://doi.org/10.1016/j.applanim.2018.10.006>
- Wikenros, C., Jarnemo, A., Frisén, M., Kuijper, D.P. and Schmidt, K., 2017. Mesopredator behavioral response to olfactory signals of an apex predator. *J. Ethol.*, **35**: 161-168. <https://doi.org/10.1007/s10164-016-0504-6>
- Wikenros, C., Kuijper, D.P., Behnke, R. and Schmidt, K., 2015. Behavioural responses of ungulates to indirect cues of an ambush predator. *Behaviour*, **152**: 1019-1040. <https://doi.org/10.1163/1568539X-00003266>
- Wiles, G.J., Bart, J., Beck, Jr. R.E. and Aguon, C.F., 2003. Impacts of the brown tree snake: Patterns of decline and species persistence in guam's avifauna. *Conserv. Biol.*, **17**: 1350-1360. <https://doi.org/10.1046/j.1523-1739.2003.01526.x>
- Winnie, J.A., 2012. Predation risk, elk, and aspen: Tests of a behaviorally mediated trophic cascade in the greater yellowstone ecosystem. *Ecology*, **93**: 2600-2614. <https://doi.org/10.1890/11-1990.1>
- Wong, B. and Candolin, U., 2015. Behavioral responses to changing environments. *Behav. Ecol.*, **26**: 665-673. <https://doi.org/10.1093/beheco/aru183>
- Zhai-Penghui, L.Y., Zhengshan, L., 2015. The current situation and evaluation of the biodiversity of hanma national nature reserve. *China Acad. J. Electron. House*, (Original article in Chinese published 2015).
- Zheng, W., Beauchamp, G., Jiang, X., Li, Z. and Yang, Q., 2013. Determinants of vigilance in a reintroduced population of pere david's deer. *Curr. Zool.*, **59**: 265-270. <https://doi.org/10.1093/czoolo/59.2.265>