

Lasting behavioural responses of brown bears to experimental encounters with humans

Andrés Ordiz^{1*}, Ole-Gunnar Støen^{1,2}, Solve Sæbø³, Veronica Sahlén¹, Bjørn E. Pedersen¹, Jonas Kindberg² and Jon E. Swenson^{1,4}

¹Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences, Postbox 5003, NO-1432, Ås, Norway; ²Department of Wildlife, Fish, and Environmental Studies, Swedish University of Agricultural Sciences, SE-901 83, Umeå, Sweden; ³Department of Chemistry, Biotechnology and Food Science, Norwegian University of Life Sciences, Postbox 5003, NO-1432, Ås, Norway; and ⁴Norwegian Institute for Nature Research, NO-7485, Trondheim, Norway

Summary

1. Some large carnivore populations are increasing in Europe and North America, and minimizing interactions between people and carnivores is a major management task. Analysing the effects of human disturbance on wildlife from a predator–prey perspective is also of conservation interest, because individual behavioural responses to the perceived risk of predation may ultimately influence population distribution and demography.

2. The Scandinavian brown bear population provides a good model to study the interactions between an expanding large carnivore population, and people who use forests extensively for professional and recreational activities. We experimentally approached 52 GPS-collared brown bears (293 approaches on foot) from 2006 to 2011, to document the reaction of bears and quantify the effect of disturbance on bear movements.

3. None of the bears reacted aggressively to the observers. Although the location of the animals was known, bears were usually in quite concealed spots and were physically detected in only 16% of the approaches (seen in 42 approaches; heard in 6). However, the bears altered their daily movement patterns after the approaches. Bears increased movement at night-time and moved less at daytime, which was most visible in days 1 and 2 after the approaches, altering their foraging and resting routines.

4. *Synthesis and applications.* We provide experimental evidence on the effect of human disturbance on a large carnivore. The lack of aggressive reactions to approaching observers reinforces the idea that European brown bears generally avoid people, although bears can respond aggressively if they feel threatened (e.g. when wounded). However, the movement patterns of the bears changed after disturbance. Separating large carnivores and people temporally and spatially is an important goal for conservation and management. Conserving the shrub cover that provides concealment to the carnivores and keeping people away from the most densely vegetated spots in the forests is a way to avoid encounters between carnivores and people, therefore promoting human safety and carnivore conservation.

Key-words: behaviour, conservation, experimental disturbance, human–wildlife interactions, large carnivores, management, people, time allocation, *Ursus arctos*

Introduction

Most studies on human–wildlife ‘conflict’ report damages caused by animals, from small birds to the largest mammals, to human property, safety or valuable resources

(Peterson *et al.* 2010). In turn, human–wildlife interactions cause a large proportion of wildlife mortality and behavioural responses that can imply demographic costs (e.g. Moore & Seigel 2006 for reptiles; Müllner, Linsenmair & Wikelski 2004 for birds; Harrington & Veitch 1992 for mammals). Behavioural responses to human disturbance are indeed of conservation and management concern, because they can be even more important for population

*Correspondence author. E-mail: andres.ordiz@gmail.com

dynamics than direct demographic effects (Pauli & Buskirk 2007).

The study of animal behaviour in recent decades has helped understand ecological patterns (Sih *et al.* 2012). An animal's perceived risk of predation influences its foraging, reproduction, hiding and fleeing behaviours (Lima & Dill 1990), and such responses are adaptive traits that influence population dynamics (Valdovinos *et al.* 2010). Given that adaptive behaviours are likely to have arisen after a long coexistence between predators and prey, disturbance stimuli could be analogous to predation risk from an evolutionary perspective (Frid & Dill 2002). Behavioural responses such as the modification of movement patterns or habitat use are often the first reaction that animals show to environmental changes and help determine the capacity of a species to cope with human-induced changes (Tuomainen & Candolin 2011). This predator–prey framework can be useful to study how large carnivores (e.g. wolves *Canis lupus*, brown bears *Ursus arctos*, lions *Panthera leo*; Linnaeus 1758) behave in a human-altered environment (Rode, Farley & Robbins 2006; Ordiz *et al.* 2011, 2012). Large carnivores are elusive animals, which stresses the need of understanding the effects of human activities on their behaviour, as cautious species are more susceptible to human disturbance and to exhibit declining populations than bolder ones (Sih *et al.* 2012).

Predation on livestock and occasional attacks to people are the most conflict-causing interactions between large carnivores and humans (Graham, Beckerman & Thirgood 2005). In turn, humans cause the majority of large carnivore mortality and have caused severe population reductions and extirpations worldwide (Woodroffe & Ginsberg 1998). However, some large carnivore populations are now increasing and some people living in recolonizing areas oppose their recovery. This is a major concern for the conservation and management of these species, whose large spatial requirements and use of multiple-use landscapes increase their contact with people, and this is occurring now in Europe (Enserink & Vogel 2006) and North America (Bruskotter & Shelby 2010).

Brown bears in Scandinavia provide a model to analyse the interactions between an expanding large carnivore population and people. This bear population was almost extinct by 1930, but recovered and reached c. 3300 bears in 2008 (Kindberg *et al.* 2011). GPS-collared bears were approached by Moen *et al.* (2012) to document their reactions when meeting people in Scandinavian forests. Most bears (80%) ran away and none behaved aggressively towards the observers, reinforcing the idea that European bears are generally not aggressive to people (Moen *et al.* 2012). Likewise, Karlson, Eriksson & Liberg (2005) approached Scandinavian wolves, which always fled from the observers.

Large carnivores often respond behaviourally to reduce encounters with humans. Bears select resting sites in denser vegetation with an increasing human activity (Ordiz *et al.* 2011); lions avoid the vicinity of cattle posts (Valeix

et al. 2012); and selection of breeding sites by wolves is influenced by villages and roads (Theuerkauf, Rouys & Jedrzejewski 2003). Yet, beyond the evaluation of the animals' fear (i.e. perceived risk, Stankovich & Blumstein 2005) and immediate reactions, it is important to document experimentally how long the effects last after the carnivores encounter people. Long-term effects of human disturbance on individual behaviour can have implications at population and community levels, and human activity can constrain the ecological role that carnivores play in ecosystems (Ritchie & Johnson 2009), thus justifying attention by management agencies (e.g. Cline, Sexton & Stewart 2007). For example, interactions of bears with human activities can have effects at the population level. Black bears *Ursus americanus* (Pallas 1780) accessing garbage near human settlements were heavier than their wild-land conspecifics and had higher densities and fecundity; ultimately, there was a human-induced redistribution of the population in the landscape (Beckmann & Berger 2003). Often, large carnivore displacement due to disturbance occurs in the opposite direction, avoiding human settlements (e.g. Hebblewhite *et al.* 2005). Beyond the direction of displacement, consequences can arise at the individual level (e.g. 'problem bears'; Elfström *et al.* 2013), population level (e.g. population redistribution; Beckmann & Berger 2003) and ecosystem level, after altering interactions between species (Hebblewhite *et al.* 2005).

We conducted approaches on foot to brown bears and analysed daily bear movement patterns before and after the approaches. Our hypothesis was that bears would become more nocturnal after encountering people, modifying their circadian foraging and resting periods. In the long term, these behavioural responses to disturbance may have consequences at population level. This requires management attention to keep large carnivores and humans separated, reducing interactions as much as possible.

Material and methods

STUDY AREA

The study area was in south-central Sweden. Elevations range from c. 200 to c. 1000 m above sea level, with most of the area below the timberline (c. 750 m). The hilly landscape is mostly covered with intensively managed forest, dominated by Scots pine *Pinus sylvestris* and Norway spruce *Picea abies*. Heather, grasses and berry-producing shrubs dominate the understorey layer. Human density ranges from 4 to 7 inhabitants km⁻². Logging, berry picking, fishing and hunting, including bear hunting, are common in the forest.

APPROACHES TO RADIO-COLLARED BROWN BEARS

From 2006 to 2011, we approached 33 female and 19 male radio-collared adult bears, 4–19 years old. Twelve of the female bears had dependent cubs in some years of the study. The bears were equipped with GPS–GSM neck collars (VECTRONIC Aerospace

GmbH, Berlin, Germany) and a VHF transmitter implant (IMP 400L, Telonics, USA). All details on marking and capturing are available in Arnemo, Evans & Fahlman (2011). The bears were approached ≤ 6 times each year, with ≥ 14 days between each approach on the same bear. Before each approach, the collar was programmed to register a GPS position every minute for 3 h. In the field, the observers (1.9 ± 0.7) tracked the bear by VHF triangulation, started the approach several hundred metres away and aimed to pass the bear at c. 50 m, with the wind towards it (downwind). The observers continued walking for 500 m and returned to the starting point, but keeping ≥ 500 m distance to the original bear location. They walked together at a normal hiking pace, talking at a normal level. When only one observer approached a bear, he/she talked to him/herself. We registered the track of the observers during the approach with a hand-held GPS receiver that recorded positions every 10 m. We conducted 293 approaches (28 in 2006, 74 in 2007, 101 in 2008, 58 in 2009, 15 in 2010, and 17 in 2011), between $11:26 \pm 59$ min and $12:41 \pm 68$ min, that is, around noon, when bears are at resting sites (Moe *et al.* 2007) and when most human activity in the forest occurs.

PRE-BERRY AND BERRY SEASONS IN RELATION WITH BEAR BEHAVIOUR AND HUMAN ACTIVITIES

The first period of brown bear activity after leaving the den in spring includes the mating season. The foraging season or hyperphagia, when bears eat primarily berries to accumulate fat for hibernation is from mid-July to den entry in October (Friebe, Swenson & Sandegren 2001). Seasonal differences in bear behaviour also appear related to changing levels of human activity (Ordiz *et al.* 2011). Therefore, we divided the field seasons into a pre-berry season (<15 July, $n = 215$ approaches) and a berry season (>15 July, $n = 78$ approaches), with 15 July being the mean date of first observing fresh berries in the scats.

STATISTICAL ANALYSES

We used the GPS positions recorded by the collars every 30 min to construct daily bear movement patterns, calculating the distance travelled by the bears every 30 min during 24 h. Using all the positions recorded up to 6 days before the approach, we built a baseline movement pattern, with which we compared the 30-min distances travelled by the bears after the experimental approaches. We chose a Bayesian model formulation with estimation using Markov chain Monte Carlo methods (MCMC) to analyse the data. This approach can easily handle missing values that occur due to lack of GSM coverage (some missing GPS positions prevented us from calculating distance travelled for a given time interval). Further, the Bayesian model makes it straightforward to account for dependencies in the data, such as temporal correlations and repeated measurements of individual bears.

We used a linear model for the response variable y (square root of distance travelled every 30 min):

$$y_{ijklm} = \lambda_{ij} + \alpha_k + \gamma_l + \eta_m + \beta_{1j}x_{day} + \beta_2x_{age} + \beta_{3j}x_{app} + \beta_{4j}x_{dist} + \beta_{5j}x_{vis} + \epsilon_{ijklm} \quad \text{eqn 1}$$

The time interval from 6 days before to 7 days after each approach was divided into 14 periods ($i = 1, \dots, 14$) defined relative to the day of approach as follows: periods 1–6 = (day –6 to –1), 7 = (day of the approach), 8 = (day +1), etc., up to

period 14 = (day +7). The model parameter λ_{ij} is the effect of daily half-hour interval j ($j = 1, \dots, 48$) within temporal period i . Further, α_k ($k = 1, \dots, 52$) is the random effect of bear k assumed to be distributed as $N(0, \sigma_b^2)$, γ_l ($l = 1, 2$) is the effect of pre-berry or berry season, and η_m ($m = 1, 2, 3$) is the sex-class effect (male, female or female with cubs). Several continuous covariates were also included: number of daylight hours (x_{day}) with regression coefficients β_{1j} , assumed to be dependent on the daily time interval j , age of the individual (x_{age}) with coefficient β_2 , number of observers (x_{app}) with time-dependent coefficients β_{3j} , minimum distance from the observers to the bear (x_{dist}) with time-dependent coefficients β_{4j} and visibility around the site where the bear was approached (x_{vis}) with time-dependent coefficients β_{5j} . Visibility was measured as sighting distance (in metres) from the bear site and was used as a proxy of vegetation cover (see Ordiz *et al.* 2011 for further details). The noise term ϵ_{ijklm} accounting for unexplained variation was assumed to be distributed as $N(0, \sigma_j^2)$; that is, the noise variance was also assumed to be dependent on daily time interval. The temporal correlation was included by assuming that the effect of a given time interval depended on the previous time interval within the same period. Specifically, we assumed

$$\begin{aligned} \lambda_{11} &\sim N(0, 1000) \text{ (vague prior distribution)} \\ \lambda_{ij} &= v \cdot \lambda_{i(j-1)} + \epsilon_{ij} \text{ for } j = 2, \dots, 48 \\ \lambda_{i1} &= v \cdot \lambda_{(i-1)48} + \epsilon_{i1} \text{ for } i = 2, \dots, 9 \end{aligned} \quad \text{eqn 2}$$

where v is an autoregressive coefficient, and ϵ is assumed to be distributed as $N(0, \tau^2)$. The variance parameter τ^2 controls the level of smoothing of the time effect. A large value induces minimal smoothing, whereas a small variance gives heavy smoothing. The sensitivity analysis of τ^2 indicated that the model parameter estimates were minimally sensitive to the choice of value for τ^2 , apart from the smoothness of λ_{ij} . In the final model fit, we used $\tau^2 = 1/5$ based on comparisons of the deviance information criterion (DIC) (Spiegelhalter *et al.* 2002) for different smoothing levels.

For all regression coefficients of continuous effects and for the parameter v , vague normal distributions $N(0, 1000)$ were assumed *a priori*. Next, for the categorical variables season and sex class, the first level was set to zero (baseline), whereas vague normal priors were assumed for the remaining levels. To complete the Bayesian formulation of the model, the inverse of all variance components (the precisions) were given gamma priors $Ga(0.001, 0.001)$, a commonly used vague prior for precisions.

The unknown model parameters were estimated by Bayesian posterior means using MCMC methods, implemented in OpenBUGS (Lunn *et al.* 2000). Due to the large number of observations, convergence was relatively fast and assessed by visual inspection of runs with differing starting values. The convergence was fastest for low levels of smoothing, but usually about 10 000 iterations were sufficient. Upon burn-in, a subsequent set of 10 000 iterations was used for parameter estimation (see Appendix S1 in Supporting Information for the OpenBUGS code). The estimated posterior distributions for the model parameters provided point estimates (mean) and credible intervals (lower 2.5% and upper 97.5% percentiles of the estimated distribution). We considered effects as statistically significant if the credible intervals of the corresponding parameters did not contain zero. The MCMC approach for parameter estimation is an iterative process allowing the missing values

to be predicted by the given model and the current estimates of the unknown model parameters (data augmentation). With the MCMC estimation method, it is also straightforward to obtain posterior mean estimates and credible intervals for any combination of the main model parameters. We used this possibility to study derived parameters defined as the time-dependent differences in the effect of the approaches.

The differences of interest are those between each of the periods 7–14 and the average effect of period 1–6; thus, posterior means and uncertainty intervals were computed for difference parameters defined by

$$\delta_{ij} = \lambda_{ij} - \bar{\lambda}_j \quad \text{eqn 3}$$

for $i = 7, \dots, 14$ and $j = 1, \dots, 48$, and where $\bar{\lambda}_j$ is the average effect of time j across periods 1 to 6. A significant positive difference implied increased movement after disturbance for the given time interval, and a negative difference implied reduced movement. We assessed the goodness of fit of the linear model with the coefficient of determination R^2 , based on all nonmissing observations and computed as $R^2 = \text{cor}(y, \hat{y})^2$ where $\hat{y}$ are the fitted values from the estimated model.

Results

None of the bears reacted aggressively to the observers in any approach ($n = 293$). Bears were seen ($n = 42$) or heard in the vegetation ($n = 6$) in 16% of the approaches. The minimum distance between observers and bears was 89 ± 68 m (≥ 50 m in 74% of the approaches;

mean $\pm$ SD). The visibility around the initial site where the bears were approached was 21 ± 11 m.

Regarding bear movements, initial model estimations showed that the effects of both age and sex class were nonsignificant; thus, these factors were removed from the model. The final model R^2 was 0.23. Based on the estimated time effects from each time period, the bears moved mostly during crepuscular and some nocturnal hours during the week prior to the approaches, with two distinct resting periods around midday and during the darkest hours around midnight (Fig. 1a). Approached bears initially moved away from their daybed and then reduced movements, which was reflected in the estimated pattern of distance travelled the day of the approach (Fig. 1b). However, the effect of the approaches on the bears lasted beyond their initial reaction. Compared to the previous week, significant periods of an increased movement at night and reduced movement during daytime were visible in the days following the approach, with a U-shaped pattern in difference from pre-approach levels most visible for days 1 and 2 (Fig. 2). Differences in movement patterns throughout the season may have occurred due to changes in day length, so the effect of day length on movement was estimated. Shortening day length had a positive effect on movement during the day and a negative effect during the night (Fig. 3). Bear movements increased in the berry season (0.491 ± 0.067 ; 95% CI = 0.37–0.62). However, the main result was that

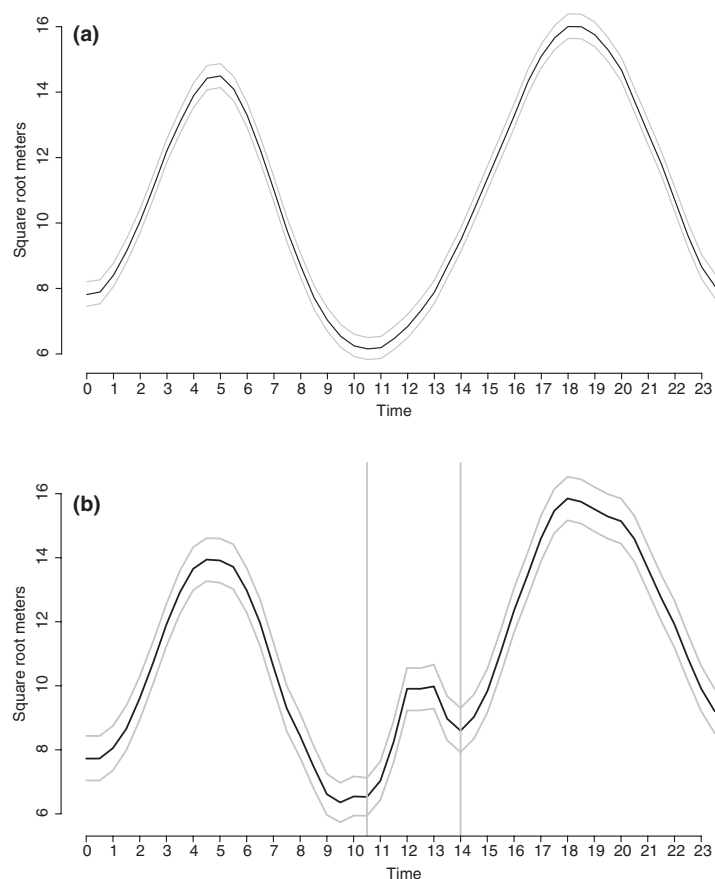


Fig. 1. (a) Estimated time effect (every 30 min during the 24 h day) on daily activity pattern of brown bears in south-central Sweden during the week before the experimental approach. The Figure shows the main resting period during midday and the second around midnight. (b) Estimated time effect on daily activity pattern of bears on the day of the approach, showing the initial escape after the disturbance event, followed by a reduction in movement. Vertical lines show the range of time when most approaches were conducted (start at $11:26 \pm 59$ min, end at $12:41 \pm 68$ min). The curves represent the mean of the distance travelled and the 95% credible intervals.

encounters with people consistently caused an increase of bear movements at night and a reduction during daytime, which persisted after correcting for daylight, berry season and random bear effects. The number of observers was quite consistent (1.9 ± 0.7) and had no significant effect on bear movements. A time-of-day-dependent effect showed that bears were most disturbed (movement pattern more altered) when vegetation cover around bear sites was denser and when observers-bear distances were shorter (Fig. 4).

Discussion

In areas where large carnivores and human populations are increasing and expanding, people often become more afraid of potential encounters with carnivores and tolerance decreases. This is occurring in Scandinavia (Moen *et al.* 2012) and elsewhere (e.g. Gurung *et al.* 2008). The most dramatic consequences of human–carnivore interactions, that is, human fatalities and retaliatory killing of animals, receive most attention, but documenting the behavioural reactions of carnivores that encounter people is also important from a management perspective, to reduce encounters and their effects for both people and carnivores of conservation concern.

The fact that none of the bears reacted aggressively to the observers and that bears were not even seen or heard in 84% of the approaches show that bears clearly avoid any confrontation with people. The outcome can be different when the encounters are perceived by carnivores as more threatening, which may explain why most people injured by bears in Scandinavia are hunters (Moen *et al.* 2012). The minimum distance between observers and bears (89 ± 68 m.) was almost double the planned 50 m., and 4 times larger than the visibility (21 ± 11 m.) around

the initial bears' sites, because the bears were in concealed places and generally moved away before the observers could get closer. However, the approaches affected the daily movement patterns of the bears. The immediate reaction after the encounters caused an average 26% increase in distance travelled by the bears compared to the same time of the day during the week prior to the approaches, immediately followed by a 10% reduction in movement (Fig. 2). Bears moved 11% and 8% more, respectively, during the darkest part of the 2 nights following an approach and for periods lasting ≥ 4 h 30 min, that is, when they previously had rested. During daytime, movement reduction was as intense in the 2 days following the encounters (10% and 11%) as in the day of approach (10%; Fig. 2). It is interesting to note that bears already had a marked resting period in the middle of the day before the approaches (Fig. 1a). As a reaction to the encounters, the bears lengthened the period of inactivity during daytime, probably relying on cover to avoid detection and the costs and risks of fleeing from people (Ordiz *et al.* 2011). The shorter the distance between observers and bear and the denser the cover, the stronger the effect of the approach on bear movements (Fig. 4). That is, bear behaviour was especially disrupted where the bear detected humans at short distance and in the highly concealed spots where bears hide and rest during the day (Ordiz *et al.* 2011; Moen *et al.* 2012).

Bears were expected to become more active during daytime as days became shorter (Fig. 3) and during the berry season, which has been reported before for this bear population (Fig. 1 in Moe *et al.* 2007) and elsewhere (Stemlock & Dean 1986). However, the expected trend towards more diurnal behaviour was disrupted by the encounters with people. This strengthens previous findings, because Ordiz *et al.* (2012) also found that bear movements

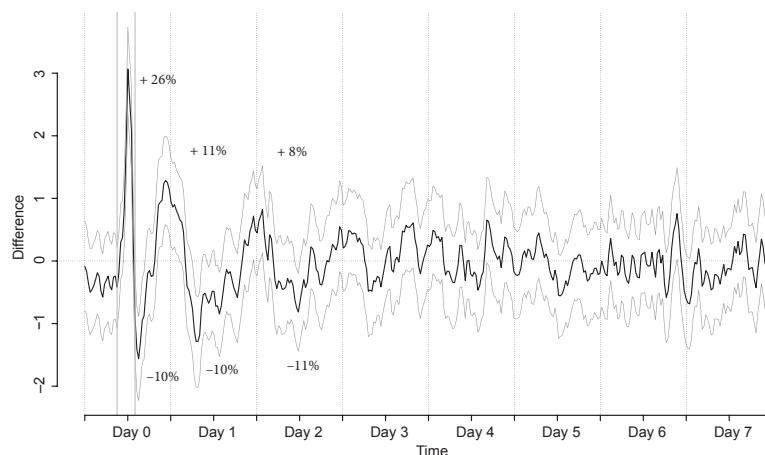


Fig. 2. Estimated differences in distance travelled by brown bears in south-central Sweden, every 30 minutes during the 24 h day, comparing the post-disturbance movement pattern of the bears, after they were experimentally approached, with the pre-disturbance movement pattern of the previous week. Two continuous vertical lines show the range of time when most approaches were conducted. The average percentage of bears' movement variation at night (+) and daytime (–) after the approaches is indicated for all significant time periods with duration ≥ 1 h 30 min. Differences at 30-min intervals were considered significant when the mean and the 95% credible intervals were all above or below zero.

Fig. 3. According to the expectation from the Bayesian model, bears would increase movements during daytime caused by shortening of the days as the autumn season advanced. The curves represent the estimated daylight effect on the distance travelled and the 95% credible intervals.

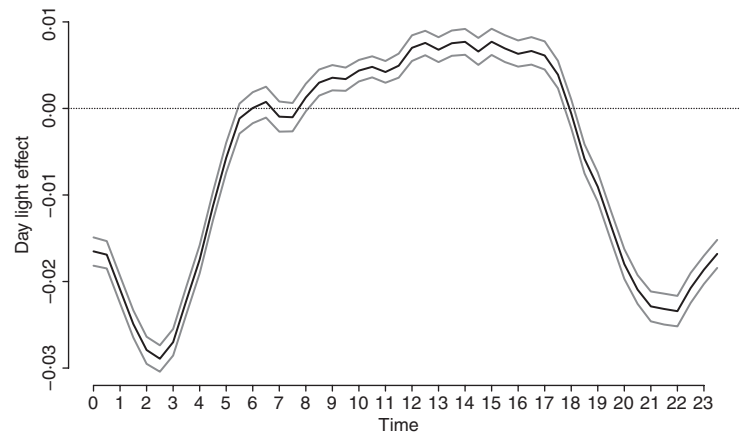
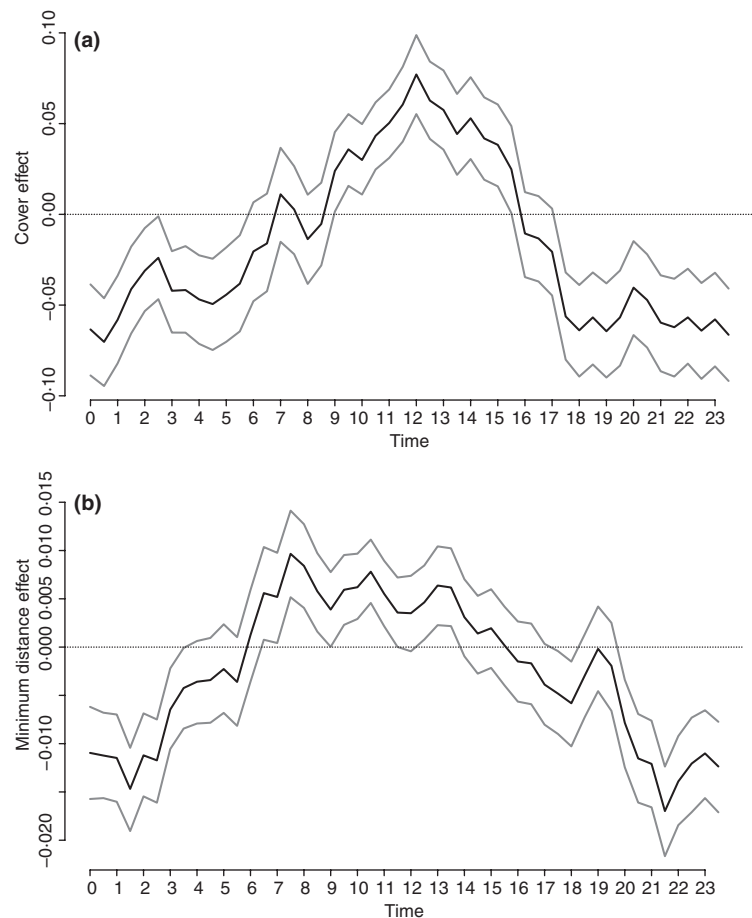


Fig. 4. Time-dependent effect of (a) sighting distance (cover) and (b) minimum distance between observers and bears. Bears approached in more open areas (larger sighting distance) and detecting the observers further away altered movement patterns less than bears approached closer and in denser spots. The curves represent the estimated effect on the distance travelled and the 95% credible intervals.



increased during night-time and decreased during daytime after the start of the bear hunting season. Moen *et al.* (2012) found that younger bears left their initial site following an encounter more often than older bears, but the difference decreased in the berry season, when human activity in the area increased. In our case, the pattern of disturbance during the days after the approach was consistent for all bears, regardless of age or sex. The effect of age also tended to be negative in our study (-0.028 ± 0.021), but not significantly so. The same result was reported on bear resting site selection, thus

reinforcing that bears consistently hide from people (Ordiz *et al.* 2011).

Many studies of the effects of human activities on wildlife utilise short-term measures, such as flight initiation distance (FID) and/or composite metrics including FID and alert distance; however, more systematic research is needed to evaluate long-term effects of disturbance (Stankowich 2008). Short-term measures may not even reflect the effects of disturbance, if animals do not have alternative places to flee to (Gill, Norris & Sutherland 2001). For brown bears, Moen *et al.* (2012) showed the

initial effects of encounters in terms of FID, and our analyses highlight the duration of the reaction and the changes in time allocation for resting and foraging.

Behavioural responses induced by human activity may not necessarily have negative effects on fitness (Gill, Norris & Sutherland 2001). However, fitness costs of human disturbance are reported for a variety of species and can negatively affect population size (Mallord *et al.* 2007) and viability (Kerbiriou *et al.* 2009). The lasting changes in bears' resting and foraging routines after disturbance deserve attention, because changes in time allocation after human disturbance may also have fitness consequences (Li *et al.* 2011). Sixty-seven percent of abandoned winter dens of Scandinavian bears had evidence of human activity within 100 m, and 3 of 5 pregnant females that abandoned dens lost cubs, compared to just 6% of 36 females that did not move (Swenson *et al.* 1997). This suggests that brown bear reproduction is affected by disturbance in addition to environmental and intraspecific factors (Ordiz *et al.* 2008). Disturbance during hyperphagia may also affect fitness, due to the strong correlation between bears' condition in the autumn and subsequent hibernation and reproductive success, which highlights the importance of storing fat during hyperphagia (e.g. Welch *et al.* 1997). The body mass of Scandinavian bears increases dramatically from spring to the onset of hibernation: c. 65% for females, c. 35% for males (Swenson *et al.* 2007). During hyperphagia, most bear populations rely on berries and/or nuts. Berries represent c. 81% of the annual digestible energy in central Scandinavia (Dahle *et al.* 1998). However, bears fattening on fruits ingest seven times less digestible energy per hour than salmon-feeding bears (Robbins *et al.* 2007). Fluctuations in berry availability and efficiency in eating berries pose additional constraints. Consequently, bears move constantly for many hours a day, as shown by our model expectation of an increased movement during the berry season, feeding at sites with the highest berry densities, and choosing the most visible berry clusters to maintain high intake rates (Welch *et al.* 1997). Good visibility should favour foraging on berries during daylight hours (MacHutchon *et al.* 1998). However, following approaches, bears reduced their activity during daytime and increased movement during the darkest part of the night. Thus, disturbance would affect energy gain by altering optimal foraging and resting, and also because responses to threats impose energetic costs (Preisser, Bolnick & Benard 2005).

The current scenario of global warming poses an extra concern. With the unique exception of some coastal populations with access to spawning salmon, all boreal populations of brown bears rely on berries during hyperphagia. Bokhorst *et al.* (2008) showed experimentally that even short warming episodes (1 week) cause a virtual elimination of fruit production in *Vaccinium* spp., which are essential berries for bears (e.g. Dahle *et al.* 1998). The entire European brown bear distribution falls within the area of highest increase in

temperature at the global scale in recent decades (see Fig. 1a in Walther *et al.* 2002). Brown bears at the southernmost edge of the distribution of bilberry *Vaccinium myrtillus* in Europe are now consuming fewer bilberries than a few years ago, which was linked to climate change (Rodriguez *et al.* 2007). Our results document that human disturbance can impede animals from exhibiting optimal activity patterns, for example foraging when it is most efficient, thus amplifying the broad effects of global warming on conservation.

Also at the population level, repeated encounters with humans may help explain the distribution of large carnivores in the landscape, with adults often living further away from human settlements than juveniles (e.g. Nellemann *et al.* 2007). The observed behavioural responses of bears to people (e.g. Moen *et al.* 2012; Ordiz *et al.* 2011, 2012; this study) may also help explain why bears (and other carnivores) are mainly diurnal in remote areas of North America, active for up to 17–18 h day⁻¹ and feeding c. 80% of the time (Welch *et al.* 1997), whereas in the more populated Europe bears are active only c. 12 h day⁻¹, with a marked period of inactivity at midday (e.g. Moe *et al.* 2007). Zedrosser *et al.* (2011) argued that the ultimate reasons for transcontinental differences in life history parameters are related to the more extended persecution of large carnivores in Europe. The nocturnal activity pattern is definitely more marked after the start of hunting seasons (Ordiz *et al.* 2012) and after our approaches. This may reflect the level of bear elusiveness due to experienced risk of human encounters and helps reveal the importance of behavioural responses as a trait involved in population resilience to human-induced environmental changes (see Introduction).

CONCLUDING REMARKS AND MANAGEMENT RECOMMENDATIONS

Brown bears avoided the approaching observers, which delivers a reassuring message for forest users and managers. However, the behavioural reaction of the bears after disturbance is of conservation concern. Large carnivores can play key ecological roles in the ecosystems they inhabit, but they themselves live in a landscape of fear instilled by human persecution (Ordiz *et al.* 2011; Valeix *et al.* 2012), which can constrain their apex role (Ritchie & Johnson 2009).

Nonlethal effects of predation risk are receiving increasing attention and appear essential to understand predator–prey interactions and population dynamics (e.g. Peckarsky *et al.* 2008). Nonlethal effects are costly and can be particularly strong in large-bodied, long-lived species (Heithaus *et al.* 2008) and in cautious animals (Sih *et al.* 2012). All of these features characterize large carnivores. The effects of human activities on carnivore dynamics should be studied from not only a demographic perspective, but also by accounting for nonlethal effects that can cause behavioural

responses leading to ecological and evolutionary consequences for the carnivores and the ecosystems they inhabit.

Nonlethal effects of nonconsumptive human activities can also be strong (Kerbirou *et al.* 2009). We did not use dogs to chase the bears, that is, we simulated hiking or berry picking, not hunting and the clear alteration of brown bears' daily activity patterns responding to mere human presence is a strong indicator of the magnitude of disturbance effects. We talked during our on-foot approaches, which presumably alerted the bears of our presence. Other parameters, for example stress levels and foraging efficiency, may help quantify the disturbance. Experimental approaches to other species have shown that on-foot observers induce a stronger response than vehicles and that talking observers lengthened FID compared to silent observers (Wolf & Croft 2010).

Prevention of problems between carnivores and people through temporal and spatial separation (Treves & Karanth 2003) and minimizing carnivore displacement by human activity (Rode, Farley & Robbins 2006) are major management issues. Management should secure the protection of cover where large carnivore populations persist, and the restoration of cover in areas where current carnivore recoveries are to succeed. At the same time, people should be kept away from areas with shrub cover that provide concealment for resting carnivores during daytime, when people are outdoors. Our call to the protection of cover is important because the shrub layer is often destroyed, considered unproductive and/or to reduce fire risk, to increase pasture for cattle or even to promote conservation of endangered species (e.g. Revilla, Palomares & Fernández 2001). Preserving cover and avoiding the most densely vegetated spots in the forests is a simple, but reliable way to avoid encounters with carnivores, which would ultimately benefit both human safety and carnivore conservation.

Acknowledgements

The Scandinavian Brown Bear Research Project (SBBRP) is funded by the Swedish Environmental Protection Agency, Norwegian Directorate for Nature Management, Swedish Association for Hunting and Wildlife Management, the Austrian Science Foundation, WWF Sweden and the Research Council of Norway (RCN). A.O. was funded by RCN and O.G.S. by the program 'Adaptive management of fish and wildlife populations'. The captures of the bears were approved by the Swedish Environmental Protection Agency (permit Dnr 412-7327-09 Nv) and the approaches by the Ethical Committee on Animal Experiments in Uppsala, Sweden (permit C 47/9). We are grateful to G. Moen, L. Scillitani and P. Greve for fieldwork and to R. Bischof, J. Rhodes and two anonymous reviewers for useful comments. This is paper no. 144 from the SBBRP.

References

Arnemo, J.M., Evans, A. & Fahlman, Å. (2011) Biomedical protocols for free-ranging brown bears, wolves, wolverines and lynx. Hedmark University College, Evenstad, Norway. Available at: <http://wolverine-foundation.org/wp-content/uploads/2011/02/bpfrws11.pdf>

Beckmann, J.P. & Berger, J. (2003) Using black bears to test ideal-free distribution models experimentally. *Journal of Mammalogy*, **84**, 594–606.

Bokhorst, S., Bjerke, J.W., Bowles, F.W., Melillo, J., Callaghan, T.V. & Phoenix, G.K. (2008) Impacts of extreme winter warming in the sub-Arctic: growing season responses of dwarf shrub heathland. *Global Change Biology*, **14**, 2603–2612.

Bruskotter, J. & Shelby, L.B. (2010) Human dimensions of large carnivore conservation and management: introduction to the special issue. *Human Dimensions of Wildlife*, **15**, 311–314.

Cline, R., Sexton, N. & Stewart, S.C. (2007) A human-dimensions review of human-wildlife disturbance: a literature review of impacts, frameworks, and management solutions. U.S. Geological Survey, Open-File Report 2007-1111, p. 88.

Dahle, B., Sorensen, O.J., Wedul, E.H., Swenson, J.E. & Sandegren, F. (1998) The diet of brown bears *Ursus arctos* in central Scandinavia: effect of access to free-ranging domestic sheep *Ovis aries*. *Wildlife Biology*, **4**, 147–158.

Elfström, M., Zedrosser, A., Støen, O.G. & Swenson, J.E. (2013) Ultimate and proximate mechanisms underlying the occurrence of bears close to human settlements: review and management implications. *Mammal Review*, doi: 10.1111/j.1365-2907.2012.00223.x.

Enserink, M. & Vogel, G. (2006) The carnivore comeback. *Science*, **314**, 746–749.

Frid, A. & Dill, L. (2002) Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology*, **6**, 16.

Friebe, A., Swenson, J.E. & Sandegren, F. (2001) Denning chronology of female brown bears in central Sweden. *Ursus: an official publication of the International Association for Bear Research and Management*, **12**, 37–46.

Gill, J.A., Norris, K. & Sutherland, W.J. (2001) Why behavioural responses may not reflect the population consequences of human disturbance. *Biological Conservation*, **97**, 265–268.

Graham, K., Beckerman, A.P. & Thirgood, S. (2005) Human–predator–prey conflicts: ecological correlates, prey losses and patterns of management. *Biological Conservation*, **122**, 159–171.

Gurung, B., Smith, J.L.D., McDougal, C., Karki, J.B. & Barlow, A. (2008) Factors associated with human-killing tigers in Chitwan National Park, Nepal. *Biological Conservation*, **141**, 3069–3078.

Harrington, F.H. & Veitch, A.M. (1992) Calving success of woodland caribou exposed to low-level jet fighter overflights. *Arctic*, **45**, 213–218.

Hebblewhite, M., White, C., Nietvelt, C., McKenzie, J., Hurd, T.E., Fryxell, J.M., Bayley, S.E. & Paquet, P.C. (2005) Human activity mediates a trophic cascade caused by wolves. *Ecology*, **86**, 2135–2144.

Heithaus, M.R., Wirsing, A.J., Thomson, J.A. & Burkholder, D.A. (2008) A review of lethal and non-lethal effects of predators on adult marine turtles. *Journal of Experimental Marine Biology and Ecology*, **356**, 43–51.

Karlson, J., Eriksson, M. & Liberg, O. (2005) At what distance do wolves move away from an approaching human? *Canadian Journal of Zoology*, **85**, 1193–1197.

Kerbirou, C., Le Viol, L., Robert, A., Porcher, E., Gourmelon, F. & Juliard, R. (2009) Tourism in protected areas can threaten wild populations: from individual response to population viability of the chough *Pyrrhocorax pyrrhocorax*. *Journal of Applied Ecology*, **46**, 657–665.

Kindberg, J., Swenson, J.E., Ericsson, G., Bellemain, E., Miquel, C. & Taberlet, P. (2011) Estimating population size and trends of the Swedish brown bear *Ursus arctos* population. *Wildlife Biology*, **17**, 114–123.

Li, C., Monclús, R., Maul, T.L., Jiang, Z. & Blumstein, D.T. (2011) Quantifying human disturbance on antipredator behavior and flush initiation distance in yellow-bellied marmots. *Applied Animal Behaviour Science*, **129**, 146–152.

Lima, S.L. & Dill, L.M. (1990) Behavioural decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, **68**, 619–640.

Lunn, D.J., Thomas, A., Best, N. & Spiegelhalter, D. (2000) WinBUGS - A Bayesian modelling framework: Concepts, structure, and extensibility. *Statistics and Computing*, **10**, 325–337.

MacHutchon, G., Himmer, S., Davis, H. & Gallagher, M. (1998) Temporal and spatial activity patterns among coastal bear populations. *Ursus*, **10**, 539–546.

Mallord, J.W., Dolman, P.M., Brown, A.F. & Sutherland, W.J. (2007) Linking recreational disturbance to population size in a ground-nesting passerine. *Journal of Applied Ecology*, **44**, 185–195.

Moe, T.F., Kindberg, J., Jansson, I. & Swenson, J.E. (2007) Importance of diel behaviour when studying habitat selection: examples from female Scandinavian brown bears (*Ursus arctos*). *Canadian Journal of Zoology*, **85**, 518–525.

- Moen, G.K., Stoen, O.-G., Sahlén, V. & Swenson, J.E. (2012) Behaviour of solitary adult Scandinavian brown bears (*Ursus arctos*) when approached by humans on foot. *PLoS ONE*, **7**, e31699.
- Moore, M.J.C. & Seigel, R.A. (2006) No place to nest or bask: Effects of human disturbance on the nesting and basking habits of yellow-blotched map turtles (*Graptemys flavimaculata*). *Biological Conservation*, **130**, 386–393.
- Müllner, A., Linsenmair, K.E. & Wikelski, M. (2004) Exposure to ecotourism reduces survival and affects stress response in hoatzin chicks *Opisthocomus hoatzin*. *Biological Conservation*, **118**, 549–558.
- Nellemann, C., Stoen, O.-G., Kindberg, J., Swenson, J.E., Vistnes, I., Ericsson, G., Katajisto, J., Kaltenborn, B.P., Martin, J. & Ordiz, A. (2007) Terrain use by an expanding brown bear population in relation to age, recreational resorts and human settlements. *Biological Conservation*, **138**, 157–165.
- Ordiz, A., Stoen, O.G., Swenson, J.E., Kojola, I. & Bischof, R. (2008) Distance-dependent effect of the nearest neighbor: spatiotemporal patterns in brown bear reproduction. *Ecology*, **89**, 3327–3335.
- Ordiz, A., Stoen, O.G., Delibes, M. & Swenson, J.E. (2011) Predators or prey? Spatio-temporal discrimination of human-derived risk by brown bears. *Oecologia*, **166**, 59–67.
- Ordiz, A., Stoen, O.G., Siebo, S., Kindberg, J. & Swenson, J.E. (2012) Do bears know they are being hunted? *Biological Conservation*, **152**, 21–28.
- Pauli, J.N. & Buskirk, S.W. (2007) Risk-disturbance overrides density dependence in a hunted colonial rodent, the black-tailed prairie dog *Cynomys ludovicianus*. *Journal of Applied Ecology*, **44**, 1219–1230.
- Peckarsky, B.L., Abrams, P.A., Bolnick, D.I., Dill, L.M., Grabowski, J.H., Luttbegg, B., Orrock, J.L., Peacor, S.D., Preisser, E.L., Schmitz, O.J. & Trussell, G.C. (2008) Revisiting the classics: considering nonconsumptive effects in textbook examples of predator-prey interactions. *Ecology*, **89**, 2416–2425.
- Peterson, M.N., Birkhead, J.L., Leong, K., Peterson, M.J. & Peterson, T.R. (2010) Rearticulating the myth of human-wildlife conflict. *Conservation Letters*, **3**, 74–82.
- Preisser, E.L., Bolnick, D.I. & Benard, M.F. (2005) Scared to death? The effects of intimidation and consumption in predator-prey interactions. *Ecology*, **86**, 501–509.
- Revilla, E., Palomares, F. & Fernández, N. (2001) Characteristics, location and selection of diurnal resting dens by Eurasian badgers (*Meles meles*) in a low density area. *Journal of Zoology*, **255**, 291–299.
- Ritchie, E.G. & Johnson, C.N. (2009) Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters*, **12**, 982–998.
- Robbins, C.T., Fortin, J.K., Rode, K.D., Farley, S.D., Shipley, L.A. & Felicetti, L.A. (2007) Optimizing protein intake as a foraging strategy to maximize mass gain in an omnivore. *Oikos*, **116**, 1675–1682.
- Rode, K.D., Farley, S.D. & Robbins, C.T. (2006) Behavioral responses of brown bears mediate nutritional effects of experimentally introduced tourism. *Biological Conservation*, **133**, 70–80.
- Rodriguez, C., Naves, J., Fernandez-Gil, A., Obeso, J.R. & Delibes, M. (2007) Long-term trends in food habits of a relict brown bear population in northern Spain: the influence of climate and local factors. *Environmental Conservation*, **34**, 36–44.
- Sih, A., Cote, J., Evans, M., Fogarty, S. & Pruitt, J. (2012) Ecological implications of behavioural syndromes. *Ecology Letters*, **15**, 278–289.
- Spiegelhalter, D.J., Best, N.G., Carlin, B.P. & van der Linde, A. (2002) Bayesian measures of model complexity and fit (with discussion). *Journal of the Royal Statistical Society. Series B, Statistical methodology*, **64**, 583–639.
- Stankovich, T. & Blumstein, D.T. (2005) Fear in animals: a meta-analysis and review of risk assessment. *Proceedings of the Royal Society of London Series B*, **272**, 2627–2634.
- Stankowich, T. (2008) Ungulate flight responses to human disturbance: a review and meta-analysis. *Biological Conservation*, **141**, 2159–2173.
- Stemlock, J.J. & Dean, F.C. (1986) Brown bear activity and habitat use, Denali National Park-1980. *Ursus: an official publication of the International Association for Bear Research and Management*, **6**, 155–167.
- Swenson, J.E., Sandegren, F., Brunberg, S. & Wabakken, P. (1997) Winter den abandonment by brown bears *Ursus arctos*: causes and consequences. *Wildlife Biology*, **3**, 35–38.
- Swenson, J.E., Adamic, M., Huber, D. & Stokke, S. (2007) Brown bear body mass and growth in northern and southern Europe. *Oecologia*, **153**, 37–47.
- Theuerkauf, J., Rouys, S. & Jedrzejewski, W. (2003) Selection of den, rendezvous, and resting sites by wolves in the Bialowieza Forest, Poland. *Canadian Journal of Zoology*, **81**, 163–167.
- Treves, A. & Karanth, K.U. (2003) Human-carnivore conflict and perspectives on carnivore management worldwide. *Conservation Biology*, **17**, 1491–1499.
- Tuomainen, U. & Candolin, U. (2011) Behavioural responses to human-induced environmental change. *Biological Reviews*, **86**, 640–657.
- Valdovinos, F.S., Ramos-Jiliberto, R., Garay-Narvaez, L., Urbani, P. & Dunne, J.A. (2010) Consequences of adaptive behaviour for the structure and dynamics of food webs. *Ecology Letters*, **13**, 1546–1559.
- Valeix, M., Hemson, G., Loveridge, A.J., Mills, G. & Macdonald, D.W. (2012) Behavioural adjustments of a large carnivore to access secondary prey in a human-dominated landscape. *Journal of Applied Ecology*, **49**, 73–81.
- Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.M., Hoegh-Guldberg, O. & Bairlein, F. (2002) Ecological responses to recent climate change. *Nature*, **416**, 389–395.
- Welch, C.A., Keay, J., Kendall, K.C. & Robbins, C.T. (1997) Constraints on frugivory by bears. *Ecology*, **78**, 1105–1119.
- Wolf, I.D. & Croft, D.B. (2010) Minimizing disturbance to wildlife by tourists approaching on foot or in a car: a study of kangaroos in the Australian rangelands. *Applied Animal Behaviour Science*, **126**, 75–84.
- Woodroffe, R. & Ginsberg, J. (1998) Edge Effects and the Extinction of Populations Inside Protected Areas. *Science*, **280**, 2126–2128.
- Zedrosser, A., Steyaert, S.M.J.G., Gossow, H. & Swenson, J.E. (2011) Brown bear conservation and the ghost of persecution past. *Biological Conservation*, **144**, 2163–2170.

Received 23 June 2012; accepted 14 December 2012

Handling Editor: Jonathan Rhodes

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. OpenBUGS code for the statistical model