

From overlooking to concealed: predator avoidance in an apex carnivore

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Abstract Many prey species select bed sites that reduce the risk of being caught off guard. We investigated bed sites used by an apex predator (gray wolf, *Canis lupus*) before and after individuals were approached by humans ($N=48$ trials). On 9 out of 10 days, the unprovoked wolves rested at sites high in the terrain with a good overview (overlooking sites). After being approached, they resettled on more concealed sites lower in the terrain. Solitary yearlings used less overlooking sites than adults both before and after disturbance. The study provides experimental evidence that wolves' behavioural response to approaching humans is analogous to predator avoidance in prey species.

Keywords Human activity · Landscape of fear · Predation risk

Introduction

A common trait among prey species is to select bed sites that reduce the risk of being caught off guard (Laundré et al. 2010). Even apex predators which have no non-human predators may exhibit such avoidance behaviour, as humans take on the predator role (Frid and Dill 2002; Ordiz et al. 2011).

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Gray wolf repeatedly use areas close to human dwellings and infrastructure (Fritts et al. 2003). Yet they are rarely observed by humans. The most obvious behavioural adaptation is their predominantly nocturnal activity pattern (Vilá et al. 1995; Ciucci et al. 1997; Merrill and Mech 2003). Also, a consistent finding is that their spatiotemporal movements are negatively related to the intensity of human activity (e.g. Theuerkauf et al. 2003; Whittington et al. 2005; Hebblewhite and Merrill 2008; Musiani et al. 2010).

The majority of wolf/human studies have been based on correlative and rather coarse-scale telemetry data. Experimental studies, particularly of finer scale behavioural responses, are scarce (but see Frame et al. 2007; Karlsson et al. 2007). In this field experiment, we show how wolves utilise local, structural aspects of the habitat as an aid in predator avoidance.

Methods

Study area and wolves

The study was carried out in four Norwegian wolf territories (59°21'–60°08'N, 11°20'–12°05'E): Moss (pack of 11–12 wolves, breeding male radio-collared), Årjäng (pack of five to nine wolves, breeding pair collared) and Mangen and Djurskog (each with one solitary yearling female dispersing from Årjäng, both collared). The area consists of mixed boreal forest, with more frequent, but lower elevations (25–255 m.a.s.) in Moss than in the other territories (130–430 m.a.s.). Moss also had a higher level of human activity, with about 12 times as many human residents (22 per km²) and 40 times as much cultivated land (37 % of the land area). At the time of study there had been no legal hunting since 1971 (when wolves were considered functionally extinct, Wabakken et al. 2001). Wolves started to recolonise the study area in the 1990s.

Provoked human disturbance

Trials were carried out June 2001–April 2002 (avoiding 6 weeks prior to and after denning, and distributing trials for each individual throughout the season). The wolves were approached at their bed sites by one person mimicking a hiker. When the focal wolf fled, the approaching person stopped and remained still until the wolf resettled, i.e. had been inactive for >1 h. Thereafter, the person carefully retreated in the opposite direction.

Investigation of bed sites

Bed sites were located by field-based triangulation. Only fixes with an estimated mean accuracy of 37 ± 5 m or better were used (Wam 2003) unless the actual bed could later be located from tracks in the snow. We investigated sites as soon as the wolves had moved away from the area. All registrations were carried out by the same team of observers (working together).

At each bed site, we recorded two parameters: (1) ‘Terrain level’ (0–100 %) = the vertical location of the bed site relative to the surrounding terrain (radius about 250 m). Thus, 0 % corresponds to the bottom of a glen, 50 % halfway up a hill and 100 % a hilltop. (2) ‘Visual distance’ = the unbroken line of view from the bed (80 cm above the ground), summed over four directional quadrants (north, east, south and west). If the view varied within a quadrant, we used the weighed mean (e.g. 80 % of the view being 20 m, 20 % being 107 m; the weighed mean = 37 m). Percentages were visually estimated; distances were paced.

Data analyses

We fitted generalised linear models (GLIMMIX in SAS/STAT® 9.2, SAS Institute Inc., NC, USA) with ‘sequence’ (before versus after disturbance) and ‘wolf age’ (adult versus yearling) as explanatory variables. The two response variables ‘terrain level’ and ‘visual distance’ were analysed

separately. Because we had repeated trials for individual wolves, we included ‘wolf identity’ and ‘trial number’ nested within ‘wolf identity’ as random effects. For trials where the Årjäng pair bedded together, only one of the paired observations was included.

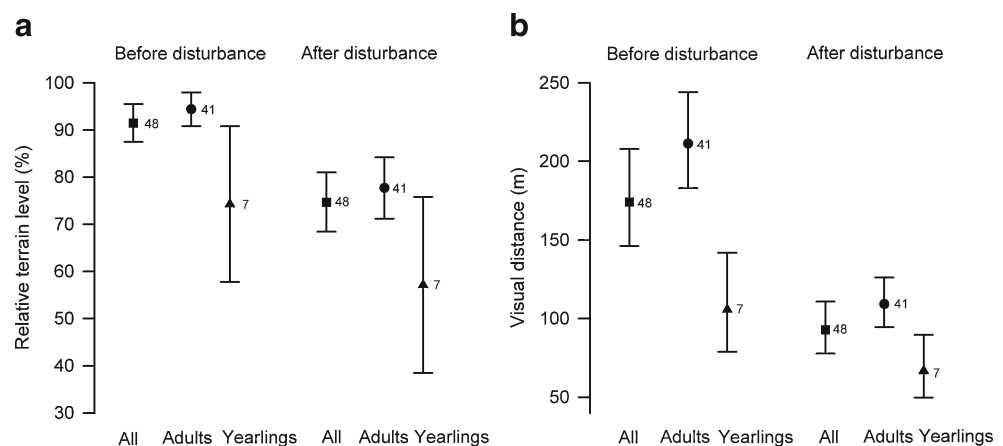
The model for terrain level was fitted with logit link function, binomial distribution (terrain level was converted to proportions) and Laplace parameter estimation (Bolker et al. 2008). Inspections of the scaled Pearson statistic and graphical diagnostics indicated adequate model fit. For visual distance, data were right-skewed, and therefore log-transformed before fitting a model with identity link function, Gaussian distribution and restricted maximum likelihood estimation (Bolker et al. 2008). Graphical diagnostics indicated a very good model fit.

Results and discussion

Prior to disturbance, the wolves rested on overlooking sites high in the terrain. The initial bed site was located at a terrain level ≥ 70 % in 45 trials (94 % of all trials), and the visual distance was ≥ 100 m in 39 trials (81 % of all trials). After being approached, the wolves resettled at concealed sites lower in the terrain (terrain level $F_{1,47}$, $P=0.038$; visual distance $F_{1,47}$, $P \leq 0.001$). Yearlings used less overlooking sites than adults (terrain level $F_{1,47}$, $P=0.071$; visual distance $F_{1,47}$, $P=0.025$), both before and after disturbance (Fig. 1).

The finding that wolves initially rested high in the terrain may to some extent have been augmented by our strict criteria for triangulation accuracy (radio signals from elevated sites are easier to detect). This does not, however, explain the differences found for sites used before versus after disturbance, as the same criteria are applied to both sets of bed sites. Furthermore, trials conducted on snow, when the accuracy criteria were relaxed, showed the same pattern (i.e. using overlooking bed sites prior to disturbance).

Fig. 1 Terrain level (a) and visual distance (b) of bed sites used by gray wolves before and immediately after provoked human disturbance (Norway 2001–2002, five radio-collared wolves). Estimated means (at measurement scale) and standard errors from GLMMs. Sample sizes are number of trials (i.e. pairs of bed sites)



Unprovoked wolves appeared to prioritise surveillance higher than concealment when choosing bed sites. The use of overlooking sites probably facilitates early detection of both human and conspecific intruders. Additionally, the wolves may prefer the more open sites for social activities, which at times occupy a lot of space (Mech 1970). Also, weather conditions may influence the choice of bed site (e.g. hilltops providing cooling winds in summer and warming sun in winter).

When the wolves were approached by humans, their strategy shifted, sacrificing optimal vigilance for better concealment. Apparently, the latter then became imperative for short-term survival. In the evolutionary context, this trade-off makes sense: originally, humans resembled stalking predators (long search, short chase), which should favour a strategy to bed at overlooking sites, even after fleeing. However, with the invention of firearms, we extended our chase to long reach and therefore, the wolves most likely to survive the intense persecution that followed were elusive animals minimising their exposure. Even the Scandinavian lynx *Lynx lynx* (with a similar history of being persecuted) escaped to safer sites when approached by humans (Sunde et al. 1998).

Interestingly, the trade-off between surveillance and concealment appeared to be less pronounced for yearling wolves. Although the sample size is limited, this indicates that younger wolves are naïve, and that the elusive behaviour of adult wolves has been acquired at least partly through repeated exposure to human encounters.

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