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Relationship between wildlife and tourism – interdisciplinary insights from Arctic fox tourism in Sweden

Malin Larm

Doctoral Thesis in Animal Ecology at Stockholm University, Sweden 2024

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Abstract

Interactions between wildlife and tourism can be studied from several different perspectives and the effects of such interactions can influence animals both positively and negatively with effects on both individual and population levels. This thesis takes an interdisciplinary approach, combining both natural and social perspectives, when studying the effects of tourism activity on a small population of the endangered arctic fox (Vulpes lagopus). We have studied arctic foxes inhabiting disturbed and undisturbed den sites in Helagsfjällen, which is the southernmost population of arctic foxes in Sweden and a popular area for recreational activities such as hiking, skiing and camping. The overall objective of the thesis has been to contribute to good management of both arctic foxes and tourism within the study area, as well as to contribute with a comprehensive study of simultaneous disturbance effects and fitness consequences of wildlife tourism activities to the scientific field of wildlife-tourism interactions. The first two papers focus on different aspects of behavioral responses of arctic foxes towards human activity, the third paper evaluates potential fitness consequences and the fourth paper focus on the tourist aspect of the interaction. Behavioral changes in response to tourism disturbance that have been identified in the foxes include changes in vigilance and probability of hiding (Paper I), temporal activity shift at the den site (Paper II) and increased tolerance to human activity (Paper I, Paper II). Juvenile summer survival was higher at disturbed dens compared with undisturbed dens during years of declining small rodent densities (Paper III). Small rodent decline years is when the predation on arctic foxes is presumed to be highest and we suggest that the positive fitness effect could be mediated by a human-induced predator refuge for the foxes in close proximity of human activity. On the tourist aspect, we have identified effects on behavior, knowledge and awareness of the situation for arctic foxes and related conservation work (Paper IV). Overall, results in this thesis showed a high level of context-dependency, which highlights the importance of considering factors such as food availability, intra-species interactions and individual traits such as previous experience with humans. Consequently, the work in this thesis together with ongoing studies of hormonal stress responses constitutes one of the more comprehensive scientific studies of tourism effects on terrestrial mammals. The output from this thesis brings important deliverables for species-specific management and conservation, but also for other species given the rapidly growing interest for wildlife tourism.

Keywords: *wildlife tourism, human disturbance, human-wildlife interaction, conservation, predation, arctic fox.*

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RELATIONSHIP BETWEEN WILDLIFE AND TOURISM – INTERDISCIPLINARY INSIGHTS FROM ARCTIC FOX TOURISM IN SWEDEN

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I **Larm M**, Brundin E, Stålhandske T & Angerbjörn A. 2020. Arctic fox responses to tourism activity. *Journal of Wildlife Management* 84:821-828.

II **Larm M,** Norén K & Angerbjörn A. 2021. Temporal activity shift in arctic foxes (*Vulpes lagopus)* in response to human disturbance. *Global Ecology and Conservation* 27: e01602.

III **Larm M,** Erlandsson R, Norén K & Angerbjörn A. 2020. Fitness effects of ecotourism on an endangered carnivore. *Animal Conservation* 23:386-395.

IV **Larm M**, Elmhagen B, Granqvist SM, Brundin E & Angerbjörn A. 2018. The role of wildlife tourism in conservation of endangered species: Implications of safari tourism for conservation of the Arctic fox in Sweden. *Human Dimensions of Wildlife* 23:257-272.

Candidate contributions to thesis articles*

	I	**II**	**III**	**IV**
Conceived the study	**Substantial**	**Substantial**	**Substantial**	**Significant**
Designed the study	**Substantial**	**Substantial**	**Substantial**	**Significant**
Collected the data	**Substantial**	**Substantial**	**Significant**	**Substantial**
Analysed the data	**Substantial**	**Substantial**	**Substantial**	**Substantial**
Manuscript preparation	**Substantial**	**Substantial**	**Substantial**	**Substantial**

* Contribution Explanation

Minor: contributed in some way, but contribution was limited.

Significant: provided a significant contribution to the work.

Substantial: took the lead role and performed the majority of the work.

I have also co-authored the following articles, which are not included in this thesis:

Larm M, Hovland AL, Palme R, Thierry AM, Miller AL, Landa A, Angerbjörn A & Eide NE. 2021. Fecal glucocorticoid metabolites as an indicator of adrenocortical activity in Arctic foxes (*Vulpes lagopus*) and recommendations for future studies. *Polar Biology* 44:1925–1937.

Lotsander A, Hasselgren M, **Larm M**, Wallén J, Angerbjörn A & Norén K. 2021. Low persistence of genetic rescue across generations in the Arctic fox (*Vulpes lagopus*). *Journal of Heredity* 112, 276-285.

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Background

Interest for nature-based tourism activities, such as wildlife tourism, is increasing world-wide (Fernández-Llamazares, 2020; Balmford et al., 2009) and many operators offers close encounters with animals in their natural habitats. Wildlife tourism is typically described as a non-consumptive use of wildlife (Higginbottom, Tribe & Booth, 2003) and have the opportunity to contribute to the conservation of endangered species (Buckley et al., 2012, Macdonald et al., 2017). However, such activities can also cause disturbance to individual animals with risk of negative consequences on e.g. fitness, distribution and demography (Larson et al., 2016). Interactions between wildlife and humans, e.g. tourism, are traditionally studied from either a natural or a social perspective, where the natural focus on the effects on animals and environments and the social focus on the effects on humans. However, already in 1966, the social scientist Aldo Leopold recognized the importance of incorporating social aspects into wildlife management when he wrote: "*The problem of game management is not how we shall handle the deer - the real problem is one of human management. Wildlife management is comparatively easy; human management difficult."* (Leopold, 1966). An interdisciplinary approach, combining natural and social perspectives, could therefore advance the development of sustainable management practices of wildlife tourism activities.

According to the definition of Nisbet (2000), disturbance is any activity that changes the behavior or physiology of an animal. There is a relatively good knowledge about different ways in which disturbance from tourism activities may exert an impact on wildlife (Larson et al., 2016). Potential behavioral changes include increased vigilance and fleeing responses, as well as activity pattern changes, such as shifts in the amount of time spent on different activities and in when activities are carried out (Ordiz, et al. 2013; Oberosler et al., 2017). Disturbance can also cause distributional changes, for example avoidance or adaptations in the use of disturbed areas (Smith et al., 2022). Physiological changes can include increased heart rate and elevated stress-hormone levels (Creel, Christianson & Schuette, 2013; Tyagi et al., 2019). Disturbance effects of human activities on wildlife are typically studied from one perspective at the time, but some studies include evaluations of simultaneous effects. Two of the more comprehensive studies of wildlife-tourism interactions are a review by Penteriani et.al. (2017) on Brown bear (*Ursus arctos*) viewing tourism in North America and a doctoral thesis by Shutt (2014) evaluating effects of ecotourism on western lowland gorillas (*Gorilla gorilla gorilla*). The bear review includes several simultaneous effects as well as attempts to quantify the consequences of tourism disturbance on an individual, population and ecological community level. For example, they found responses of individual bears to vary e.g. between different sex and age classes, group compositions and with habituation as well as depending on situational factors such as availability and quality of alternative feeding sites, with potential negative consequences on both individual, population and ecological community levels (Penteriani et al., 2017). The gorilla study reveals behavioral and physiological responses of gorillas to human activities, for example that physiological stress responses of gorillas increased during the habituation process and then returned to similar levels as unhabituated individuals when they became fully habituated. It also considers both a tourist and an epidemiological aspect and has a strong integration between research and management (Shutt, 2014). These two studies highlight several important aspects to consider when studying interactions between wildlife and humans, both in how individual animals responds to a disturbance and various effects that tourism activities can have on individual, population and ecological community levels. Both studies also emphasize the importance of integrating research and management.

Many animals are presumed to perceive humans as a potential predator and apply anti-predator strategies in the response towards an approaching human. Responding to a perceived predation risk is thus a fitness trade-off, where the response should be optimized rather than maximized (Ydenberg & Dill, 1986; Frid

& Dill, 2002; Beale & Monaghan, 2004). Responses of an individual animal are context dependent and may vary depending on several different individual and situational factors, such as sex, age, group composition, food availability, habitat quality, physical condition, personality traits and previous experience with humans (Bejder et al. 2006; Stankowich 2008). Responses of individual animals to a disturbance can in turn affect the geographical distribution of the population, by causing redistributions within and between areas. If groups or individuals vary in their sensitivity to the human activity, it could also modify the demographic structure of the population (Frid & Dill, 2002; Nevin & Gilbert, 2005). Further, differences in susceptibility to human activities between species could alter intra-species interaction dynamics within an ecological community (Dill, Heithaus & Walters, 2003; Smith et al., 2018). Different responses between species could for example reduce species competition or create a refuge through spatial and/or temporal displacement of a predator (Leighton, Horrocks & Kramer, 2010; Muhly et al., 2011). It could also have implications on an ecological community level if a species ecological role and functions for the ecosystem are affected (Wilson et al., 2020; Ordiz et al., 2021).

On a population and ecological community level, tourism activities can also bring positive effects. Such effects can be economic contributions to conservation (Buckley et al., 2012), attitudinal and behavioral changes (Ballantyne et al., 2011) and incentive for governments and local communities to preserve species and environments and thereby avoid more exploitative activities and land uses (Naidoo & Adamowicz, 2005). The benefits of nature experiences for human health and recreation can also be an argument for protection of wildlife and environments (Trombulak et al., 2004).

Within the field of conservation biology there is also a challenge of combining scientific research with practical management (Granquist & Nilsson, 2016). After the managing authorities have defined management objectives, e.g. as "Limits of acceptable change" (Stankey et al., 1985) or other types of critical/acceptable levels of disturbance, knowledge gained from scientific studies and recommendations provided by researchers can be incorporated into the management of both tourists and wildlife to keep disturbance at the acceptable level (Reynolds & Braithwaite, 2001; Hagen et al., 2012). The acceptable level of disturbance could be either a biological decision based on the sensitivity to disturbance in the targeted species or population, or based on ethical criteria, eg. that any reaction on human presence is undesirable (e.g. as defined for Svalbard, see Overrein 2001). Further, it is important to consider disturbance effects on both an individual and a population level. Individual animals may be negatively affected by a disturbance without considerable negative effect on the population level. Also, potential positive effects of a wildlife tourism activity may to some extent be able to compensate for negative effects on a population level.

A wildlife tourism experience can be seen as a trade-off, where increased visitor opportunities and satisfaction typically implies more disturbance caused to the viewed animals (Reynolds & Braithwaite, 2001). Generally, encountering wildlife is the main focus of a wildlife tourism activity, and close encounters with opportunities for photographing the animals yields high visitor satisfaction (Shutt, 2014; Dybsand, 2020). However, there are other factors apart from encountering wildlife that can increase visitor satisfaction, without increasing disturbance to the wildlife. That could for example be high-quality guiding, surrounding activities, observations of other species or signs of the focal species, educational features as well as the feeling of an authentic experience (Margaryan and Wall-Reinius, 2017; Dybsand, 2020; Dybsand & Fredman, 2020). For activities taking place in nature where opportunities to enforce regulations are limited, education is also essential in motivating visitors to voluntarily follow regulations such as behavioral guidelines or codes of conduct (Orams, 1997; Marschall, Granquist & Burns, 2017; Öqvist et al., 2018). Another main component is the expectations of the experience beforehand. If the expectations of visitors are realistic, satisfaction is likely to be higher as expectations can be met (Shutt, 2014; Dybsand, 2020).

Arctic foxes and tourism in Fennoscandia

The arctic fox (*Vulpes lagopus*) is one species for which the tourist interest is increasing, both in Fennsocandia, Svalbard and Iceland. The arctic fox has a circumpolar distribution, inhabiting the Arctic and subarctic tundra. Although it is still abundant in many parts of the distribution range, in Fennoscandia the arctic fox is classified by the IUCN as endangered in Sweden (Swedish red list, 2020) and Norway (Norwegian red list, 2021), and critically endangered in Finland (Hyvärinen et al., 2019). During the late 19th and early 20th century, arctic foxes in Fennoscandia were heavily hunted for their valuable fur, which led to a drastic population decline (Lönnberg, 1927). In the 1920´s, the arctic fox was protected by law in all Fennoscandian countries, in Sweden 1928, Norway 1930 and Finland 1938 (Elmhagen et al., 2017a). Despite the protection, the population did not recover (Hersteinsson et al., 1989). The main threats to the Fennoscandian arctic fox today are the expansion of the dominant competitor and potential predator red fox (*Vulpes vulpes*) into the mountain tundra (Elmhagen et al., 2017b), and increasing irregularities in the cyclic dynamic of the main prey, small rodents (Angerbjörn et al., 2021; Ims, Henden & Killengreen, 2008; Ims et al., 2017). After 20 years of successful conservation actions, in form of red fox culling and supplemental feeding (Angerbjörn et al., 2013), as well as release of captive breed foxes (Landa et al., 2017) the population is now increasing and the conservation status has improved from critically endangered (CR) to endangered (EN) in Sweden 2015 (Swedish red list, 2020) and in Norway 2021 (Norwegian red list, 2021). The arctic fox is, however, still far from a viable population level and dependent on the conservation actions.

The arctic foxes in Fennoscandia have a fluctuating population dynamic that is closely connected to the cyclic abundance of small rodents in the tundra (Kaikusalo & Angerbjörn, 1995; Ims & Fuglei, 2005; Angerbjörn et al., 2013). Every 3-5 years, the small rodents reach peak densities, which is typically followed by a phase of rapid decline and a phase of extremely low densities, before they begin to increase towards a new peak. The arctic fox litter sizes in Fennoscandia varies between 1-18 weaned juveniles, with numerous and large litters during the small rodent increase and peak phases and fewer and smaller litters during the decrease and low phase (Angerbjörn et al., 1995). Arctic fox survival is also strongly influenced by the small rodent cycles, where juvenile mortality can reach 90% at declining prey abundance (Meijer et al., 2008). During years of high small rodent abundance, red foxes, wolverines (*Gulo gulo*), golden eagles (*Aquila chrysaetos*), white tailed eagles (*Haliaeetus albicilla*) and other predator populations in the tundra also flourish (Ims & Fuglei, 2005). Generally, alternative prey species such as hares (*Lepus timidus*), ptarmigan (*Lagopus lagopus* and *Lagopus muta*) and other birds also increase during small rodent peak years as the predator species focus their foraging on small rodents (Landa et al., 1997; Nyström et al., 2006).

Helagsfjällen is a subarctic mountain area that holds one of the largest and the southernmost populations of arctic foxes in Sweden, consisting of approximately 40-60 adult individuals (Angerbjörn et al., 2013; Wallén et al., 2021). The area is also one of the main areas for recreational tourism activities in Sweden, with an extensive network of hiking and skiing trails and several mountain cabins operated by the Swedish Tourist Association (Svenska Turistföreningen, STF). During the summer season (June to September), hiking is the predominant activity in Helagsfjällen. Even though some visitors hike and camp outside of the marked trails, most hike along the trails between the mountain cabins and stations and make day hikes in their surroundings. Some arctic fox dens are located close to one of these cabins or hiking trails and the foxes at these dens experience human activity frequently during the summer.

Figure 1. Location of the study area Helagsfjällen in Sweden, where arctic fox responses to tourism disturbance were studied during 2015 – 2020. (Larm et al. 2020a).

Most dens, however, are located farther from the cabins and trails and hence rarely experience humans. Since 2011, STF Helags mountain station offers guided arctic fox safari tours to an active den during the summer. As the arctic fox is endangered and the location of their dens is confidential information, the tours operate on a special permission from the County Administrative Board (Länsstyrelsen). To limit disturbance to the foxes the tours are allowed to be held only two days a week during July to September, staying in the vicinity of the den for no more than 4 hours at a time. The guided tours always stay at 300 m from the den, which is the recommended minimum distance to keep during an arctic fox encounter (Länsstyrelsen in Eide, 2015; Norwegian Environmental Agency, 2017; Swedish Environmental Protection Agency, 2017). A maximum of 8 participants are allowed on each tour and all participants are required to sign an agreement to not share the location of the den. Given that the interest for tourism activities in relation to arctic foxes is increasing, it is becoming an increasingly important aspect to consider in arctic fox management and conservation.

Figure 2. Photos of the camera monitoring and the guided arctic fox safari tours. a) Automatic wildlife cameras used to monitor the activity of the arctic foxes at the den site. b) A group of tourists on an arctic fox safari tour watching the den through spotting scopes from the observation spot located approximately 300 m from the den. (Larm et al., 2021b).

Aims

The aim of this thesis has been to take an interdisciplinary approach, combining both natural and social perspectives, in investigating various aspects and fitness consequences of the interaction between tourism and wildlife. More specifically, I have studied the effects of tourism activity on a small population of the endangered Arctic fox (*Vulpes lagopus*) in Sweden, with an overall objective to contribute to good management of both arctic foxes and tourism within the study area, as well as to contribute with a comprehensive study of simultaneous disturbance effects and fitness consequences of a wildlife tourism activity to the growing scientific field of tourism-wildlife interactions. In *Paper I* and *Paper II* we investigate different behavioral responses of arctic foxes to human activity and compare responses between disturbed and more undisturbed den sites. *Paper I* focus on behavioral responses at different distances from the den site, with the objective to provide a scientific basis for a recommended minimum approach distance to arctic foxes and their den sites in Fennoscandia. In *Paper II* we investigate both temporal shifts in the arctic foxes use of their den site and direct behavioral responses towards varying levels of disturbance during a guided arctic fox tour. In *Paper III* we attempt to evaluate the fitness consequences of tourism disturbance for the arctic foxes by comparing juvenile survival between dens of varying levels of tourism disturbance. We also investigate how the consequences of human disturbance on the arctic foxes vary with the fluctuating availability of natural food and predation pressure that is characteristic to the alpine tundra ecosystem. *Paper IV* focus on the tourist aspect of the interaction and is based on a survey conducted within different groups of visitors in the study area. It investigates effects of arctic fox information provided in different contexts on visitor’s knowledge, awareness and attitudes about the situation for arctic foxes and related conservation work. Finally, we also perform an experiment on captive arctic foxes in Norway to validate a method for analyzing fecal glucocorticoid metabolites as an indicator of physiological stress in arctic foxes (Larm et al., 2021a). The validation study is not included in the thesis, but is an essential first step for future studies of physiological responses to human disturbance and other stressors in arctic foxes, measured by levels of fecal glucocorticoid metabolites.

General methodology

The studies included in this thesis are mainly based on data that have been collected during the yearly summer fieldwork within the Swedish arctic fox project in the Helagsfjällen mountain area (*Paper I-IV)*. Every summer, all known den sites in the area were visited in July to determine occupancy (Figure 3) and litter sizes. During the inventories, juvenile foxes were also captured using Tomahawk live traps and ear-tagged (Dalton Rototags) with unique color combinations. The ear-tags allow for remote identification of individual foxes which can be used to asses survival and movement between dens and areas. To determine juvenile summer survival (*Paper III*), dens with a litter were revisited in August to estimate the number of remaining juveniles (see Elmhagen et al., 2014 for field methods). The phase of the small rodent cycle (*Paper III*) was determined for each summer following Henden et al. (2009), based on data from the Swedish small rodent monitoring program obtained during spring and autumn (Ecke, 2018). In addition, an index of the small rodent abundance (*Paper III*) was obtained from small rodent trap lines conducted during the summer field work (Figure 3), following Hellström et al. (2014).

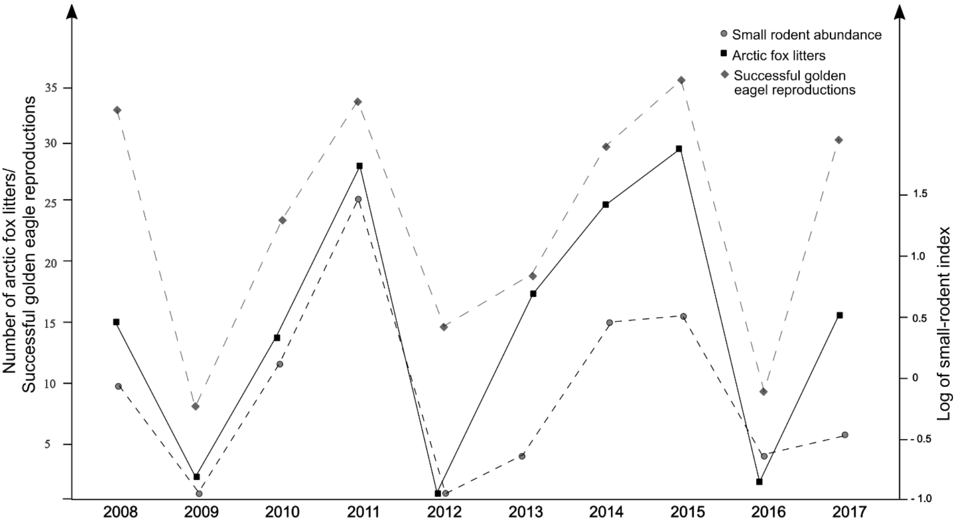

Figure 3. Rodent abundance and number of arctic fox litters in the Helagsfjällen area during 2008-2017, and successful golden eagle breeding in Jämtland County for the same period. (Larm et. al. 2020b).

In *Paper I,* experimental human approaches were conducted toward adult arctic foxes to study their behavioral responses to an approaching human, using a modified version of the protocol described in Choi et al. (2019). The behaviors displayed by the fox were recorded at predetermined distances, as well as the distance where the fox became vigilant, first barked and hid or fled. In *Paper II*, behaviors of both foxes and tourists were observed during the guided arctic fox safari tours to investigate the mutual direct relationship between them. Activity and behavioral observations were also obtained from automatic camera traps placed on the dens (*Paper I & II*).

In *Paper I - III*, dens were categorized as either disturbed or undisturbed by tourism activity based on their distance to hiking trails and mountain cabins. Dens located within 1 km of a hiking trail and/or within 2 km of a mountain cabin were categorized as disturbed (Figure 4). All of these dens were visible from a trail or cabin and saw humans on a daily basis during July and August. Undisturbed dens were located farther than 1 km from a trail and 2 km from a mountain cabin. As the trails channel the vast majority of hikers, the foxes at the undisturbed dens rarely encountered humans.

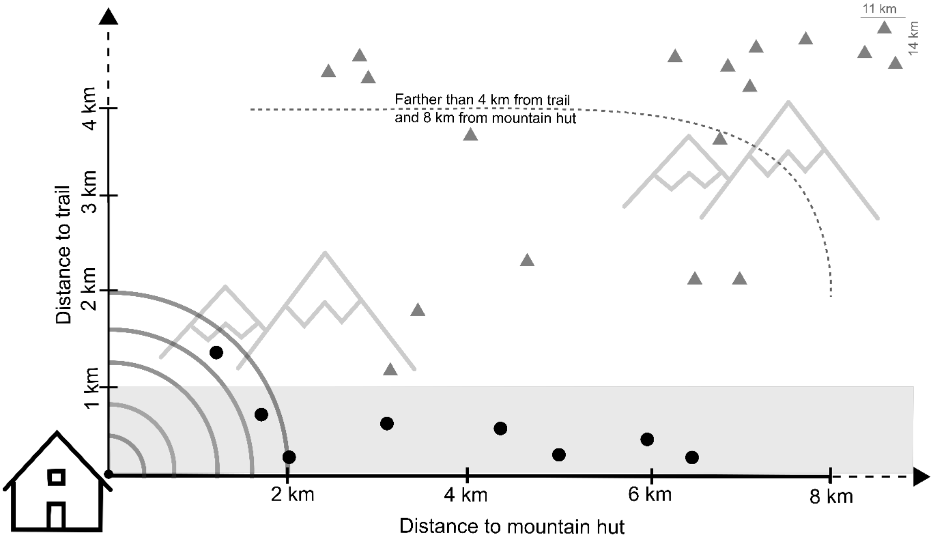

Figure 4. The location of the arctic fox dens included in the study in relation to hiking trails and tourist mountain cabins, around which the vast majority of the tourism activity is centered. Dens classified as disturbed by tourism activities (●) are located within 1 km of a trail and within 2 km of a cabin and are all within eyesight of a trail or cabin. Dens classified as undisturbed (▲) are located farther than 1 km from a trail and farther than 3 km from a cabin and none of the dens is within eyesight of a trail or cabin. Dens beyond the dotted line are farther than 4 km from a trail (up to 11 km) and 8 km from a cabin (up to 14 km). (Larm et al., 2020b).

The questionnaire used to study visitor knowledge, awareness and attitudes in *Paper IV* was distributed to five different groups of respondents at three locations in the Helagsfjällen area (Table 1). At STF Helags mountain station, the questionnaire was distributed to three different groups, one group were visitors to the mountain station that did not participate in an arctic fox safari tour and the other two were tour participants responding either before or after a tour. Respondents at the other two locations were used as control groups.

Table 1. The arctic fox specific survey questions explored in the study. Questions marked with * were added to the survey in 2016. (Larm et al., 2018).

Survey questions
1) Can you mention one or more reasons to why the arctic fox is endangered in Sweden? *(Free text)*
Can you mention one or more conservation actions taken to preserve the arctic fox in Sweden? *(Free text)*
2) Do you belive it is important to preserve the arctic fox in Sweden? *(Yes / No / Don't know)*
3) Do you know the minimum distance you should keep to an arctic fox or an arctic fox den site? *(100 m / 300 m / 500 m / Don't know) **
What other actions can you take to decrease your disturbance when encountering arctic foxes? *(Free text) **
4) Respondents that stated human disturbance and/or exploitation as a reason to why the arctic fox is endangered in question 1. *(Free text)*

Results and Discussion

Behavioral responses

In *Paper I* we confirmed that a minimum approach distance of 300 m is enough to avoid causing most foxes to hide or flee, but there is individual variation and many foxes became vigilant at longer distances than 300 m (Figure 5), some already at the start distance of 500 m. The foxes at the disturbed dens, who are more used to human activity, tolerated closer approaches before increasing their vigilance and before they hid or fled compared with foxes at undisturbed dens. However, the probability of hiding increased rapidly when approached within approximately 200 m. at both disturbed and undisturbed dens (Figure 6). Based on *Paper I,* we provide a scientific basis for the recommend minimum distance of at least 300 m to arctic foxes and den sites in Sweden and Norway (Norwegian Environmental Agency, 2017; Swedish Environmental Protection Agency, 2017).

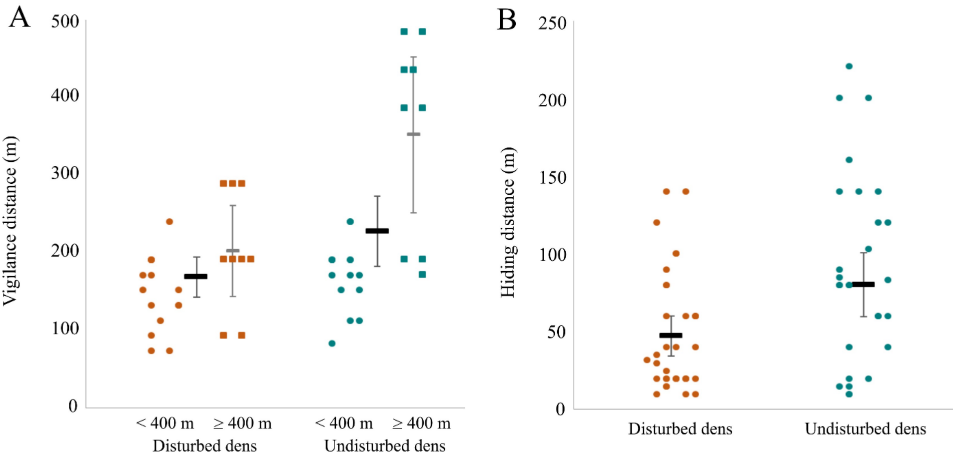

Figure 5. (A) Vigilance distance for arctic foxes at disturbed dens (● <400 m, ■ ≥400 m) and undisturbed dens (● <400 m, ■ ≥400 m), with approaches starting at <400 m on the left and ≥400 m to the right. Mean and error bars to the left (black) represent all approaches and to the right (grey) only approaches with a start distance of ≥400 m. (B) Hiding distance for disturbed dens (●) and undisturbed dens (●). (Larm et al., 2020a).

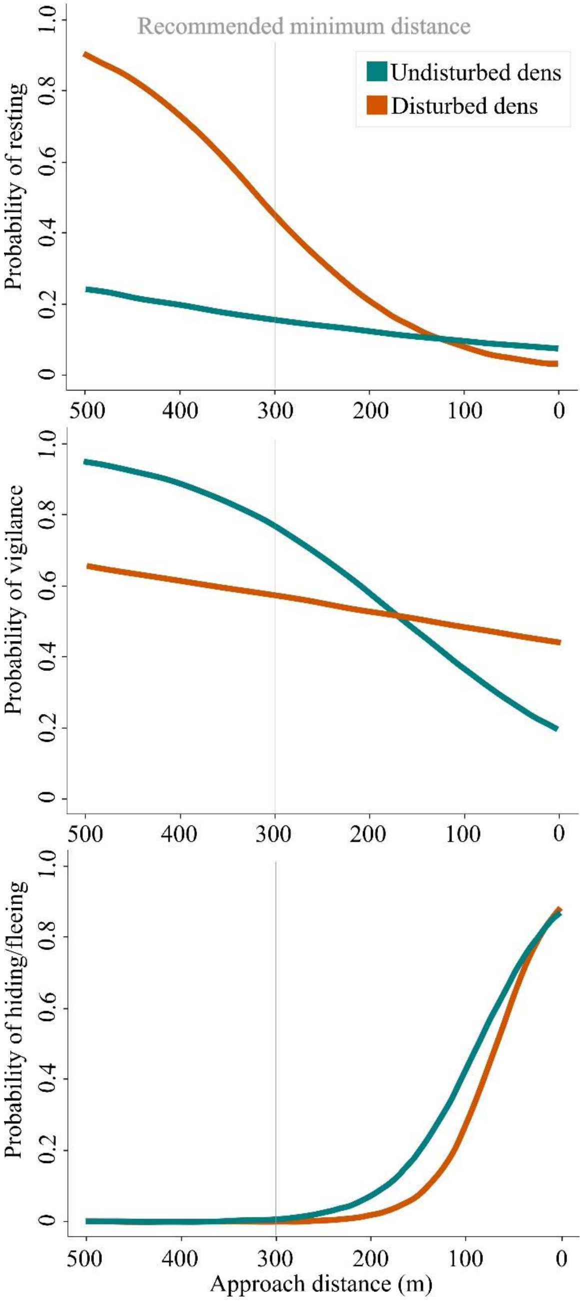

Figure 6. Probability of an arctic fox resting, being vigilant, or hiding or fleeing at decreasing approach distances for disturbed and undisturbed dens, as predicted by the generalized linear models. The grey vertical line marks the current recommended minimum distance (300m). (Larm et al., 2020a).

In *Paper II* we observed both juvenile and adult foxes to increase their presence at the den when the disturbance level from the tour group increased during arctic fox safari tours (Figure 7). The adult foxes also guarded the juveniles more, i.e. they were active during a larger part of the time when there were juveniles at the den during a tour compared with the same time at days with no tour (Figure 7).

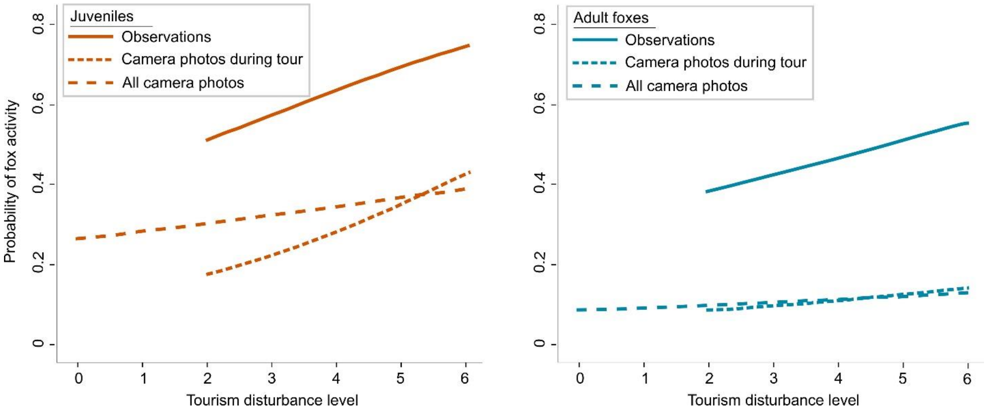

Figure 7. Three different probability estimates of adult and juvenile arctic fox activity with increasing disturbance level of the tour group during 13 guided tours in 2015. Solid lines are based on observation during the tour, short dotted lines (from 2 to 6) are based on camera photos taken during the tours and long dotted lines (from 0 to 6) are based on camera photos from all days during tour time (10:00 – 14:00), where disturbance level 0 is based on days with no tour. (Larm et al., 2021b).

The foxes at the den visited during the guided tours also shifted their use of the den site temporally (Figure 8). They were more active at the den during the day and less active during the night, compared with the two undisturbed dens, who both had activity peaks at dawn and dusk and lower activity at the den during daytime. The daytime is also when the disturbance from tourism is highest, which indicates that they may be less comfortable to leave the den site and the juveniles when humans are present (*Paper II*). Such shifts in the distribution of the activity could affect foraging and provisioning for the juveniles, as well as increase energy expenditure and exposure to predators (Frid & Dill, 2002; Nevin & Gilbert, 2005; Rode et al., 2007).

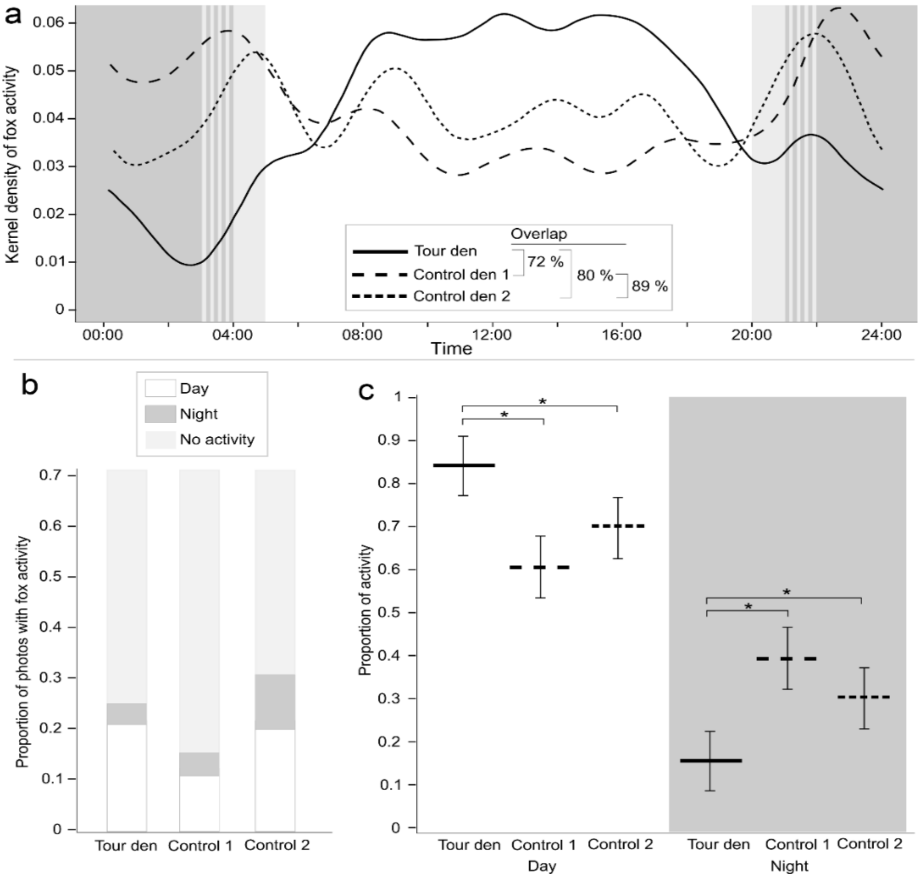

Figure 8. a) Comparison of diurnal activity distribution between the arctic fox den visited during the guided tours (solid line) and two undisturbed control dens (dotted lines). White background represents time with daylight, dark grey nighttime and light grey dawn and dusk. b) The proportion of photos with arctic fox activity taken during day (including dawn and dusk; white) and night (dark grey) at each of the three dens. c) The mean (± 95% CI) proportion of the activity spent at the den during day and night at the three dens. The foxes at the tour den were more active at the den during the day, and less during the night, compared with both of the two undisturbed control dens. (Larm et al., 2021b).

Fitness consequences

Investigating fitness consequences of animal's responses to disturbance is complex. Most studies focus on identifying different responses of animals, but without attempting to quantify the fitness consequences and ecological significance of a disturbance. In *Paper III* we aimed to identify fitness effects of the tourism disturbance on the arctic foxes. By comparing juvenile summer survival at disturbed and undisturbed dens, we surprisingly found that the survival was higher at disturbed dens than at undisturbed dens, but the effect was only found during years of declining small rodent densities (Figure 9). During the decline phase, the predation on arctic foxes is at the highest as the large tundra predators, such as eagles and red foxes, need to switch to alternative prey when small rodents are scarce (Elmhagen et al., 2000). Eagles, but also red foxes and wolverines, have previously been seen to avoid human activity to a larger extent than the arctic fox (May et al., 2006; Krebs, Lofroth & Parfitt, 2007; Kaisanlahti-Jokimaki et al., 2008; Martin et al., 2011). The probable mechanism behind the increased survival at disturbed dens could thus be a human-induced predator refuge for the foxes in close proximity of human activity. Such effects on the intra-species dynamics have been seen in other species as well (Nevin & Gilbert, 2005; Leighton et al., 2010; Muhly et al., 2011) and have the potential to alter species distribution and interactions, which could have consequences on an ecosystem level (Hebblewhite et al., 2005; Muhly et al., 2011; Smith et al., 2018).

All inhabited dens in the Helagsfjällen area are provided with supplementary food through feeding stations filled with dog pellets at the dens (Angerbjörn et al., 2013). It is thus difficult to determine the potential effects of tourism on the foraging and food provisioning for the juveniles. In *Paper III*, the juveniles at the disturbed dens were not in a poorer physical condition than the juveniles at undisturbed dens, suggesting that the tourism activity did not affect the mortality due to starvation, even during years of low availability of natural food. However, the diurnal activity distribution of the foxes at the undisturbed dens in *Paper II* can be assumed to represent an optimal trade-off between hunting, guarding of juveniles and resting. Since the foxes at the disturbed dens had shifted their activity pattern and increased the time they spent guarding the juveniles during the tourist visits, it is possible that the foraging and food provisioning for the juveniles had been compromised, but could be compensated for by the supplemental food.

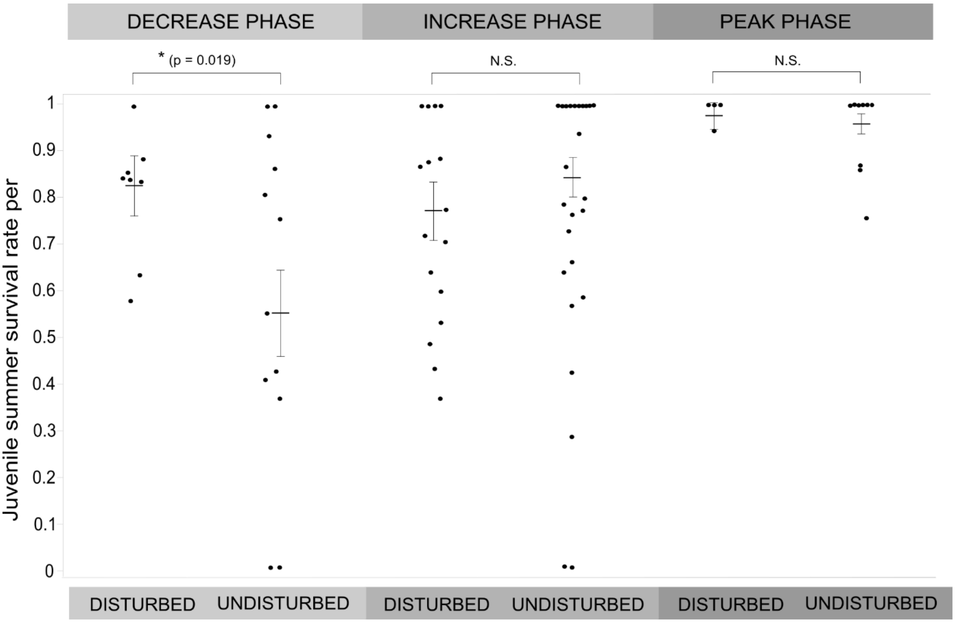

Figure 9. Differences in juvenile summer survival between dens that are disturbed and undisturbed by tourism activities for the different phases of the small-rodent cycle. The juvenile survival was higher at disturbed dens during decrease years, while there was no difference in survival during increase years. The peak year (2011), where the juvenile survival was very high among all dens is included in the figure for reference. (Larm et al., 2020b).

Context dependency

Overall, results in this thesis showed a high level of context-dependency. In *Paper III*, the fitness consequences of the tourism activity varied with the phase of the small rodent cycle, probably due to changes in the interaction between arctic foxes and predators. The small rodent density affects the abundance of both arctic foxes, predators and other prey species such as hares and ptarmigans, and thereby also affects the intra-species interaction dynamics within the system (Ims & Fuglei, 2005). For the arctic foxes it also affects the food availability, breeding success and survival, which makes small rodent dynamics crucial to take into consideration in any study of arctic foxes in a tundra ecosystem. The varying contexts between years made it possible to identify the predator refuge effect as the probable mechanism behind the difference in juvenile survival presented in *Paper III*, as it was only seen during small rodent decrease years, when the predation on arctic foxes generally is at the highest. The constantly fluctuating tundra ecosystem and strong context dependency makes the arctic foxes a good model system for studies of how the disturbance effects vary depending on situational factors, such as food availability and intra-species interactions.

There were also individual variations in responses toward human presence depending on previous experience with tourism disturbance, where foxes at disturbed dens were more tolerant than foxes at undisturbed dens (*Paper I*). Personality differences between foxes can also affect individual responses to humans, where bolder individuals have a higher tolerance to approaching humans than more shy individuals (Choi et al., 2019). In farmed arctic foxes, boldness was also related to fecal glucocorticoid metabolite concentrations, which reflects the physiological stress level of the animal (Larm et al., 2021a). Bolder individuals had lower levels of fecal glucocorticoid metabolites compared to more shy individuals, which is similar to what have been observed in several other species (Martin & Realé, 2008; Malmkvist et al., 2003). In wild arctic foxes, it can be difficult to distinguish whether a high tolerance towards humans is due to habituation or boldness. In other cyclic species, fecal glucocorticoid metabolite levels also fluctuate over the different phases (Sheriff, Krebs & Boonstra, 2011). In addition, there may be an interaction between phase dependent factors, such as food availability and predation, and other stressors, such as human disturbance, which could result in different responses to disturbances depending on the context (Dantzer et al., 2014).

Tourist perspective

After participation in a guided arctic fox safari tour, the questionnaire revealed an increased knowledge about the arctic foxes and their situation in Fennoscandia as well as increased awareness of the behavioral guidelines for minimizing disturbance during arctic fox encounters (*Paper IV*). Knowledge and awareness can be a first step towards improved attitudes and behaviors (Ballantyne et al., 2011) and improve the acceptance for behavioral guidelines such as a code of conduct (Öqvist et al., 2018), but whether that was the case for the arctic fox tour participants is yet not known.

During a guided tour, the noise and movement level of the participants was higher when juveniles were present on the den compared with when no foxes or only adults were active (*Paper II*). Such effects of juveniles and charismatic animals have previously been seen in other species and settings as well (Patterson & Bitgood, 1988). That indicates that viewing the juveniles play at the den elicits positive emotions and excitement in the tour participants. Positive emotions in connection to a wildlife tourism experience is also something that can facilitate attitudinal and behavioral changes, particularly changes related to the viewed species and environment (Orams, 1997; Ballantyne et al., 2007).

A positive visitor experience can in turn be positive for the conservation of the wildlife and environment and be an incentive for their protection. The information provided before a tour is important for creating realistic expectations of e.g. the possibility to view the animals and degree of interaction (Shutt, 2014;

Dybsand, 2020). During a tour, a guide can mitigate a negative experience or unmet expectations to some extent, for example through educating about the species and environment and by providing surrounding activities (Margaryan and Wall-Reinius, 2017; Dybsand, 2020; Dybsand and Fredman, 2020). A guide can also be an important role model following the behavioral guidelines such as a code of conduct (Littlefair & Buckley, 2008; Öqvist et al., 2018). Based on tour evaluations performed by the arctic fox tour operator, participants were overall very satisfied with the experience and the performance of the guide and found the information provided by the guide to be an important part of the tour experience. Most also stated that they would share the knowledge and experience with friends and family.

Altogether, the effects found on tour participants can be considered positive for the conservation of the arctic foxes. The improved knowledge and awareness, positive emotions during a guided tour and satisfaction with both the experience and the performance of the guide, provides a good basis for actual attitudinal and behavioral changes and for the participants to become ambassadors for the conservation of the arctic fox in Fennoscandia. These findings highlight the link between wildlife experiences and recreational values (Trombulak et al., 2004). Finally, parts of the participation fee from the tours is donated to the conservation work, which contributes to the supplemental feeding for all arctic foxes in the Helagsfjällen area.

Concluding remarks

In conclusion, this thesis has identified several different direct and indirect effects on the behavior, activity pattern and tolerance towards humans in arctic foxes exposed to human activity, as well as increased juvenile survival at disturbed dens during years of high predation on arctic foxes (Figure 10). It has also identified effects on the behaviors, knowledge and awareness of tourists (Figure 10). However, due to the high context-dependency of responses of individual animals to disturbance and the associated ecological consequences on individual and population levels (Penteriani et al., 2017), it is difficult to determine effects as exclusively positive or negative.

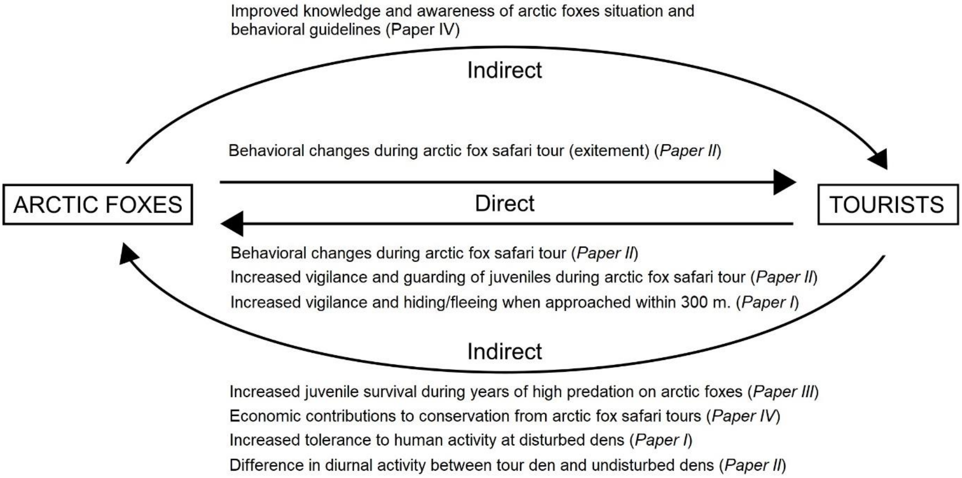

Figure 10. Schematic model summarizing the different direct and indirect effects on both arctic foxes and tourists identified in the studies included in this thesis.

The apparent challenge with guided tours to arctic fox dens is to minimize the negative effects on the foxes while ensuring a positive visitor experience. The highly variable ecological conditions between the phases of the small rodent cycle challenges the management even more as the effects on the foxes may vary between years; foxes being more vulnerable in years when rodents decline (*Paper III)*. It is therefore important that guidelines and regulations are strict enough to reduce negative effects during those years, or develop adaptive strategies taking small rodent phase into account. Responses can also vary between foxes due to individual traits, such as differences in experience with humans (*Paper I & II)* and personality (Choi et al., 2019). In *Paper I*, we provide a scientific basis for the recommended minimum distance of 300 m to the foxes and their dens. We confirm that 300 m is enough for most foxes to not flee or hide, but is not enough to avoid causing vigilance and changes in activity patterns. At distances shorter than 200 m, the probability of hiding or fleeing increased rapidly, which stresses the importance of communicating and adhering to the recommendations.

Even though the foxes at disturbed dens seem to tolerate closer approaches than foxes at undisturbed dens, they changed their behavior and were present at the den together with the juveniles more during a guided tour compared to days without a tour (*Paper II*). That indicates that the adults may still perceive the presence of humans as a threat. Potential effects of such changes in behavior and activity on the foraging and food provisioning for the juveniles could have been mitigated by the ongoing supplemental feeding. If the supplemental feeding stops, it will be important to reevaluate the disturbance effects and investigate potential fitness consequences when the foxes no longer have access to nearby supplemental food. It is further important to acknowledge that the effects found in the studies included in this thesis are for the current tourism pressure, if that changes in the future, impacts on wildlife are likely to change as well.

Based on evaluations of the guided arctic fox safari tours, the visitor satisfaction was high (*Paper IV*). Many of the visitors appreciate the knowledge-based guiding, extensive information about the arctic fox, as well as about other animals and plants in the surrounding environment. They also appreciated the fact that revenue from the tours was donated to the conservation of the foxes and said that they were likely to recommend the experience to friends and family. The positive experience in combination with increased knowledge and awareness have the potential to generate positive attitudes to regulations and behavioral changes that eventually could create ambassadors for the conservation of the arctic foxes. Maintaining a high-quality guiding experience is thus important for obtaining high visitor satisfaction without compromising the conservation of the arctic foxes.

Following on the successful validation of fecal glucocorticoid metabolites as an indicator of physiological stress done in close cooperation with Norwegian Institute of Nature Research (Larm et al., 2021a), studies of physiological responses of wild arctic foxes have been started. Fecal samples from wild arctic foxes have been collected in several different mountain areas in Sweden and Norway, with the aim to study fecal glucocorticoid metabolite levels of arctic foxes in relation to disturbance from human and red fox activity, both on a larger scale between mountain areas with different disturbance levels and within an area in relation to local variations in human and red fox activity.

Consequently, the work in this thesis together with the ongoing work on physiological stress responses will contribute with one of the more comprehensive scientific studies of tourism effects on terrestrial mammals. Although the weight of this thesis is mostly on the ecological perspective of the wildlife-tourism interaction, important insights have also been gained from incorporating the tourism perspective. The output from this thesis brings important deliverables for species-specific management and conservation, but also for other species given the rapidly growing interest for wildlife tourism.

Future work

Some projects that will complement the work in this thesis are already ongoing. As mentioned, fecal samples of wild arctic foxes have been collected in Sweden and Norway that will be used to study physiological stress in response to human activity and other stressors. A new, improved and extended questionnaire study was also conducted during the summers of 2018 and 2019 together with protocols filled out by the tour guide with information about each tour. The aim of that study is to connect the responses of the guided tour participants to questions about awareness, attitudes and willingness to pay for arctic fox conservation to both the objective and subjective tour experience.

Further, there is an interesting development of the tourism currently ongoing within the Helagsfjällen area, where the studies of this thesis were conducted. The local reindeer herders argue that the current level of tourism activities causes too much disturbance to the reindeers, which has resulted in that the Swedish Tourist Association have been obliged to scale down on the services they offer during the coming years. For example, one mountain cabin that was located in close proximity of some arctic fox dens have already been closed. We can only speculate in what effects these changes will have on tourism activities and the recreational use of the area, but regardless, the changes in tourism pressure will offer interesting opportunities for research on tourism disturbance effects.

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Svensk sammanfattning

Intresset för naturturism och att observera vilda djur ökar både i Skandinavien och globalt sett. Interaktionen mellan turism och vilda djur kan studeras ur flera olika aspekter, inom både ett naturvetenskapligt och ett samhällsvetenskapligt perspektiv. Effekten av sådana interaktioner på vilda djur kan vara både positiva och negativa och påverka såväl enskilda individer som hela populationer. Ofta studeras aspekter av störning från turism på vilda djur enskilt och få studier kombinerar flera olika aspekter eller undersöker vilka ekologiska konsekvenser störningen kan ha för djuren.

I den här avhandlingen kombinerar jag ett naturvetenskapligt och ett samhällsvetenskapligt perspektiv på interaktionen mellan turism och vilda djur. Jag har studerat effekter av turismstörning i den sydligaste populationen av fjällräv (*Vulpes lagopus*) i Sverige, som finns i Helagsfjällen i Jämtlands län. Området kring Helagsfjällen är populärt för olika typer av friluftsaktiviteter, så som vandring, skidåkning och tältning. Till en fjällrävslya i området genomförs även guidade fjällrävsturer sommartid.

Det övergripande målet med avhandlingen har dels varit att bidra till en god förvaltning av både fjällrävar och turister inom studieområdet och dels att bidra vetenskapligt med en omfattande studie av olika aspekter av interaktionen mellan turism och vilda djur tillsammans med en undersökning av de ekologiska konsekvenserna. Jag har studerat olika aspekter av hur fjällrävar reagerar på mänsklig närvaro och jämfört reaktionerna mellan fjällrävar som bor i lyor med hög respektive låg turismstörning. De första två kapitlen i avhandlingen fokuserar på olika beteendemässiga reaktioner hos fjällrävarna på mänsklig närvaro, i det tredje kapitlet undersöks de ekologiska konsekvenserna och i det fjärde kapitlet studeras effekter på besökare i området och deltagare på de guidade fjällrävsturerna.

För att studera fjällrävarnas reaktioner på mänsklig närvaro vid olika avstånd från lyan genomförde vi upprepade mänskliga närmanden mot fjällrävar på deras lyeplats (*Kapitel 1*). Vid ett avstånd på 300 meter gömde sig de första fjällrävarna. Många fjällrävar hade dock ökat sin vaksamhet vid längre avstånd än 300 meter, vissa redan vid 500 meter där närmandena startade. Fjällrävar på lyor med hög nivå av turismstörning tolererade mänsklig närvaro på närmare avstånd från lyan än fjällrävar på mer ostörda lyor, vilket indikerar att de kan ha habituerats till mänsklig närvaro, dvs. lärt sig att människor inte utgör ett hot. Resultaten från studien tillför en vetenskaplig grund till de rekommendationer som finns i Sverige och Norge om att hålla ett minimiavstånd på 300 meter till fjällrävar och deras lyeplatser. På lyan som besöks av guidade turer ändrade fjällrävarna sin användning av lyeplatsen till att vara mer aktiva på lyan under dagtid, jämfört med två ostörda lyor (*Kapitel II*). Under de guidade turerna ökade också både vuxna rävar och valpar sin närvaro på lyan när turisterna rörde sig och lät mer. Dessa resultat tyder också på att fjällrävarna inte uppfattar människor som ett direkt hot, men samtidigt tycks de inte vilja lämna lyeplatsen dagtid, när risken för störning från människor är som störst, i samma utsträckning som fjällrävar på ostörda lyor.

Genom att jämföra valpöverlevnad under sommaren på störda och ostörda lyor fann vi förvånande att överlevnaden var högre för valpar på störda lyor (*Kapitel III*). Effekten fanns dock bara under år med nedåtgående täthet av smågnagare, när predationen på fjällrävar antas vara som högst eftersom de utgör ett alternativ byte till smågnagare för större rovdjur. Vi föreslår att den ökade valpöverlevnaden skulle kunna vara en effekt av att mänsklig närvaro orsakar större störning för andra stora rovdjur jämfört med fjällräven och att predationen på fjällrävsvalpar inom områden med hög turismstörning därmed minskar.

För att studera den turistiska aspekten av interaktionen genomfördes en enkät-studie till fem grupper av besökare i området, varav två grupper var deltagare på de guidade fjällrävsturerna. Studien visade att efter deltagande i en fjällrävstur hade besökarna fått ökad kunskap och medvetenhet kring fjällrävarnas situation, bevarandearbetet för fjällrävar och om riktlinjer för att minska sin störning på fjällrävar (*Kapitel IV*). Deltagarna på de guidade turerna uppgav att de var nöjda och hade en positiv upplevelse av de guidade turerna. Ökad kunskap och medvetenhet tillsammans med positiva upplevelser av vilda djur kan exempelvis leda till positiva förändringar i attityder och beteenden kopplade till bevarande och ökad acceptans för riktlinjer för att minska störning. Vi vet dock inte om det uppfylldes för deltagarna på de guidade fjällrävsturerna.

Slutligen genomförde vi även en lyckad validering av en metod för att analysera fysiologisk stress i avföring från fjällräv. Valideringen är inte inkluderad i avhandlingen, men utgör ett första steg för framtida studier av utsöndrade nivåer av stresshormon hos fjällrävar vid störning från exempelvis människor. Prover har redan samlats in från vilda fjällrävar i olika fjällområden i Sverige och Norge för studier av effekten av störning från mänsklig närvaro och rödräv.

Sammanfattningsvis utgör delarna i denna avhandling, tillsammans med det pågående arbetet på hormonella stressresponser, en omfattande vetenskaplig kartläggning av effekter av turismstörning på ett vilt däggdjur. Resultaten från avhandlingen kan först och främst bidra till förvaltningen och bevarandet av fjällräv, men kan också ge insikter för andra arter som påverkas av det ökande intresset för naturturism.

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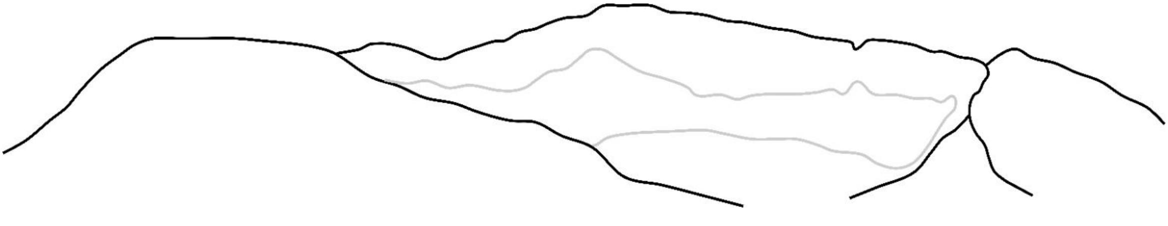

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Note

Arctic Fox Responses to Tourism Activity

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ABSTRACT As the interest for nature-based tourism activities increases, it is important to provide evidence-based guidelines for wildlife-human interactions to minimize the disturbance caused to wildlife. In Fennoscandia, the endangered arctic fox (*Vulpes lagopus*) is subject to increasing tourism interest and some regions recommend a minimum approach distance of 300 m, but the guidelines have not been scientifically validated. We conducted experimental human approaches towards arctic fox den sites to study activity and behavioral changes in response to the approaching observer. The first arctic foxes hid when approached within 300 m, but many had increased their vigilance already at the start distance of 500 m. At approximately 200 m, the hiding probability increased rapidly at dens disturbed and undisturbed by tourism activities. Arctic foxes at disturbed dens allowed the observer to approach more closely before they increased their vigilance and before they hid compared to foxes at undisturbed dens. We confirm that a minimum distance of 300 m might be sufficient for most arctic foxes to refrain from hiding, but a longer distance would be required to avoid causing any disturbance. We recommend a minimum approach distance of ≥300 m to be implemented in all Fennoscandian regions inhabited by the arctic fox. © 2020 The Wildlife Society.

KEY WORDS arctic fox, human disturbance, human-wildlife interaction, minimum approach distance, nature-based tourism, wildlife tourism.

Nature-based human activities, such as wildlife tourism, may cause disturbance to wildlife (Czech et al. 2000, Snyder 2007) by affecting activity budgets (Kitchen et al. 2000, Li et al. 2011), habitat use (Nevin and Gilbert 2005), distribution (Gill et al. 1996, Bejder et al. 2006, Carrete and Tella 2010), risk perception (Rodriguez-Prieto et al. 2008, Geffroy et al. 2015), and inter-species interactions (Muhly et al. 2011, Larm et al. 2019). Disturbance is any activity that changes the behavior or physiology of an animal (Nisbet 2000). Many animals are presumed to perceive humans as a potential predator and respond to an approaching human in a similar way as they would to an approaching predator (Gill et al. 1996, Frid and Dill 2002, Beale and Monaghan 2004). Antipredator responses such as avoidance and fleeing can be costly because it takes time and energy away from fitness enhancing activities such as foraging and parental care and may displace an animal from a preferred habitat (Ydenberg and Dill 1986, Steidl and Anthony 2000, Frid and Dill 2002). Responding to a perceived predation risk is thus a fitness trade-off where the response should be optimized rather than maximized (Ydenberg and Dill 1986). A common measurement of the trade-off between risk avoidance and fitness enhancing activities is flight initiation distance, which is the distance from an approaching observer or object where the focal animal flees or hides. An animal may become vigilant, however, and respond behaviorally and physiologically long before it decides to take flight (Ydenberg and Dill 1986) and it has been suggested that the effect of a disturbance can be determined by the risk perceived by the affected animal rather than the actual risk (Gill et al. 2001). Thus, in accordance with the disturbance definition, an animal may be disturbed long before it takes flight (Tarlow and Blumstein 2007).

Several individual and situational factors may influence this trade-off and the responses of an individual animal to a disturbance. Such factors could be sex, age, time of year, group composition, food availability, physical condition, personality traits, and previous experience of humans (Gill et al. 2001, Bejder et al. 2006, Stankowich 2008). Predictable and recurring human activities, like many wildlife tourism and recreational activities, may cause an animal to decrease its responses towards the activity over time as it learns not to perceive it as a threat (i.e., habituate; Higham and Shelton 2011).

Codes of conduct and behavioral guidelines for wildlife encounters often include a minimum approach distance to decrease disturbance to the targeted wildlife (Holmes et al. 2005, Aanes 2011, Midgely and Burns 2014). It is preferable to base recommendations on scientific studies, which could detect subtler effects such as physiological stress responses and increases in vigilance (Blumstein et al. 2003, Holmes et al. 2005). Scientifically based or evaluated guidelines are available for royal penguins (*Eudyptes schlegeli*; Holmes et al. 2005) and several species of waterbirds

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(Carney and Sydeman 1999, Schlacher et al. 2013). Studies of flight initiation distances may also include recommendations for the management to minimize disturbance, such as for ungulates (Stankowich 2008), desert bighorn sheep (*Ovis canadensis nelsoni*; Papouchis et al. 2001), brown bears (*Ursus arctos*; Penteriani et al. 2017), and yellow-bellied marmots (*Marmota flaviventris*; Li et al. 2011). Even though flight initiation distance is somewhat consistent within species (Blumstein et al. 2003), the level of disturbance deemed acceptable by wildlife managers may vary between populations of the same species depending on management objectives (Holmes et al. 2005). As an example, Iceland, Svalbard, and Fennoscandia are all inhabited by the arctic fox (*Vulpes lagopus*), but the conservation status and management objectives for the arctic fox differ between the 3 areas. In Iceland, where the arctic fox is numerous and subject to extensive hunting (Unnsteinsdottir et al. 2016), the recommended minimum distance from an artic fox or den site is 40 m (Midgely and Burns 2014). In Svalbard, the conservation status of the arctic fox is similar, but because the management objective is to minimize any disturbance to maintain the pristineness of the Svalbard flora and fauna, the recommended minimum distance is set to 500–1,000 m (Aanes 2011). In Fennoscandia on the other hand, the arctic fox is endangered (Norwegian Red List 2015, Swedish Red List 2015) and the management objective is to increase the population to a viable level. Some human disturbance is tolerated as long as it does not affect population viability negatively. In Norway, arctic fox dens are protected and Norway and some regions in Sweden have a recommended minimum distance from arctic foxes or den sites of 300 m (Länsstyrelsen Jämtlands län in Eide 2015, Norwegian Environmental Agency 2015, Swedish Environmental Protection Agency 2017), whereas other regions have no specific recommendations. Today, that distance is based on an educated guess rather than empirical data. Field experience is important in the management and conservation of species, but the effectiveness and credibility of the guidelines would be strengthened if it were combined with empirical data (Granquist et al. 2019).

Our objectives were to investigate the behavioral responses of arctic foxes to human activity at different distances from their den site and compare the responses between den sites disturbed and undisturbed by tourism. Because foxes at disturbed dens are more used to human presence, we predicted that they would tolerate closer approaches before they increased their vigilance and hid, compared to foxes at undisturbed dens. We also expected the activity distribution to diverge from the baseline earlier during the experimental approach at undisturbed dens compared to disturbed dens.

STUDY AREA

We conducted our study during 3 summers from 2016 to 2018 in Helagsfjällen in central Sweden (Fig. 1). Helagsfjällen is a subarctic mountain region of about 3,400 km^2 mainly located above the tree line at 700–800 m above sea level. The landscape is dominated by low hills covered in alpine tundra vegetation, characterized by low shrubs and bushes. The highest peaks reaches up to 1,500–1,800 m above sea level., where the terrain is dominated by rocks. The area has strong seasonal variation in temperature and weather conditions, with mild summers and cold, snow-rich winters. There are no roads through the area and it is mainly used for reindeer (*Rangifer tarandus*) herding, recreational tourism, and small game hunting. Helagsfjällen holds the largest and southernmost arctic fox population in Sweden, consisting of approximately 40–60 adult individuals (Angerbjörn et al. 2013). In Fennoscandia, the arctic fox uses the same den sites from year to year and the dens are most important during summer when the juveniles depend on the den for shelter (Elmhagen et al. 2014). Arctic fox litter sizes in Fennoscandia vary between years from 1 to 18 weaned juveniles, depending on the fluctuating availability of its main prey, small rodents (Angerbjörn et al. 1995). The main predator and competitor species to the arctic fox are golden eagle (*Aquila chrysaetos*), red fox (*Vulpes vulpes*), and wolverine (*Gulo gulo*; Tannerfeldt and Angerbjörn 1996).

Figure 1. Location of the study area Helagsfjällen in Sweden, where we studied arctic fox responses to tourism activity during July and August in 2016–2018.

The Helagsfjällen area is popular for recreational tourism during summer (Jun–Sep) and winter (Feb–Apr). An extensive network of hiking and skiing trails run through the area and the Swedish Tourist Association (Svenska Turistföreningen) offers accommodation at several mountain huts along the trails. We classified the dens included in the study as disturbed or undisturbed by the tourism activity in the area. The dens classified as disturbed were located within 1 km of trails or within 2 km of mountain huts. In the open tundra they were all within eyesight of the trail or hut and the arctic foxes inhabiting these dens could see humans on a daily basis during summer. One of the disturbed dens was also subject to guided arctic fox safari tours that was operated by Helags mountain station hut managers 2 times/week during summer. The dens classified as undisturbed were located >2 km from any trail or >7 km from any mountain hut. Because the trails channel most hikers in the area, the arctic foxes at these dens would rarely encounter humans.

METHODS

Field Methods

To study the vigilance distance, hiding distance, and distribution of different activities of arctic foxes, we used observations from 65 experimental human approaches towards 6 arctic fox dens performed in summer from 2016 to 2018 (Table S1, available online in Supporting Information). We performed the approaches between 0700 and 2200, primarily at occasions when we wanted to approach the den for other reasons (e.g., setting traps, collecting fecal droppings). Consecutive approaches towards the same fox were >2 hours apart, but usually we did not approach a fox more than once a day. The start distance varied between 160–500 m, mainly because we complemented the approaches made for this study with approaches from another study that used the same method but with a closer start distance to increase the sample size. In addition, the topography did not allow for full distance approaches at all den sites. The approaching observer walked towards the den and stopped for 30 seconds at predetermined distances (500, 450, 400, 350, 300, 250, 200, 180, 160, 140, 120, 100, 80, 60, 40, 20 and 0 m from the den) to record all activities displayed by the observed fox during that time (lying head down, lying head up, sitting, standing, moving, hiding or fleeing, watching observer, watching side, and barking). The observer also recorded the approach distance where the fox first displayed vigilance (watching the observer), barked, hid, or fled (Table 1), and additional information about time, trial order, wind direction, and whether there were cubs or other adult foxes present at the den. We also recorded the hiding distance of other adults present during the approach.

We placed automatic cameras at 5 dens in the area during summers 2015 to 2017, set to take a photo every 5 minutes. We derived a baseline activity distribution for disturbed and undisturbed dens separately from all photos taken between 0700 and 2200 during July and August, the same time span during which the approaches were performed (Table S1). We excluded photos taken during an approach from the baseline. In all photos with adult fox activity (11% of 83,961 photos), we classified the activity of the adult foxes in order of increasing vigilance as resting (lying, head down), vigilant (lying, head up, sitting), or moving (standing or moving). We used the relative distribution of the activities derived from the photos for comparison to the activity distribution of the foxes during the experimental approaches. For the disturbed dens ($n = 3$), we performed camera monitoring and experimental approaches at the same dens, and for the undisturbed dens, we performed camera monitoring and approaches at 1 den, only camera monitoring at 1 den, and only approaches at 2 dens (Table S1).

We conducted all research procedures in this study in accordance with Swedish law and procedures were approved by the Swedish Board of Agriculture (Jordbruksverket) and an ethical board (Umeå djurförsöksetiska nämnd, permits A130-07, A131-07, A36-11, A37-11, A18-14, A19-14, A10-17). The camera monitoring was approved by the County Administrative Board in Jämtland (Länsstyrelsen Jämtland).

Statistical Analyses

We fitted linear models for the vigilance and hiding distances with time, trial order, wind direction (towards or from den), litter (yes or no), cubs present on the den (yes or no), start distance, and tourism disturbance level (disturbed or undisturbed) as explanatory variables in the original model. We examined the explanatory variables for collinearity using plots but did not find any relations. We fitted an additional model for vigilance distance on a subset of the data with a start distance of ≥400 m ($n = 19$) to remove potential effects of start distance. We included all explanatory variables used in the full model except start distance. We conducted a stepwise reduction of the original models by eliminating the least significant variable in each step. We then compared the models using corrected Akaike's Information Criterion (AIC_c) values. When the difference in AIC_c values was <2, we selected the simpler model (Table S2, available online in Supporting Information). We performed the experimental approaches during July and beginning of August, apart from 2 approaches

Table 1. Classifications of arctic fox activities and overview of the different activity measurements used in the study of arctic fox responses to tourism activity in Helagsfjällen, Sweden, 2016–2018.

	Resting	Vigilant[a]	Moving	Hide or flee[b]
Baseline from camera photos	Lying, head down	Lying, head up Sitting	Standing Moving	
Activities during approaches	Lying, head down	Lying, watching side Lying, watching observer Sitting	Standing Moving	Hides in den Flees from den

[a] Vigilance distance was the distance from the observer where the fox first watched the observer.

[b] Hiding distance was the distance from the observer where the fox first hid or fled.

in September. We excluded the 2 late approaches from the analyses of vigilance and hiding distances because the arctic foxes behave differently at the den site in September compared to July and August, when the cubs are younger.

We compared the activity distributions during the experimental approaches to the baseline activity distribution using chi-square tests. We compared the mean distribution of activities for disturbed and undisturbed dens at each approach distance to the baseline activity distribution derived from camera photos. For the experimental approach data to be comparable to the photos, vigilance began when the fox lifted its head, rather than when the fox first watched the observer. To test for differences in response distance between disturbed and undisturbed dens, we also used generalized linear models (Bates et al. 2015) with resting, vigilance, and hiding as binomial response variables predicted by disturbance level (disturbed or undisturbed), approach distance (0–500 m), and the interaction between them. We performed all analyses in R (R Core Team 2018) and RStudio version 1.1.419 (RStudio 2017).

RESULTS

The mean start distance of the experimental approaches was 289 m for disturbed dens ($n = 35$) and 310 m for undisturbed dens ($n = 28$). The vigilance distance (when the fox first watches the observer) was related to tourism disturbance and start distance ($\chi_1^2 = 14.78$, $P < 0.001$). Foxes at undisturbed dens started to be vigilant at longer distances (238 ± 46 m [95% CI]) compared to foxes at disturbed dens (177 ± 27 m; Fig. 2A). The vigilance distance was positively correlated with start distance ($r^2 = 0.55$, $P < 0.001$). When we analyzed the approaches ≥400 m separately to remove the effect of start distance, the difference increased between disturbed ($n = 10$, 211 ± 60 m) and undisturbed dens ($n = 9$, 364 ± 102 m; $\chi_1^2 = 7.16$, $P = 0.02$; Fig. 2A). The hiding distance was also longer at undisturbed dens (80 ± 21 m) than at disturbed dens (47 ± 13 m; $\chi_1^2 = 10.32$, $P = 0.002$, Fig. 2B) but was not affected by start distance (Table S2).

The mean activity distribution derived from the camera photos varied slightly between disturbed (6,984 photos) and undisturbed dens (2,899 photos). At disturbed dens, the activities were distributed as 30.6% resting (lying, head down), 55.7% vigilant (lying head up, sitting), and 13.7% moving (standing or moving). At undisturbed dens, the foxes spent 20.8% of the active time resting, 65.2% vigilant, and 14% moving (Fig. 3, baseline activity). The activity distribution during the experimental approaches changed as the distance between the approaching observer and the den decreased (Fig. 3). The foxes at undisturbed dens shifted from resting to vigilance at longer distances compared to the foxes at disturbed dens, at 500 m most foxes were already vigilant (Fig. 3). At disturbed dens ($n = 35$), the first foxes hid when approached within 140 m and at that distance the activity distribution also started to differ significantly from the baseline activity derived from camera photos (140 m: $\chi_3^2 = 8.94$, $P = 0.03$; Table S3, available online in Supporting Information). At undisturbed dens ($n = 30$), the activity distribution started to differ from the baseline activity at an approach distance of 200 m (200 m: $\chi_3^2 = 73.43$, $P < 0.001$; Table S3), and 1 fox hid when approached within 300 m. The probability predicted by the generalized linear models of a fox resting, being vigilant, or hiding or fleeing changed nonlinearly with decreasing approach distances and the responses differed significantly between disturbed and undisturbed dens (resting: $\chi_1^2 = 23.94$, $P < 0.001$, vigilance: $\chi_1^2 = 22.51$, $P < 0.001$, hiding: $\chi_1^2 = 3.97$, $P = 0.046$; Fig. 4).

DISCUSSION

We investigated activity and behavioral responses of arctic foxes towards human activity at different distances

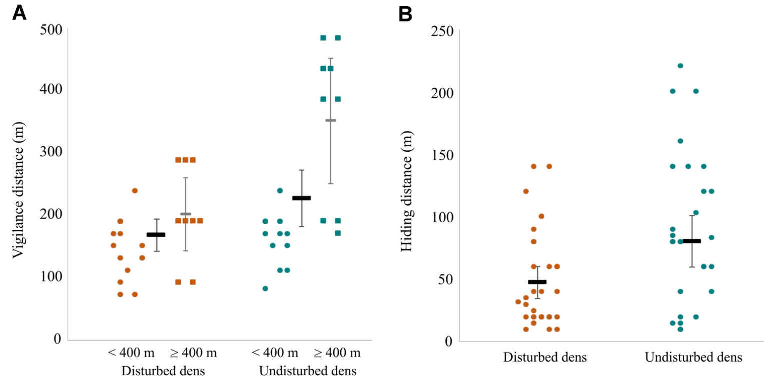

Figure 2. Vigilance distance (A) for arctic foxes at disturbed dens (● <400 m, ■ ≥400 m) and undisturbed dens (● <400 m, ■ ≥400 m) in Helagsfjällen, Sweden, 2016–2018, with approaches starting at <400 m on the left and ≥400 m to the right. Mean and error bars to the left (black) represent all approaches and to the right (grey) only approaches with a start distance of ≥400 m. We also present hiding distance (B) for disturbed dens (●) and undisturbed dens (●).

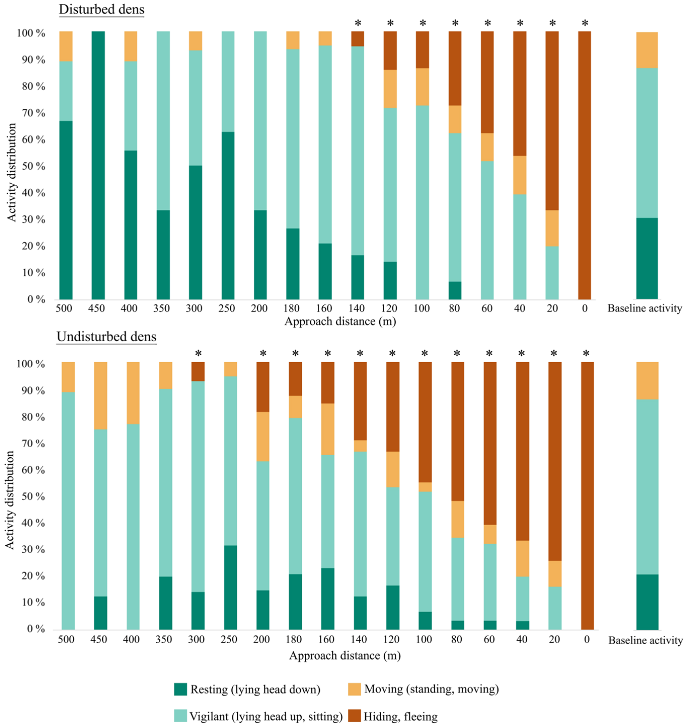

Figure 3. Distribution of different activities during experimental approaches toward arctic foxes in Helagsfjällen, Sweden, 2016–2018, compared to the baseline activity distribution derived from camera photos for disturbed and undisturbed dens separately. Asterisks indicate distances where the distribution differs significantly from the baseline activity distribution.

from the den to reinforce the Fennoscandian guidelines for arctic fox encounters. During our experimental approaches, the first fox hid at 300 m and the upper bound of the 95% confidence interval for the vigilance distance was 284 m for the undisturbed dens (238 ± 46 m; Fig. 2). This confirms that the 300 m recommended today (Länsstyrelsen Jämtlands län in Eide 2015, Norwegian Environmental Agency 2015, Swedish Environmental Protection Agency 2017) might be sufficient to avoid causing disturbance to most arctic foxes. Some foxes, however, were vigilant already at the start distance of 500 m, indicating that the vigilance distances presented in this study might be underestimated and that some foxes might be disturbed by human activity at even longer distances than 500 m from the den site (Figs. 3 and 4). Because disturbance begins when an animal increases its vigilance (Nisbet 2000, Tarlow and Blumstein 2007), 300 m is not a large enough distance to avoid causing disturbance to the most susceptible foxes. Further, the hiding or fleeing probability did not increase linearly with decreasing approach distance. Instead, there was a threshold approach distance at approximately 200 m, after which the probability increased rapidly at disturbed and undisturbed dens (Fig. 4). Visits within 200 m, for example by researchers and wildlife managers, should therefore be minimized.

In accordance with our hypotheses, we found the vigilance and hiding distances to be shorter at dens disturbed by tourism activity compared to undisturbed dens (Fig. 2). As predicted, the approach distance where the activity distribution of the foxes diverged from the baseline was also longer at undisturbed dens. According to a previous study with the same arctic fox population, juveniles of bolder parents had a higher weekly survival during the summer. The boldness trait was largely determined by shorter latency to rise from lying down and shorter latency to hide when approached by a human observer (Choi et al. 2019). The decreased vigilance and hiding latency found at disturbed dens in this study thus suggests a relationship between tourism activity and increased boldness. It is difficult to distinguish whether the increased boldness is a habituation response to the disturbance or due to bolder arctic foxes inhabiting the more disturbed dens. Choi et al. (2019) reported increasingly passive responses over trials in juveniles, who were tested repeatedly. In addition, we did not observe

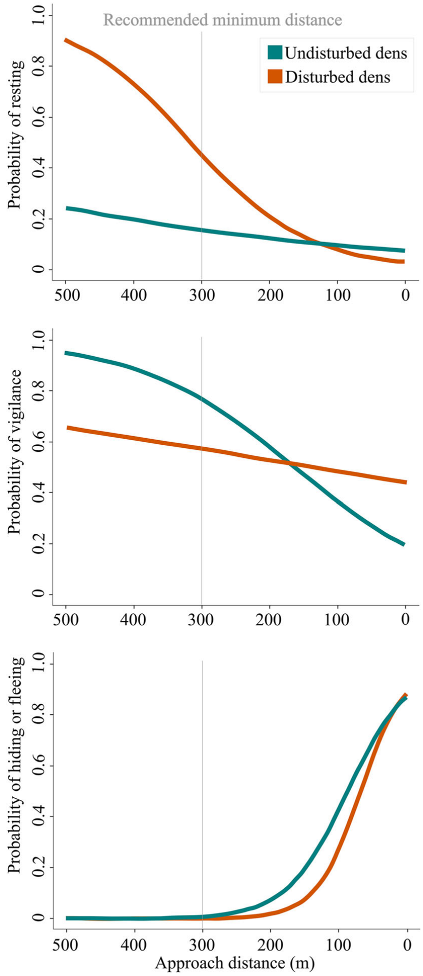

Figure 4. Probability of an arctic fox resting, being vigilant, or hiding or fleeing at decreasing approach distances for disturbed and undisturbed dens in Helagsfjällen, Sweden, 2016–2018, as predicted by the generalized linear models. The grey line marks the current recommended minimum distance (300 m).

any foxes abandoning den sites close to human activity. This suggests that arctic foxes at disturbed dens, similar to several other species (Yorio and Boersma 1992, Steidl and Anthony 2000, Stankowich 2008), develop bolder behavior as they habituate to humans. Arctic foxes potential to tolerate and habituate to humans may also alter their interactions with other, more susceptible species. In a preceding study we found juvenile survival to be higher at disturbed dens during years of high arctic fox predation, likely because the tourism activity creating a predator refuge for arctic foxes close to trails and mountain huts (Larm et al. 2019). Larm et al. (2018) reported that participation in a guided arctic fox tour resulted in greater awareness of the conservation status of the arctic fox and greater knowledge of behavioral guidelines (e.g., approach distances).

Individual and situational variations influence responses towards humans in a wide range of species. For example, sex and age differences affected responses in desert bighorn sheep (Papouchis et al. 2001) and yellow-bellied marmots (Li et al. 2011). Responses of ungulates (Stankowich 2008) and brown bears (Nevin and Gilbert 2005) varied with group composition and responses of bottlenose dolphins (*Tursiops* spp.; Bejder et al. 2006) and burrowing owls (*Athene cunicularia*; Carrete and Tella 2010) varied with personality traits. Previous experience of human activity is also an important factor influencing animal responses. Several researchers have compared flight initiation distance between habituated and non-habituated populations and in concordance with this study reported decreased responses towards human activity in habituated populations of ungulates (Stankowich 2008), bald eagles (*Haliaeetus leucocephalus*; Steidl and Anthony 2000), and magellanic penguins (*Spheniscus magellanicus*; Yorio and Boersma 1992). But habituation to disturbance from human activity means that the animal has already changed its behavior in response to human activities. Habituation can sometimes be positive (e.g., for animals subject to intensive wildlife tourism), which highlights the complexity in applying the definition of disturbance as any activity that changes the behavior or physiology of an animal (Nisbet 2000). In addition, physiological responses are difficult to study but may occur at even longer distances than behavioral changes. For example, wandering albatrosses (*Diomedea exulans*) started to display behavioral responses when approached within 10 m (Villiers et al. 2005), whereas physiological responses started already at 5 times that distance (Weimerskirch et al. 2002). When setting a minimum approach distance, it is important to acknowledge that an animal may be disturbed even though it does not show any signs of disturbance and to take individual and situational variations into consideration.

MANAGEMENT IMPLICATIONS

According to the management objectives for the arctic fox in Fennoscandian, some human effects can be tolerated as long as it does not affect the viability of the population in a negative way. An informed decision based on empirical data can now be made and we strongly advise a minimum distance of ≥300 m to be implemented in all Fennoscandian regions inhabited by the artic fox. Because the effects of tourism activity on arctic fox are not fully understood and the interest for nature-based tourism is increasing, further monitoring will be important to ensure that the tourism activity does not affect population viability negatively. The probability of foxes hiding or fleeing increased rapidly at approximately 200 m; this should be taken into account by researchers and wildlife managers that sometimes need to come closer to the den sites, so that visits within 200 m are avoided if possible.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's website.

Supporting Information

9 January 2020

Larm et al. 2020. Arctic Fox Responses to Tourism Activity. Journal of Wildlife Management.

Table S1. Number of camera photos (from 2015–2017) and experimental approaches (from 2016–2018) at the 7 arctic fox dens in Helagsfjällen, Sweden, included in the study. The camera photos are the number of photos taken during July and August, between 0700 and 2200, where at least 1 adult arctic fox was active at the den.

	Camera photos					Approaches				
Dens	2015	2016	2017	2018	Total	2015	2016	2017	2018	Total
Disturbed	1,038	2,534	3,412		6,984		7	19	9	35
Den A	446	203			649			4	1	5
Den B	592	1,554	1,699		3,845		4	5	8	17
Den C		777	1,713		2,490		3	10		13
Undisturbed	2,288	460	151		2,899		2	17	11	30
Den D								11	5	16
Den E									4	4
Den F	615	273	151		1,039		2	6	2	10
Den G	1,673	187			1,860					

Table S2. Full corrected Akaike's Information Criterion (AIC_c) model comparisons for the linear models used to analyze hiding distance and vigilance distance (2 models, 1 on the full data set and 1 on a subset of the data with a start distance of ≥400 m) based on human approaches performed towards arctic foxes in Helagsfjällen, Sweden, 2016–2018.

	Hiding distance	AICc	Δ AICc
1)	Tourism + Cubs up (Y/N) + Trial + Time + Wind + Start distance + Litter (Y/N)	685.56	12.55
2)	Tourism + Cubs up (Y/N) + Trial + Time + Wind + Start distance	682.87	9.86
3)	Tourism + Cubs up (Y/N) + Trial + Time + Wind	680.30	7.29
4)	Tourism + Cubs up (Y/N) + Trial + Time	678.21	5.20
5)	Tourism + Cubs up (Y/N) + Trial	676.17	3.16
6)	Tourism + Cubs up (Y/N)	674.30	1.29
7)	Tourism	673.01	

	Vigilance distance	AICc	Δ AICc
1)	Tourism + Start distance + Wind + Cubs up (Y/N) + Trial + Litter + Time	588.95	12.36
2)	Tourism + Start distance + Wind + Cubs up (Y/N) + Trial + Litter	585.98	9.39
3)	Tourism + Start distance + Wind + Cubs up (Y/N) + Trial	583.35	6.76
4)	Tourism + Start distance + Wind + Cubs up (Y/N)	581.01	4.42
5)	Tourism + Start distance + Wind	578.63	2.04
6)	Tourism + Start distance	576.59	

	Vigilance distance ≥ 400 m	AICc	Δ AICc
1)	Tourism + Time + Litter (Y/N) + Trial + Cubs up (Y/N)	247.04	21.40
2)	Tourism + Time + Litter (Y/N) + Wind + Trial	240.26	14.62
3)	Tourism + Time + Litter (Y/N) + Wind	234.88	9.24
4)	Tourism + Time + Litter (Y/N)	230.80	5.16
5)	Tourism + Time	227.73	2.09
6)	Tourism	225.64	

Table S3. Comparison of the distribution of different activities (resting, vigilant, moving, and hiding or fleeing) displayed by arctic foxes during the study in Helagsfjällen, Sweden, 2016–2018. We compared the activity distribution at different approach distances to a baseline activity distribution derived from camera photos using chi-square tests for foxes at disturbed (used to tourism activity) and undisturbed (not used to tourism activity) dens separately. Asterisks indicate significant difference.

Disturbed dens

Distance	df	χ^2	*P*	
500	3	5.82	0.121	
450	3	4.60	0.204	
400	3	2.80	0.424	
350	3	0.52	0.915	
300	3	2.74	0.434	
250	3	4.35	0.226	
200	3	3.11	0.375	
180	3	1.10	0.777	
160	3	2.87	0.413	
140	3	8.94	0.030	*
120	3	37.56	<0.001	*
100	3	55.44	<0.001	*
80	3	188.92	<0.001	*
60	3	348.43	<0.001	*
40	3	492.27	<0.001	*
20	3	1,003	<0.001	*
0	3	1,787	<0.001	*

Undisturbed dens

Distance	df	χ^2	*P*	
500	3	2.82	0.421	
450	3	1.07	0.785	
400	3	3.93	0.269	
350	3	0.25	0.969	
300	3	7.80	0.050	*
250	3	2.28	0.516	
200	3	73.43	<0.001	*
180	3	29.75	<0.001	*
160	3	50.40	<0.001	*
140	3	157.75	<0.001	*
120	3	239.43	<0.001	*
100	3	395.14	<0.001	*
80	3	505.89	<0.001	*
60	3	646.16	<0.001	*
40	3	788.22	<0.001	*
20	3	953.39	<0.001	*
0	3	1,410	<0.001	*

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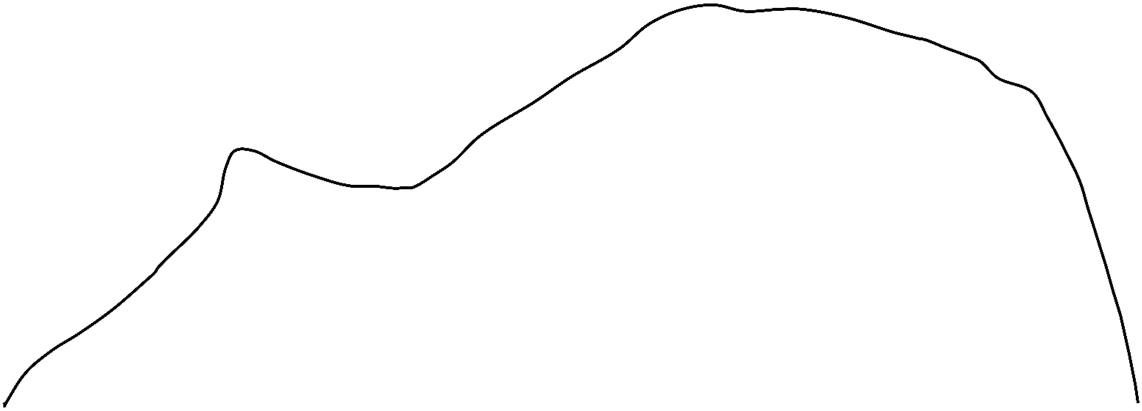

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Original Research Article

Temporal activity shift in arctic foxes (*Vulpes lagopus*) in response to human disturbance

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ABSTRACT

The rapidly growing interest for nature-based recreational activities threaten biodiversity values and increases the disturbance caused to wildlife. Several studies have demonstrated spatial and temporal activity shifts of animals in response to human disturbance. However, most studies investigate effects on how animals use an area of high tourism disturbance, such as a tourist resort or hiking trail, and not the effects of human disturbance at a key site for the animal, such as a denning or breeding site. In this study, we use photos from remote camera monitoring of arctic fox (*Vulpes lagopus*) dens with the aim to investigate the effects of various levels of tourism disturbance on the diurnal activity pattern and vigilance of breeding adult arctic foxes at the den site. We find a temporal shift towards a higher daytime activity at the den in response to high intensity tourism (71 ± 3.9% in disturbed areas compared with 53 ± 6.2% in undisturbed areas), which stands in contrast to an increased nocturnality seen in studies of many other species, including another study of arctic foxes. We suggest that the difference could be explained by the higher cost of avoiding a key site for the animal, as in this study, compared with avoiding a more general human disturbance in an area within the distribution range of the animal, as in most other studies. Increased time spent avoiding the perceived threat of humans could compromise other important activities and have potential negative effects on e.g. hunting or provisioning for the juveniles. Human disturbance focused at a key site, such as a denning or breeding site, can thereby be expected to have larger consequences than what is observed in most studies of disturbance effects on wildlife. Based on observations of both tourists and arctic foxes during close encounters in an area of high intensity tourism, we also find that they both respond behaviorally to each other. The potential for positive or negative feedback mechanisms in such relationships between tourists and wildlife highlights the importance of considering both sides of the complex interaction to find a balance between preserving biodiversity and ensuring continued possibilities for recreation.

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1. Introduction

The interaction between wildlife and recreational tourism is a complex balance between preserving biodiversity and ensuring continued possibilities for recreation. The increasing interest in nature-based recreational activities

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(Snyder, 2007; Balmford et al., 2009) threaten biodiversity values (Czech et al., 2000) and can cause disturbance to wildlife (Higginbottom et al., 2001). However, recreational tourism activities are also crucial for financing large parts of conservation actions for many endangered species (Buckley et al., 2012) and can lead to improved conservation attitudes, behaviors and support for conservation actions among tourists and recreationists (Higginbottom et al., 2001). It is therefore important to develop them in a sustainable direction and to consider both the natural and the social perspective of the interaction.

The behavioral responses of animals to human activities can vary depending on their tolerance to the disturbance (Higham and Shelton, 2011). Many animals presumably perceive humans as a threat to which they respond in a similar way as they would to a predator (Frid and Dill, 2002; Beale and Monaghan, 2004). Further, the response of an animal towards a perceived threat can be interpreted as a trade-off, where fitness-enhancing activities such as foraging and caring for juveniles are traded for anti-predator responses such as fleeing and avoidance of a perceived threat (Frid and Dill, 2002; Beale and Monaghan, 2004). The tolerance and the risk-foraging trade-off can vary between individual animals depending on several different individual and situational factors, such as sex, age, breeding status, group composition, time of year, food availability, physical condition, previous experience with humans and personality traits (Knight and Cole, 1995; Gill et al., 2001; Bejder et al., 2006). Thus, the response may not directly reflect an animal's susceptibility to the disturbance, i.e. the most vulnerable individual does not necessarily show the strongest response, but the response can rather be related to the cost of leaving the site or current activity. For example, leaving a high-quality site with good abundance of food and shelter or low abundance of predators could carry a higher cost than leaving a low-quality site, especially if alternative sites are scarce or of lower quality (Gill et al., 2001). Animals can avoid a human disturbance through a spatial or temporal change of activity, i.e. they can either move away from a disturbed area, or adjust their activity in time to the human disturbance (Nevin and Gilbert, 2005; Martin et al., 2010). A spatial or temporal redistribution could result in increased energy expenditure (Tyler, 1991; Nevin and Gilbert, 2005), change in population demography (Bejder et al., 2006) and change in species interactions (Muhly et al., 2011; Smith et al., 2018; Larm et al., 2020b). A temporal change could also cause animals to shift activities from a preferred time (Yasue, 2005), for example to forage more at sub-optimal times of the day, which could have potential fitness consequences connected to higher risk exposure and that longer foraging time is needed to fill the energy requirements.

Animals that are exposed to a reoccurring and predictable human disturbance can learn what to expect from an encounter with humans and how to respond appropriately to it depending on the experienced consequences (Bejder et al., 2009). If the encounter has no consequences for the animal, i.e. it is neither beneficial nor harmful, habituation can occur as the animal responds less and less to a disturbance. Because habituation is a process of increased tolerance over time (Bejder et al., 2009) it will be the effect of a long-term disturbance. However, our understanding of risk-foraging trade-offs and sublethal effects in such situations is limiting (Gaynor et al., 2020) and effects should preferably be measured in terms of fitness (Larm et al., 2020b). A recent review on changes in temporal activity found a general shift towards an increased nocturnality in response to various human activities, spanning from settlements and agriculture to tourist resorts and hiking trails (Gaynor et al., 2018). However, the trade-off of to spatially or temporally adjust the activity in areas or during times of high human activity may vary from the trade-off to respond to human disturbance focused at a key site for the animal, such as a breeding or denning site.

A recent review of the effects of tourism and recreation on a wide array of both wildlife and plant species in northern Fennoscandia concluded that tourist resorts exert the greatest disturbance, while e.g. hiking trails and camping have a moderate effect (Tolvanen and Kangas, 2016). The endangered Fennoscandian arctic fox (*Vulpes lagopus)* is subject both to visits from guided tours at the denning site and to a general disturbance of human activity at hiking trails and tourist mountain huts in close proximity of their denning sites. Therefore, it is a suitable study species for investigating activity and behavioral effects of varying levels of tourism disturbance at a key site. Previous studies show that the arctic foxes are behaviorally affected by human presence, where foxes in highly disturbed areas were more tolerant to approaching humans compared with foxes in less disturbed areas (Larm et al., 2020a). However, the link between disturbance from tourism activities, different behavioral changes and their potential fitness consequences have not been clearly established. In this study, we use photos from remote camera monitoring of arctic fox dens with the aim to investigate whether the diurnal activity and vigilance of adult foxes at the den differ between areas of varying levels of disturbance from human activities. Apart from the general trend that animals become more nocturnal as a response to human disturbance (Gaynor et al., 2018), there are also reports of arctic foxes in Svalbard that turned to be more nocturnal as a response to snow mobile tourism (Fuglei et al., 2017). The basic hypothesis in our study would thus be an increased nocturnality in areas of high-intensity tourism. However, indications of a different risk-foraging trade-off at a key site have been observed in wolfs (*Canis lupus*) with site-dependent pups (Wam et al., 2014) and in breeding bald eagles (*Haliaeetus leucocephalus*; Steidl and Anthony, 1996), that both had a higher tolerance to approaching humans compared with their non-breeding conspecifics. Our own previous studies on arctic foxes also indicates a potential habituation response in highly disturbed areas (Larm et al., 2020a), which could mitigate responses of avoidance. For this study, we would therefore instead predict that the breeding arctic foxes in areas of high-intensity tourism would respond by an increased presence at the den during daytime to guard the juveniles, as well as an increase of vigilant behaviors. To address the mechanisms behind potential behavioral responses, we also use a smaller dataset with behavioral observations of both foxes and tourists from one highly disturbed area, where we compare the same parameters between days with varying human activity. Finally, using observations of both arctic foxes and tourists from the same highly disturbed area, we also attempt to reveal the behavioral interplay between foxes and tourists during a close encounter.

2. Methods

2.1. Study system

The study was carried out during July and August in 2015–2017 in the Helagsfjällen mountain region (63°N, 12°E), located in central Sweden. Helagsfjällen is an area of approximately 3400 km^2, located mainly above the tree line at 700 – 800 m.a.s.l. The landscape is dominated by low mountains covered in alpine tundra vegetation such as low shrubs and bushes. There are some higher mountain peaks reaching up to 1500–1800 m.a.s.l., where the terrain is dominated by rocks. Helagsfjällen have strong seasonal climate variations, with cold, snow-rich winters and mild summers.

Helagsfjällen is one of the core areas for the arctic fox in Fennoscandia (the Sweden, Norway and Finland peninsula), with a population of approximately 40–60 adult individuals (Angerbjörn et al., 2013). The arctic fox is a mesopredator in the Fennoscandian tundra, preying mainly on cyclic small rodents (Angerbjörn et al., 1995). Predators and competitors of arctic foxes are golden eagles (*Aquila chrysaetos*), red foxes (*Vulpes vulpes*), wolverines (*Gulo gulo*) and sea eagles (*Haliaeetus albicilla*; Tannerfeldt and Angerbjörn, 1996). The arctic foxes use their large dens for protection and the same den sites are used from year to year (Dalerum et al., 2002). Surrounding the den, they have a home range of approximately 20–25 km^2 (Angerbjörn et al., 1997). Even though the den is maintained throughout the year it is most essential during the summer when the juveniles are reared (Elmhagen et al., 2014). The foxes mate during late March - early April after which the juveniles are born late May – early June and appear outside the den in early July. After the summer rearing period the juveniles start to leave the natal den in September - October (Eide, 2015). The arctic fox is classified as endangered or critically endangered in the Fennoscandian countries (Norwegian Red List, 2015; Hyvärinen et al., 2019; Swedish Red List, 2020) following extensive hunting in the early 20th century. Today, the main threats to the Fennoscandian arctic fox population are the expansion of the competing red fox into the tundra (Elmhagen et al., 2017) and irregularities in the small rodent cycles (Reid et al., 2013). As a conservation measure, all inhabited arctic fox dens in Helagsfjällen are supplementary fed with ad libitum access to dog food in feeding stations located 50–100 m from the den site. The supplemental food is mainly used by the foxes when the availability of natural food is low (Thierry et al., 2020).

2.2. Tourism disturbance and guided arctic fox safari tours

Helagsfjällen is a popular area for recreational activities such as hiking, backcountry skiing and small game hunting. The Swedish Tourist Association (Svenska Turistföreningen) runs several tourist mountain huts in the area with approximately 65,000 (2015) accommodated stays per year (Jämtland Härjedalen Turism, 2015). An extensive network of hiking and skiing trails connects the tourist mountain huts. One tourist hut operates guided arctic fox safari tours to an inhabited den site. The number of participants has increased rapidly since the start in 2011 to between 80 and 120 persons per summer. Since the arctic fox is endangered in Sweden, the location of the dens is confidential and the tours operate with special permission from the County Administration Board (Länsstyrelsen Jämtlands Län in Eide, 2015). When the study was conducted, tours were held up to two times per week during July - September, which corresponds to the time when juveniles are present at the den. A maximum of 8 participants were allowed per tour and they could stay by the den site for no longer than 4 h. The tour was led by a guide who provided information about arctic fox biology and the mountain ecosystem and made sure the disturbance to the foxes was kept to a minimum. The group observed the den from a predetermined spot approximately 300 m away from the den using spotting scopes (Fig. 1b). The observation spot was located on a hillside facing the den and was visible from the den. The group typically arrived at the den between 10:00 – 11:00 in the morning and stayed for 3 – 4 h.

All dens used in this study were classified as either disturbed or undisturbed by tourism activities based on their distance to trails and tourist mountain huts according to the same definitions used in previous studies within the same population (Larm et al., 2020a, 2020b). Dens located within 1 km of a hiking trail and/or within 2 km of a tourist mountain hut were classified as disturbed (n = 4) and the other dens as undisturbed (n = 2) by tourism activity. Among the disturbed dens, two dens were exposed to a high intensity of tourism activities (den A and B, Table 1). Den A was located close both to a well-used hiking trail and a well-visited tourist mountain hut around which many people made day hikes, while den B was visited by the guided tours and was also located close to a tourist hut. The two other disturbed dens (den C and F, Table 1) had a moderate intensity of tourism activity because they were both located far from a tourist hut, but within 300–350 from hiking trails used daily during the study period. The two undisturbed dens (den D and E, Table 1) were located far from both hiking trails and tourist huts and therefore experienced a low intensity of tourism activity.

2.3. Confounding factors

Predation, competition and food availability are all factors with potential to influence the responses of the foxes towards the disturbance from tourism activities. The main predator of arctic foxes, golden eagles, move easily over vast areas and could therefore be assumed to be evenly distributed over the relatively small Helagsfjällen area. However, eagles have been found to be less abundant in areas with high human activity (Kaisanlahti-Jokimäki et al., 2008). A higher summer survival of juvenile arctic foxes was also recorded at dens in close proximity of tourism activities during years of high arctic fox predation, presumably as an effect of the human activity creating a predator refuge (Larm et al., 2020b). The competition for food and den sites can be expected to decrease with increasing altitude, since the abundance of the main competitor, the red fox, is highest at

Fig. 1. Photos of the camera monitoring and the guided arctic fox safari tours. a) Automatic wildlife cameras used to monitor the activity of the arctic foxes at the den site were placed to cover the most active part of the six monitored dens. b) A group of tourists on an arctic fox safari tour watching the tour den through spotting scopes (Den B) from the observation spot located approximately 300 m. from the den.

Table 1
Information about the dens used in the study and overview of the three different datasets.

Year	Den	Hiking trail	Tourist hut	Guided tours	Disturbance category	Altitude (m.a.s.l.)	Productivity (NDVI)			
2015	A	750 m	1,8 km		High	1073	0.47			
2015	B	1,2 km	2 km	X	High	1017	0.65			
2015	C	350 m	6.5 km		Moderate	1142	0.52			
2015	D	2,3 km	7.9 km		Low	989	0.66			
2015	E	3,8 km	7 km		Low	1182	0.52			
2016	B	1,2 km	2 km	X	High	1017	0.65			
2016	F	300 m	5 km		Moderate	1037	0.65			
2017	A	750 m	1.8 km		High	1073	0.47			
2017	B	1,2 km	2 km	X	High	1017	0.65			
2017	F	300 m	5 km		Moderate	1037	0.65			
2017	D	2,3 km	7.9 km		Low	989	0.66			
		Dataset I			**Dataset II**				**Dataset III**	
Year	Den	Days	Photos day	Photos night	Tour days Days	Photos	No tour days Days	Photos	Tours	Observations
2015	A	38	7581	2340						
2015	B	55	10,803	2198	12	2785	37	9173	13	460
2015	C	30	7166	583						
2015	D	40	11,253	3522						
2015	E	43	9550	2243						
2016	B	41	8012	1650	3	812	12	3022	5	187
2016	F	27	5699	1575						
2017	A	8	1530	313						
2017	B	52	11,975	2204						
2017	F	53	11,264	3700						
2017	D	16	1696	549						

lower altitudes closer to the tree line (Herfindal et al., 2010). The abundance of the most important prey species, the Norwegian lemming (*Lemmus lemmus*) is on a territory scale negatively related to the primary productivity (Le Vaillant et al., 2018). To control for potential confounding effects of competition and availability of natural prey on the responses of the arctic foxes to tourism activity, we use the altitude of the den site as a proxy for red fox abundance and productivity (normalized difference vegetation index, NDVI, Erlandsson, 2019) within a circular area with a radius of 1 km around the den site as a proxy for availability of natural prey.

2.4. Camera monitoring and handling of photos

We used automatic wildlife cameras to monitor the activity of adult and juvenile arctic foxes at six different dens with variable levels of disturbance during July – August in 2015 – 2017 (dataset I; Fig. 1a; Table 1). All dens were not monitored all years and only dens with an arctic fox litter were included in this study, because foxes without a litter are not bound to a den in the same way as foxes rearing juveniles. The cameras were positioned to cover the most active part of the dens and set to take one photo every fifth minute throughout the day and night. Photos where the whole or parts of the monitored area was not visible due to either technical errors or natural factors like fog, rain, snow or high grass were excluded. Activity was defined as presence of foxes in the photo (yes/no) and the activity level was measured for adults and juveniles separately based on the proportion of photos with fox activity. All photos with adult activity were categorized according to the behaviors displayed by the adult/adults present in the photo. The behaviors were categorized as resting (lying with head down), vigilant (lying with head up or sitting) or moving (standing or moving). If more than one adult fox were present in a photo, it was categorized according to the fox with the highest vigilance level.

We also compared the distribution of the adult activity between daytime and nighttime, where we defined daytime as the time between dawn and dusk (3 am – 22 pm in July and 4 am – 21 pm in August). We calculated an index value of the distribution of the activity between day and night for each day based on the proportion of photos with fox activity during day and night (activity during day / activity during day + activity during night). Calendar days with less than five valid photos from either day or night were excluded from the analyses. Days with no activity at all were also excluded because it was not possible to calculate a proportion between day and night for those days.

A subset of the photos from the den visited by the guided tours (Den B) during 2015 and 2016 (dataset II; Table 1) were used for comparisons of activity and behaviors between days of high-intensity tourism activity (days with a tour) and days of lower-intensity tourism activity (days with no tour). The tour days start at 10:00 on a day with a tour and last for 24 h until 10:00 the following day.

2.5. Observations during the tours

We used a specific dataset from 2015 and 2016 collected at a den of high intensity tourism (den B). Here, the activity of both tourists and foxes were observed every fifth minute during the guided tours (dataset III; Table 1) according to a method previously used by Erlandsson et al. (2017). In 2015, the same guide performed all tours and observations, while in 2016, another person was trained by the guide to perform the observations. For the tourists, noise and movement levels were scored on a scale from 1 to 3 at each observation. For the noise level, score 1 was used for quite tourists, score 2 for tourists talking quietly, and score 3 for tourists talking loudly. For the movement level, score 1 was used for minimal movements, score 2 for movements while sitting down and score 3 for when someone was standing or walking around. The noise and movement levels were strongly correlated and they were therefore later combined to a tourist disturbance level between 2 and 6. For the observations of fox activity, the number of adult and juvenile foxes were noted every 5th minute in the same way as for the photos. A total of four different adult individuals inhabited the den during 2015 and 2016.

2.6. Detectability assessment

To assess how well the cameras detected activity, we compared the presence of adult and juvenile foxes in the photos with the direct observations during the tours at the tour den. It was assessed at two different scales, both how much of the total adult and juvenile activity that was captured by the cameras and how well they could detect whether there were any adults and juveniles present at the den or not.

2.7. Permits and handling of animals

The fieldwork and handling of animals was conducted in accordance with Swedish law and was approved by the Swedish Board of Agriculture (Jordbruksverket) and Swedish Environmental Protection Agency (Naturvårdsverket; permit NV-01959–14). Ethical permits were given by an ethical board (Umeå djurförsöksetiska nämnd; permits A18–14 and A19–14).

2.8. Statistical analyses

All analyses were performed in R version 3.6.2 (R Core Team, 2019) and RStudio version v1.2.5033 (R Studio, 2019). To identify potential confounding effects of competition and food availability, altitude and productivity (NDVI values) were compared between disturbed and undisturbed den sites using *t*-tests.

We compared the proportion of activity spent during day and night using linear mixed effect models. For the between den comparison (dataset I), the proportion of activity spent during daytime was used as the response variable, the tourism disturbance level of the den (High/Low) as fixed effect and den was set as a random effect because the same dens were used for several years. For the comparison between tour days and no tour days at the tour den (dataset II), the same response variable was used, but with tour day or no tour day as the fixed effect and year (2015 or 2016) as random effect.

We analyzed the behavioral differences between dens for each day (dataset I), i.e. the proportional display of the different behaviors (resting, vigilance and moving). The proportion of the different behaviors were then compared using linear mixed effect models with tourism disturbance level (High/Low) as fixed effect and den as random effect. Behavioral differences between tour days and no tour days at the tour den (dataset II) were analyzed in the same way, but with tour day/no tour day as fixed effect and year (2015 or 2016) as random effect.

The responses of the foxes to the tourists were analyzed using three different probability estimates of juvenile and adult activity in relation to the disturbance level from the tourists. The estimates were based on observations during a tour in dataset III (tourist disturbance level 2–6) and camera photos in dataset II taken during a tour (tourist disturbance level 2–6) as well as camera photos taken both during a tour and during tour time (10:00 – 14:00) on days with no tour (tourist disturbance level 0–6). To estimate the probability of fox activity depending on the disturbance level of the tourists, we used generalized linear models for adults and juveniles separately. Presence of adult or juvenile foxes (yes or no) from either observations or camera photos was used as a binomial response variable and the disturbance level of the tourists (0–6 or 2–6) was used as the explanatory variable. During days with no tour, the tourist disturbance level was set to 0.

The disturbance level of the tourists in dataset III was compared between observations when there were no foxes active, when only adults were active and when juveniles were active using a linear model with tourist disturbance level during a tour (2–6) as the response variable and presence of adults (yes or no) and presence of juveniles (yes or no) as explanatory variables.

3. Results

3.1. Comparison of activity and behaviors between disturbed and undisturbed dens, dataset I

There were arctic foxes active in 12–36% of all valid camera photos ($n_{photos} = 107{,}406$, Table 1) from the six different dens during 2015–2017 ($n_{dens} = 11$). The adult foxes at disturbed dens ($n_{dens} = 8$) spent a higher proportion of their activity at the den during daytime than during nighttime, while the adult foxes at undisturbed dens ($n_{dens} = 3$) had a more even distribution of their activity at the den between day and night (Fig. 2). The activity index of the proportion of adult fox activity spent during the day was 71 ± 3.9% [LMER estimate ± SE] at disturbed dens and 53 ± 6.2% at undisturbed dens (likelihood ratio: $\chi^2_{[1]} = 7.58$, $P = 0.006$).

The distribution of time spent on the different activities was not related to the level of disturbance from tourism activities. The adult foxes at disturbed dens spent 21 ± 3% of their active time at the den resting, 59 ± 3% vigilant and 20 ± 3% moving. At undisturbed dens, the adult foxes spent 14 ± 5% of the active time at the den resting, 66 ± 5% vigilant and 19 ± 5% moving (vigilant: $\chi^2_{[1]} = 0.69$, $P = 0.4$, resting: $\chi^2_{[1]} = 0.25$, $P = 0.6$, moving: $\chi^2_{[1]} = 0.41$, $P = 0.5$).

3.2. Comparison of activity and behaviors between tour days and no tour days at the tour den, dataset II

Focusing on the photos from the den visited by guided tours (den B, Table 1) during 2015 and 2016 we compared the activity and behavior of the adult foxes between days when the den was visited by a guided tour and days with no tour. During tour days ($n_{days} = 15$), the adult foxes were active in 22 ± 4% [LMER estimate ± SE] of the photos, which did not differ from days with no tour ($n_{days} = 49$), when the activity level was 27 ± 20% (likelihood ratio: $\chi^2_{[1]} = 1.47$, $P = 0.23$).

Further, there was no difference in the distribution of the activity during day and night between tour days ($n_{days} = 10$) and days with no tour ($n_{days} = 43$). The activity index value of the proportion of adult fox activity spent during the day was 75 ± 11% [LMER estimate ± SE] during tour days and 71 ± 10% during no tour days ($\chi^2_{[1]} = 0.13$, $P = 0.7$).

During 2015 and 2016, the adult foxes at the tour den spent 48% of the active time vigilant, 38–40% resting and 11–14% moving. There was no difference between tour days (n_{days}=11) and no tour days ($n_{days} = 46$) in the proportion of active time the adult foxes spent vigilant ($\chi^2_{[1]} = 1.40$, $P = 0.24$), resting ($\chi^2_{[1]} = 2.48$, $P = 0.12$) or moving ($\chi^2_{[1]} = 0.08$, $P = 0.78$).

3.3. Responses of arctic foxes and tourists to each other during a guided tour, dataset III

Based on the parallel observations of foxes and tourists from the tour den in 2015 ($n_{tours} = 13$), the probability of fox activity during a tour was found to be positively related to the disturbance level of the tourists, for both adult and juvenile foxes (Fig. 3). The three different probability estimates of juvenile and adult activity in relation to the disturbance level from the tour were based on observations during the tour (disturbance level 2–6; $n_{obs} = 460$) and camera photos taken both during a tour (disturbance level 2–6; $n = 677$) and between 10:00 – 14:00 during days when there was no tour (disturbance level 0–6; $n = 2870$). The probability estimates of fox activity based on observations were highest for both adults and juvenile foxes as they capture all activity, while camera photos capture a large part, but not all, of the activity. The probability of juvenile fox activity was positively related to the tourism disturbance level for all three estimates, observations during a tour (likelihood ratio: $\chi^2_{[1]} = 7.05$, $P = 0.008$, $r = 0.26$), camera photos taken during the same tours (likelihood ratio: $\chi^2_{[1]} = 9.59$, $P = 0.002$, $r = 0.32$) and camera photos from both days with and with no tour (likelihood ratio: $\chi^2_{[1]} = 14.02$, $P < 0.001$, $r = 0.10$). For the adults, the probability of activity followed the same pattern for the estimates based on observations during a tour (likelihood ratio: $\chi^2_{[1]} = 3.83$, $P = 0.05$, $r = 0.18$) and from camera photos taken during both tour and no tour days (likelihood ratio: $\chi^2_{[1]} = 4.04$, $P = 0.044$, $r = 0.16$), but not for camera photos taken only during the time of a tour (likelihood ratio: $\chi^2_{[1]} = 1.14$, $P = 0.28$, $r = 0.09$). The small sample of observations from 2016 (n_{tours}=5, $n_{obs} = 187$), shows a similar pattern (Fig. 4).

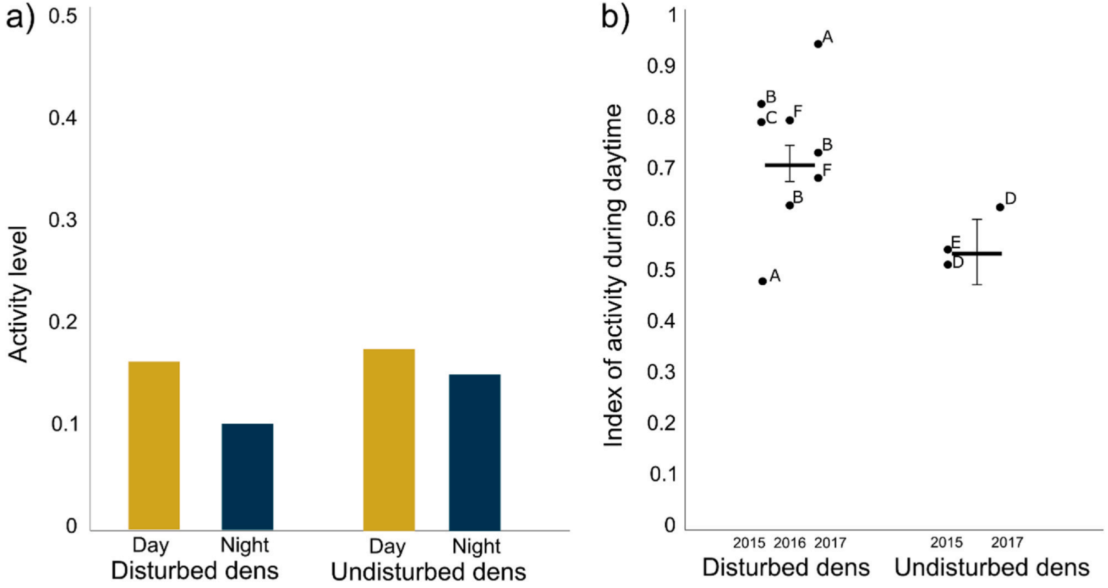

Fig. 2. Adult arctic fox activity at dens disturbed and undisturbed by human activity. a) Mean proportion of photos from day and night with adult arctic fox activity for disturbed and undisturbed dens. b) Index value of the activity spent during daytime (LMER estimate ± SE) at dens disturbed and undisturbed by human activity. The dots represent the mean index value of the different dens and years. A value of 0.5 means that the activity was equally high during both day and night, while a lower index value means that the foxes were active in a higher proportion of the photos during the night compared with the day.

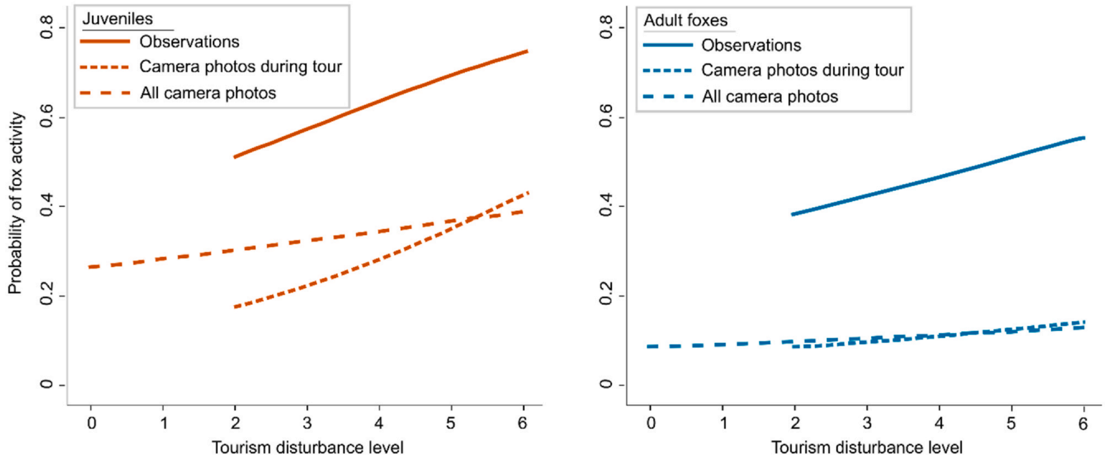

Fig. 3. Three different probability estimates of adult and juvenile arctic fox activity with increasing disturbance level of the tour group during 13 guided tours in 2015. Solid lines are based on observation during the tour, short dotted lines (from 2 to 6) are based on camera photos taken during the tours and long dotted lines (from 0 to 6) are based on camera photos from all days during tour time (10:00 – 14:00), where disturbance level 0 is based on days with no tour.

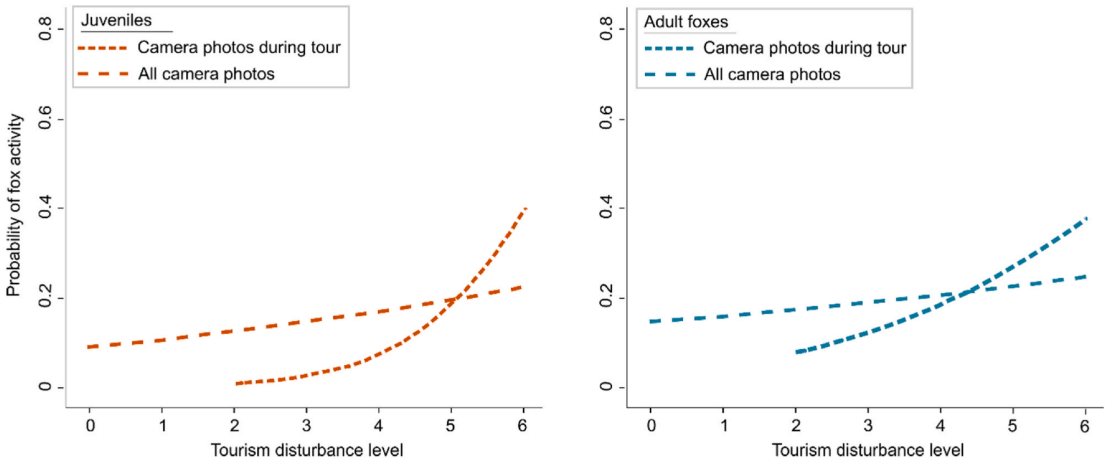

Fig. 4. Probability estimate of adult and juvenile arctic fox activity with increasing disturbance level of the tour group during 5 guided tours in 2016. Short dotted lines (from 2 to 6) are based on camera photos taken during the tours and long dotted lines (from 0 to 6) are based on camera photos from all days during tour time (10:00 – 14:00), where disturbance level 0 is based on days with no tour.

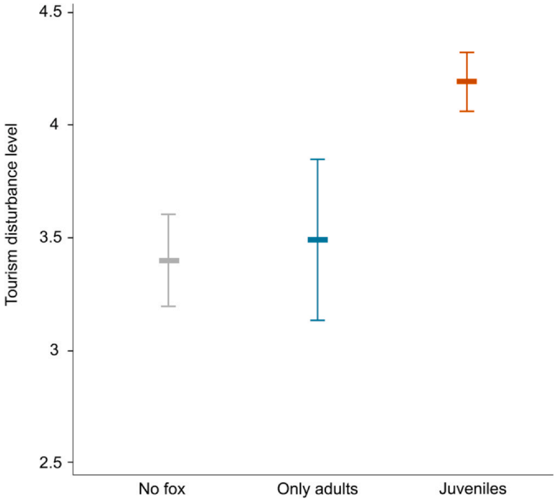

Fig. 5. The disturbance level (mean ± 95% CI) of the tourists was higher when juvenile arctic foxes were active relative to when no foxes were active and when only adults were active.

The disturbance level of the tourists also varied with the activity of the foxes, the disturbance level for the tour group was 3.49 ± 0.2 [95% CI] when no foxes were present at the den, 3.57 ± 0.34 when only adults were present and 4.26 ± 0.13 when juveniles were present (Fig. 5). The difference in disturbance level was not significantly different when only adults were present ($n_{obs} = 48$) compared with when no foxes were present ($n_{obs} = 161$) at the den ($F_{[1]} = 0.788$, $P = 0.37$), but when juveniles were present ($n_{obs} = 251$) the disturbance level was higher ($F_{[1]} = 3.97$, $P = 0.047$).

3.4. Detectability assessment

By comparing the camera photos and observations during a tour (n = 460), we found that the cameras detected 56 ± 5% [95% CI] of all adult activity during that time and could determine whether there was any adult activity or not (regardless of how many adults were active) 59 ± 5% of the time. For the juveniles, 55 ± 4% of all activity was detected and the photos could determine 65 ± 5% of the time whether any juveniles were present on the den or not.

The results of the three different estimated probabilities for fox activity, based on observations and camera photos, show the same positive relationship with the disturbance level from the tours for both adults and juveniles. That indicates that the cameras detect a representative sample of the activity and can be used to study relative differences in activity, but that the absolute amount of activity will be underestimated (Fig. 3).

3.5. Confounding factors

The altitude of the den site and primary productivity of the territory was compared between disturbed and undisturbed dens to control for potential confounding factors of competition and food availability, but no differences were found. The mean altitude was 1067 and 1086 m.a.s.l. for the disturbed dens and the undisturbed dens respectively ($t = -0.25$, $P = 0.81$) and the mean productivity value (NDVI) was 0.57 and 0.59 for the disturbed dens and the undisturbed dens respectively ($t = -0.20$, $P = 0.85$).

4. Discussion

The objective of this study was to investigate activity and behavioral responses of arctic foxes towards varying levels of tourism disturbance at a key site. In concordance with our predictions, we found that adult arctic foxes in areas of high intensity tourism activity spent a larger proportion of their total activity at the den during daytime, compared with foxes in areas of lower intensity of tourism activities. There was, however, no difference in the distribution of the activity between day and night during days of high intensity tourism compared with days of lower intensity tourism at the den visited during the guided tours. This suggests that the foxes adapt their activity pattern temporally to an anticipated tourism disturbance rather than in direct response to a disturbance event. The shift to a higher activity during daytime at the disturbed dens compared with undisturbed dens indicates that the adult foxes perceive the human presence as a potential threat and are not comfortable leaving the den site during daytime, when the risk of disturbance from tourism activities is the highest. If the distribution of activity over the day at undisturbed dens is assumed to result in an optimal trade-off between hunting, guarding and resting, it is possible that the shift to a higher daytime activity at the den site could compromise hunting and food provisioning of arctic foxes in areas of high intensity tourism.

However, several different factors could affect that trade-off. In another study area in Sweden, arctic foxes have been observed to abandon their natal dens in response to human disturbance and to a red fox attack (Elmhagen et al., 2014). Moving to avoid disturbance would be a costly response for the arctic foxes as they use already established large dens, which are located several kilometers apart (Angerbjörn et al., 1997). It can thus be challenging to find a new den site of equal quality, especially during a year of high small-rodent abundance when most high-quality dens are already occupied. In Helagsfjällen, where this study was conducted, such spatial responses to human disturbance have not been observed. Instead, despite the disturbance from tourism activities, the arctic foxes have remained in areas of high intensity tourism and the dens with the highest levels of tourism disturbance have been among the most productive in the mountain region (Swedish Arctic Fox Project, 2019). A previous study even found that arctic fox juveniles at disturbed dens had a higher summer survival during years of high predation on arctic foxes, possibly due to the human activity creating a predator refuge (Larm et al., 2020b). A lower predation pressure could contribute to the quality of the den site, making the trade-off of leaving even more costly, which could further explain the temporal rather than spatial shift in activity observed in this study. It is possible that a reduced predation pressure could explain why arctic foxes at disturbed dens did not display more vigilant behaviors, compared with foxes at undisturbed dens.

There was no difference in altitude or productivity of the den sites, which were used as proxies for red fox presence and food availability respectively, between the disturbed and undisturbed dens included in this study. However, even though the food availability is fairly similar between dens, there are large variations between years as the small-rodent abundance fluctuates in 3–4-year cycles (Stenseth, 1999). The availability of natural food could be an important factor affecting the trade-off between protecting the juveniles and foraging, where the cost of remaining at the den would be greater during years of low food abundance. However, even though the foxes prefer natural prey when available, the supplemental feeding reduce the variation in juvenile physical condition between years of varying small-rodent abundance (Tannerfeldt et al., 1994) and likely also the cost of reduced hunting intensity. The supplemental feeding thereby makes it difficult to evaluate potential fitness consequences of the human disturbance, as it could mitigate potential negative effects on foraging and food provisioning for juveniles. However, due to the supplemental feeding, the food availability is not likely to cause the differences observed in this study, but if it would be reduced or stopped in the future, the effect of tourism disturbance on the arctic foxes may increase, especially during years of low small-rodent abundance. Given the relatively small sample sizes in this study, it would be valuable to extend the spatial and temporal sampling, both to validate the results and to investigate potential effects of the small-rodent phase and the supplemental feeding.

The temporal shift in activity to a higher proportion of activity spent during daytime stands in contrast to the general shift towards increased nocturnality in response to human activity found by Gaynor et al. (2018), as well as to the increased nocturnality observed in arctic foxes in Svalbard in response to snow mobile traffic during winter (Fuglei et al., 2017). However, our study was conducted during the breeding season and on foxes with a litter at the den site. During the winter the arctic foxes do not have juveniles to protect and provide for and the snow mobile traffic was not focused to the denning sites. The difference can thus likely be explained by the larger trade-off needed to leave a key site than to just avoid a site with human activity together with other factors influencing the cost of the trade-off. That interpretation is in concordance with the higher tolerance towards approaching humans observed in wolfs with site-dependent pups (Wam et al., 2014) and breeding bald eagles (Steidl and Anthony, 1996), compared with their non-breeding conspecifics.

Changes in activity were also observed during the guided tours at the tour den, where the probability of both juvenile and adult presence at the den increased when the disturbance (noise and movement) from the tourists increased. There was, however, no difference in vigilant behaviors displayed by the adult arctic foxes between tour days and no tour days. In a previous study within the same arctic fox population, most foxes at disturbed dens were not behaviorally affected by human presence at 300 m from the den, which is the distance that is kept during a guided tour (Larm et al., 2020a). However, that study was conducted by a single observer walking silently towards the den to increase the disturbance. During a guided tour, the group is stationary at the observation spot located approximately 300 m from the den, the disturbance instead consists of the noise and movement level of the group (Knight and Cole, 1995). In the human approach study, the responses of the adult foxes increased with the increasing disturbance as the observer approached the den (Larm et al., 2020a). However, in contrast to the increased presence of the arctic foxes at the den with increasing disturbance from the tour group, the foxes instead hid or fled when they were approached by the observer. This shows that the distance kept to the arctic foxes and their den site is a key component in reducing disturbance and emphasizes the importance of keeping a minimum distance of 300 m to the den site, especially with other factors, such as noise and movement, potentially increasing the disturbance. Further, it is possible that the foxes have become habituated to the disturbance caused by the tours as they have learned that the group will stay at the observation spot and behave in a predictable way. However, even though a higher tolerance towards humans could be a result of habituation in areas of high-intensity tourism, it could also have other explanations, such as that bolder foxes inhabit dens in more disturbed area. To confirm whether it is due to habituation, repeated monitoring of tolerance levels over time would be needed (Bejder et al., 2009).

For the tour participants, the disturbance level was higher when juveniles were present at the den relative to when only adults were present. Based on experiences from the guided tours, the increased noise and movement is due to excitement watching the juvenile foxes play at the den. At zoos, the interest of the tourists has also been found to increase for example when juvenile animals are present and when watching a charismatic or rare species (Patterson and Bitgood, 1988). We have previously found that participation in a guided arctic fox safari tour increased the knowledge and awareness of the conservation work and behavioral guidelines for the arctic foxes (Larm et al., 2018), but it is not known whether that translated into actual behavioral changes in the tour participants. However, positive emotions in connection to a wildlife experience, as seen in the tour participants in this study, can facilitate both attitudinal and behavioral changes, especially those connected to the specific wildlife and environment of the experience (Orams, 1997; Ballantyne et al., 2007). Tour guides also play a crucial role, both by educating and acting as role models for the appropriate attitudes and behaviors (Littlefair and Buckley, 2008; Apps et al., 2015). With the current trend in wildlife tourism from eco-tourism to ego-tourism (Granquist et al., 2019), the wish to get close encounters with the animals and take photos for remembering and showing the experience to others directly or through social media often transcends the willingness to not disturb (Shutt, 2014). Targeted education, eg. through a guide, can then also be important to give the visitors appropriate expectations and perceptions of the experience, as well as to enhance the experience and connection without disturbing the animals (Schänzel and McIntosh, 2000; Shutt, 2014; Dybsand, 2020).

A similar relationship as the one between foxes and tourists has also been found in harbor seals (*Phoca vitulina*) in Iceland, where the presence of seals affected the behaviors of the tourists at a seal viewing site and as the disturbance caused by the tourists increased, the strength of the behavioral responses of the animals also increased until they finally decided to take flight (Granquist and Nilsson, 2016). Such feedback mechanisms could enhance both positive and negative effects, but would be difficult to detect if both perspectives were not considered simultaneously (Liu et al., 2007; Shutt, 2014; Granquist and Nilsson, 2016; Muntefering et al., 2019). Knowledge about behavioral effects on both wildlife and tourists are also important for constructing codes of conduct that target the actual problems and find appropriate and effective solutions (Granquist and Nilsson, 2016; Muntefering et al., 2019). The development of sustainable wildlife tourism practices would benefit from more interdisciplinary studies, as minimizing negative effects on wildlife and the environment, while ensuring visitor satisfaction, are both key factors (Reynolds and Braithwaite, 2001). The value of biodiversity conservation for human health and possibilities for recreation is also not to be underestimated, as economic and psychological incentive for protecting natural areas often render more support than the intrinsic values of nature and wildlife themselves (Schänzel and McIntosh, 2000; Trombulak et al., 2004).

5. Conclusions

The temporal shift towards a higher daytime activity at the den in response to high intensity tourism activity observed in this study stands in contrast to the increased nocturnality seen in many other species, including another study of arctic foxes in a different context. This suggests that temporal activity shifts may differ depending on whether the disturbance takes place at a key site for the studied animal, as in this study, or if it is a more general human disturbance in an area within the distribution range of the animal, such as a tourist resort or hiking trail. Given the larger trade-off of leaving a key site, human disturbance focused at for example a denning or breeding site, can be expected to have larger consequences than what is observed in most studies of disturbance effects on wildlife.

Based on this and previous studies within the same population, we can further conclude that there is a mutual relationship between arctic foxes and tourists with both direct and indirect effects in both directions. The potential for positive or negative feedback mechanisms in such relationships between tourists and wildlife highlights the importance of considering both sides simultaneously. As both minimizing negative effects on the animals and environment and ensuring visitor satisfaction are important for a wildlife tourism activity to be sustainable, these are promising results since sustainable practices benefit both the wildlife and environment as well as humans through the recreational value of such experiences. The challenge is to adjust the tourism activities in such a way so that positive feedback loops between wildlife and tourists can balance negative effects.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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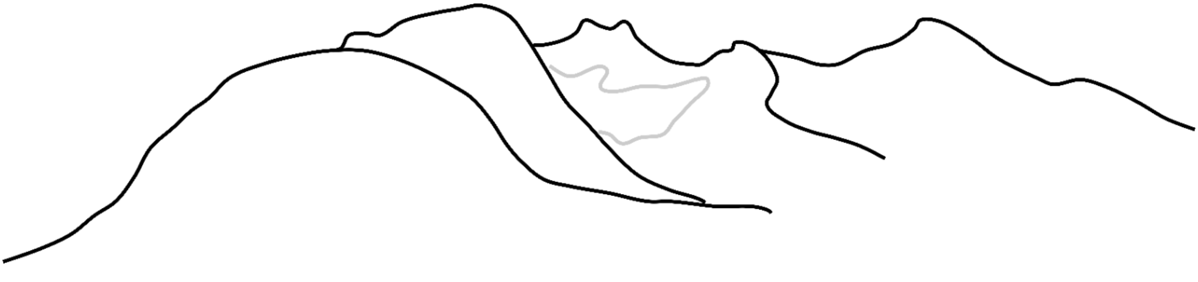

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Fitness effects of ecotourism on an endangered carnivore

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Keywords
carnivore conservation; ecotourism; fitness; predator refuge; researcher disturbance; tourism disturbance; tourism management; wildlife tourism.

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Abstract

Nature-based recreational and tourism activities can exert significant direct and indirect impacts on wildlife, through behavioral, physiological and distributional changes. Despite many studies demonstrating such changes, few attempts have been made to quantify the fitness consequences and evaluate their biological significance. Helagsfjällen in Sweden is a core area of the endangered Fennoscandian arctic fox *Vulpes lagopus*, and a popular area for recreational tourism. Some dens in the area experience daily disturbance from tourism during the summer season, while others are virtually undisturbed. We used a long-term dataset (2008–2017) of 553 juveniles in 74 litters to investigate summer juvenile survival, which is an important fitness component for the arctic fox. We found that the mean juvenile survival rate increased from 0.56 at undisturbed dens to 0.83 at disturbed den during years of decreasing small-rodent abundance, where predation on the arctic fox is presumed to be highest. We suggest that the increased survival could be mediated by a human activity-induced predator refuge for the arctic foxes in close proximity of trails and mountain huts. Our study demonstrates a possible positive indirect effect of nature-based tourism on wildlife and is one of a few studies attempting to quantify this impact. It highlights the importance of context for how animals are affected by disturbance. We also demonstrate that studying how the effects of tourism activity vary depending on the context could provide opportunities for identifying the mechanisms behind these effects, which can be an important link between scientific research and the management of wildlife and tourism activities.

Introduction

Nature-based recreational activities like wildlife tourism can exert both significant positive and negative impacts on wildlife (Czech, Krausman & Devers, 2000). Impacts can be either direct or indirect and affect animals on a scale from individuals to entire populations and ecological communities (Higginbottom, Northrope & Green, 2001). The interest for recreational and tourism activities in natural areas is increasing rapidly worldwide and many visitors are seeking more and more intense experiences at remote locations (Snyder, 2007; Geffroy *et al.*, 2015). Even non-consumptive activities like wildlife watching may cause disturbance and can be intrusive in the sense that they have an explicit focus on exploring nature and wildlife that often have little previous experience of humans. In addition, tourism activities tend to target charismatic species that are rare and/or endangered (Reynolds & Braithwaite, 2001). On the other hand, organized tourism activities in natural areas often incorporate conservational and educational features with potential to generate positive effects to compensate for disturbance. Such positive effects could, for example, be economic contributions from wildlife tourism, which is crucial for conservation of many species worldwide. It can also provide income for local communities, increasing the incentive to support protection of biodiversity and avoid more exploitative land uses (Jones, Diggle & Thouless, 2015; Buckley, Morrison & Castley, 2016).

Several previous studies have found that tourism can affect individual animals directly and indirectly by inducing behavioral, physiological and distributional changes (Le Corre, Gélinaud & Brigand, 2009; Benítez-López, Alkemade & Verweij, 2010; Penteriani *et al.*, 2017). The direct effects on individual animals are typically negative or neutral (Higginbottom *et al.*, 2001). Changes in behavior or physiology could compromise activities like foraging and parental care, with potential fitness consequences. If tourism activity causes individuals to leave disturbed areas, it could affect the distribution and demography of the population (Frid & Dill, 2002; Bejder *et al.*, 2006). The impact of a disturbance on individual animals is, however, context-dependent and may vary according to several context-related factors, such as food availability, time of year and group composition as well as the sex, age, previous experience with humans, physical condition and personality traits of the individual (Knight & Cole, 1995; Gill, Norris & Sutherland, 2001; Bejder *et al.*, 2006).

In contrast, effects of tourism activity on a population or ecological community level are generally more indirect and can be either positive, negative or neutral (Buckley, 2009). Effects on one species could indirectly affect other interacting species (Higginbottom *et al.*, 2001; Leighton, Horrocks & Kramer, 2010). For example, it could alter the interaction dynamics between competitors or predators and prey if their susceptibility and responses to the activity differ (Dill, Heithaus & Walters, 2003; Smith *et al.*, 2018). It would then benefit the more tolerant species by reducing the competition for resources or creating a predator refuge through spatial and/or temporal displacement of predators (Leighton *et al.*, 2010; Muhly *et al.*, 2011).

Despite relatively good knowledge of the different ways in which tourism activity may exert an impact on wildlife, few studies have attempted to quantify fitness consequences and evaluate their biological significance for population demography (Nevin & Gilbert, 2005*b*; Griffin *et al.*, 2007; Buckley *et al.*, 2016). One exception is the study by Penteriani *et al.* (2017) on brown bears *Ursus arctos* in North America, which includes several simultaneous effects as well as investigations of fitness consequences. The disturbance effects varied between different groups of bears and depended for example on the availability and quality of alternative feeding sites. However, despite potential negative effects on the fitness of individual bears, no negative effect was found on their population demography (Nevin & Gilbert, 2005*a*,*b*). Such empirical knowledge allows informed decisions around the management of wildlife as well as of wildlife tourism activities. Studying fitness consequences may be of particular importance for small and endangered populations, where even small impacts on population size and demography could be of significance for the viability of the population.

In Fennoscandia, the endangered arctic fox *Vulpes lagopus* (Swedish Red List, 2015) inhabits the tundra regions of the Swedish and Norwegian mountains. Like many mammal and bird species in the tundra, they have a fluctuating population dynamic, closely connected to the cyclic abundance of small rodents (Ims & Fuglei, 2005; Angerbjörn *et al.*, 2013; Fig. 1). Arctic fox litter sizes in Fennoscandia varies between 1 and 18 weaned juveniles in accordance with the abundance of small rodents (Angerbjörn *et al.*, 1995). During years of high small-rodent abundance, predator populations in the tundra flourish, among them the arctic fox, red fox *Vulpes vulpes*, wolverine *Gulo gulo*, golden eagle *Aquila chrysaetos* and white tailed eagle *Haliaeetus albicilla* (Kaikusalo, 1982; Landa *et al.*, 1997; Ims & Fuglei, 2005; Nyström *et al.*, 2006). Following a small-rodent peak, the decline is often abrupt (Turchin *et al.*, 2000) and the large carnivore populations need to switch their diet to other food sources (Landa *et al.*, 1997; Nyström *et al.*, 2006). The arctic fox is a mesopredator in the tundra ecosystem and a potential prey species for the larger predators. During years of declining small-rodent abundance, entire litters of arctic fox juveniles can be killed by golden eagles (M. Larm & A. Angerbjörn, pers. obs.). Furthermore, the interactions between the arctic fox and its superior competitors and potential predators, red foxes and wolverines (Tannerfeldt & Angerbjörn, 1996), could increase as they are attracted by supplemental food provided for the arctic foxes at the den sites as a conservation measure (Stoessel *et al.*, 2018). Consequently, as the small-rodent cycle affects the abundance of both predators and alternative prey species, it also affects the dynamic of the intra-guild interactions.

The aim of this study was to quantify the impact of nature-based tourism activity and researcher presence on the fitness of an arctic fox population in the Swedish mountain tundra. We investigated the effect on summer survival of juveniles, which is a crucial fitness component as it affects the recruitment of individuals to the small population (Meijer *et al.*, 2008). We expected the survival to be context-dependent and vary between the different phases of the small-rodent cycle. The study had a pseudo-experimental setup, with dens classified as either disturbed or undisturbed by tourism activity, depending on their distance to trails and tourist mountain huts, and with prey availability and predation pressure varying between years. Supplemental food has previously been shown to improve physical condition and increase survival of juveniles, especially when the availability of natural prey is low, reducing potential variations in mortality due to starvation between dens and years (Tannerfeldt, Angerbjörn & ArvidSon, 1994; Angerbjörn *et al.*, 2013). If we can confirm that there is no difference in juvenile physical condition between dens disturbed and undisturbed by tourism activities, potential variations in juvenile summer survival could likely be attributed to predation.

Materials and methods

Study system

Study area and study species

The study was conducted in Helagsfjällen (62.55 N, 12.30 E), a sub-arctic mountain area of about 3400 km^2 located in the county of Jämtland in central Sweden. The area holds the largest and southernmost arctic fox population in Sweden, consisting of approximately 40–60 adult individuals (Angerbjörn *et al.*, 2013; Swedish Arctic Fox project, personal observations). Extensive data down to the level of individual animals allow for reliable estimates of survival, which along with knowledge of tourism and other influencing factors makes the Helags arctic fox population a good model system for studying fitness effects of tourism.

The survival and causes of mortality of arctic foxes vary between years with the highly fluctuating small-rodent abundance (Meijer *et al.*, 2013; Erlandsson *et al.*, 2017). Generally, most arctic foxes die due to starvation or predation, but diseases and parasite infections can also contribute to the mortality (Elmhagen *et al.*, 2017). As no signs of disease or parasite outbreaks were observed in the area during the years of the study, we expected juvenile survival to mainly be

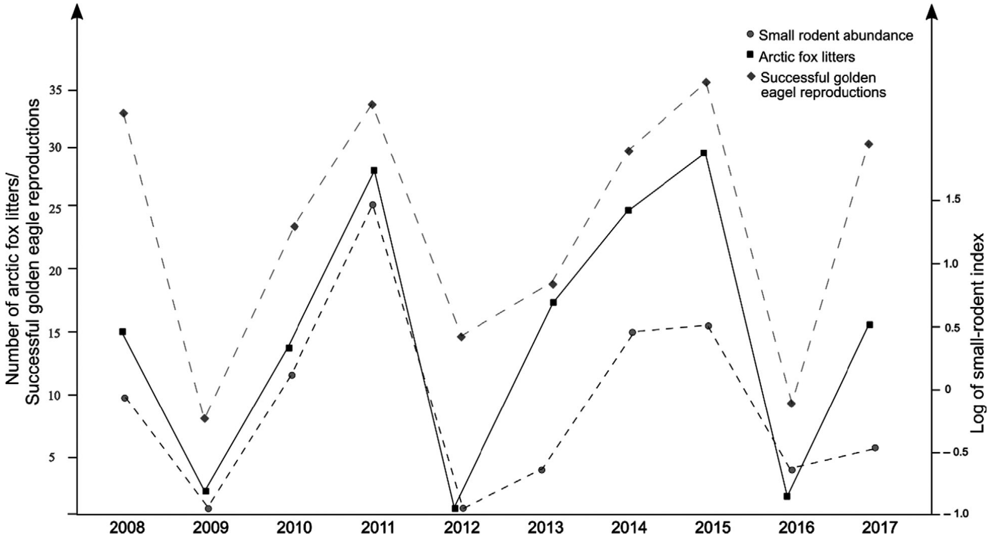

Figure 1 Small-rodent abundance and number of arctic fox litters in the Helagsfjällen area and number of successful of golden eagle reproductions in Jämtland County during the years of the study 2008–2017 (a value of 0.1 was added to the small-rodent trapping values of zero for the plotting).

related to food provisioning and predation, which, in turn, could be affected by tourism activity and researcher presence. Supplemental food was provided at all known and inhabited arctic fox den sites in the area during the study period 2008–2017. Feeding stations were located within approximately 50–100 m of the den site and were checked and refilled regularly, ensuring ad libitum access to dog food. The supplemental food is used by the foxes as a complement when the abundance of natural food is low. The amount of food consumed varies between dens and years depending on local prey availability, litter size and individual needs, thereby reducing variations in food provisioning for the juveniles (Tannerfeldt *et al.*, 1994; Angerbjörn *et al.*, 2013).

Tourism activity

Helagsfjällen is a popular area for recreational and tourism activities and the Swedish Tourist Association (Svenska Turistföreningen) runs several mountain huts in the area, connected by an extensive network of hiking and skiing trails. According to guest night data from the Swedish Tourist Association, the tourism visits in the area have increased from approximately 20 000 to 28 000 guest nights per year during the study (Swedish Tourist Association, 2008–2012; Jämtland Härjedalen Turism, 2010–2016). Based on data from trail use counters complemented by guest books and estimates by the staff at the mountain huts the trails are hiked by a minimum of zero to five (some days the weather does not allow for hiking) and up to 20–50 hikers per day during the summer season (June–September). The vast majority of hikers keep to marked trails when walking between huts, while many visitors take day hikes outside of the trails in the surroundings of the mountain huts. However, the absolute majority of the tourists are interested in the hiking and naturalistic sceneries and do not search for arctic foxes. In combination with the locations of arctic fox den sites being confidential for the sake of protecting the foxes, planned visits to den sites are fairly rare, but dens located close to mountain huts may experience accidental visits.

We classified each den site as either disturbed or undisturbed by tourism activity (Fig. 2; Supporting Information Table S1). Due to the bareness of the tundra, the range of sight can be several kilometers and the dens classified as disturbed all had a trail and/or hut within sight, which none of the undisturbed dens had. Dens classified as disturbed were all located within one km of a well-used trail and/or within two km of a tourist mountain hut. Foxes occupying those dens were estimated to see humans on a daily basis during the yearly study period July–August. The undisturbed dens were located farther than 1 km from a well-used hiking trail and more than 3 km from a mountain hut (no dens in the study were located between 2 and 3 km from a mountain hut). As the trails channel the vast majority of hikers in the area, the arctic foxes at the dens far from the trail system rarely encounter humans. Disturbed and undisturbed dens were well distributed over the study area, controlling for large-scale environmental variations such as topography. We also compared values of the altitude, productivity [normalized difference vegetation index (NDVI), Erlandsson, 2018],

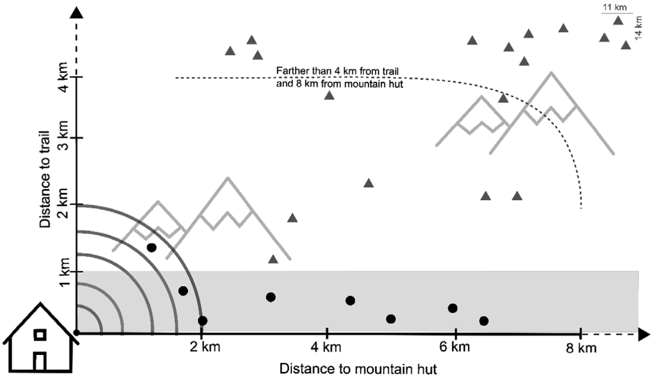

Figure 2 The location of the arctic fox dens in the study in relation to hiking trails and tourist mountain huts, around which the vast majority of the tourism activity is centered. Dens classified as disturbed by tourism activities (●) are located within 1 km of a trail and within 2 km of a hut and are all within eyesight of a trail or hut. Dens classified as undisturbed (▲) are located farther than 1 km from a trail and farther than 3 km from a hut and none of the dens is within eyesight of a trail or hut. Dens beyond the dotted line are farther than 4 km from a trail (up to 11 km) and 8 km from a hut (up to 14 km).

and litter size of each den site to detect potential confounding differences in territory quality between disturbed and undisturbed dens.

Researcher presence

In addition to tourism activity, dens were also visited by researchers and volunteers from the Swedish arctic fox project during yearly inventories. The procedure for den visits follow a standard protocol (see Elmhagen *et al.*, 2013 for a detailed description) and mainly includes observations from the tent (100–300 meters from the den) and ear-tagging. The number of days with researcher presence at each den during the yearly study period July–August depended on, for example weather, trapping success and the sort of data that were collected and varied between dens and years from 2 to 8+ days (there were only four events of eight or more days of researcher presence during the study) (Supporting Information Table S1).

Field methods

Juvenile survival

The study was based on survival data of 553 juveniles in 74 litters distributed over 26 den sites during 2008–2017, a period covering two full rodent cycles (disturbed: $n_{\text{dens}} = 8$, $n_{\text{litters}} = 29$, undisturbed: $n_{\text{dens}} = 18$, $n_{\text{litters}} = 45$, Table 1). During yearly inventories, all known den sites were visited after weaning (July) to determine occupancy and reproductive status. Following the protocol used by Meijer, Norén & Angerbjörn (2011) and Erlandsson *et al.* (2017), all breeding dens were monitored until a robust estimate of the litter size was made, approximately 24–48 h depending on weather conditions and fox activity. Most breeding dens were revisited or monitored by camera in August to estimate the juvenile summer survival (survival rate = number of juveniles in August/number of juveniles in July). As juveniles remain bound to the den throughout August, we expect all surviving juveniles to be detected. Only dens with a minimum of 3 weeks between the first and second counts were used in the survival estimates. To account for differences in time between the counts (between 21 and 66 days), the survival rate was standardized to 30 days following Krebs (1989) by calculating a daily survival rate and multiplying that by 30 days. The standardized survival rate was not related to the number of days between the counts (correlation test, $n_{\text{litters}} = 74$, $t = 1.22$, $p = 0.23$). Maternal experience has previously been shown to affect the summer juvenile survival, where litters reared by a female with previous breeding experience had a higher survival compared to litters of first-time breeders during years of high predation (Meijer *et al.*, 2011; Erlandsson *et al.*, 2017). As data on maternal experience were not available for all litters in the study, it was not possible to include in the model. To control for a potential bias, we instead compared the maternal experience between disturbed and undisturbed dens for the litters where data were available ($n = 47$ of 74 litters).

Juvenile physical condition

In connection with the yearly den inventories, juveniles were trapped for ear-tagging (Dalton rototags) using baited Tomahawk live traps, allowing remote identification of individuals. During handling, weight (±5 g) and left hind foot length (±1 mm) were recorded following a standardized protocol. If a juvenile was trapped more than once, the same measurements were taken again for validation. To assess how well-nourished individuals were, a juvenile physical condition index was calculated based on these measurements following

Table 1. An overview of the arctic fox data used in the study along with the small-rodent phase and index as well as golden eagle reproductions for each year

	Year										
	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	Total
Number of litters studied	12	NR	9	13	NR	12	16	8	0	4	74
Disturbed dens	4	–	2	4	–	5	7	4	–	3	29
Undisturbed dens	8	–	7	9	–	7	9	4	–	1	45
Number of cubs	91	NR	58	163	NR	47	99	67	0	28	553
Disturbed dens	41	–	14	56	–	22	47	37	–	22	239
Undisturbed dens	50	–	44	107	–	25	52	30	–	6	314
Small-rodent abundance											
Small-rodent phase	↘ Decrease	↓ Low	↗ Increase	↑ Peak	↓ Low	↗ Increase	↗ Increase	↘ Decrease	↓ Low	↗ Increase	
Small-rodent index	0.97	0	1.33	27	0	0.29	2.98	3.1	0.21	0.36	
n (trap nights)	826	≥500	450	510	1440	686	1376	775	476	1390	
Golden eagle reproductions	33	8	24	34	15	18	30	36	10	31	

The low years in the small-rodent cycle (2009, 2012 and 2016) were not included in the analysis due to few or no reproductions (NR) during these years.

Tannerfeldt *et al.* (1994), where weight increase allometrically with hind-foot length. The individual index scores were compared between years and disturbed/undisturbed dens. Since the index was measured on juvenile foxes that had no supplemental food, the average condition would be 1.0 (Tannerfeldt *et al.*, 1994).

Small-rodent and golden eagle abundance

Each summer was classified as either increase, peak, decrease or low phase of the small-rodent cycle following Henden, Ims & Yoccoz (2009), based on data from the Swedish small-rodent monitoring program obtained during spring and autumn (Ecke, 2018). In addition, an index of the small-rodent abundance during the summer (number of rodents/100 trap nights) was calculated from small-rodent trap lines in Helagsfjällen, following Hellström, Nyström & Angerbjörn (2014). Data about golden eagle reproductions were obtained from the County administrative board (Länsstyrelsen Jämtland, personal communication). These data represent the reproductions in all Jämtland County and not only the mountain area, but was considered a proxy of golden eagle presence in the study area. As intra-guild interactions vary over the small-rodent cycle, the phase of the cycle was used in the analyses rather than the index as it describes the relative food availability and predation risk. The small-rodent and golden eagle index were only used descriptively (Fig. 1).

Permits and handling of animals

The handling and trapping of both arctic foxes and small rodents was done in accordance with Swedish law. It was approved by the Swedish Board of Agriculture (Jordbruksverket) and ethical permits were given by an ethical board (Umeå djurförsöksetiska nämnd; permits A130-07, A131-07, A36-11, A37-11, A18-14, A19-14 and A10-17). The trapping of foxes was also approved by the Swedish Environmental Protection Agency (Naturvårdsverket; permits 412-7884-07 Nv, NV-01959-14, NV-02547-17).

Statistical analyses

To investigate the effect of tourism and researcher presence on juvenile survival, we fitted a generalized mixed-effect model with individual juvenile summer survival as binomial response variable and with small-rodent phase, week of inventory (during the inventory period 1–25 July), tourism activity (disturbed/undisturbed) and number of days with researcher presence (2 to 8+) as explanatory variables. We also included interaction terms between small-rodent phase and tourism activity as well as small-rodent phase and researcher presence. Litter ID was included as a random factor to group juveniles within the same litter. A stepwise reduction of the model was performed, removing the least significant variable in each step, until all variables contributed significantly. Years with low small-rodent abundance were excluded because there were no or very few reproductions during these years (2009 – 0 litters, 2012 – 0 litters and 2016 – 2 litters).

To test whether the juvenile condition was affected by tourism activity, we fitted a mixed-effect model with juvenile physical condition index as the response variable, rodent phase, tourism activity and the interaction term between them as explanatory variables. Litter ID was included as a random factor. In addition, the altitude, productivity (NDVI values) and litter sizes were compared between disturbed and undisturbed den sites using *t*-tests to identify potential confounding differences in territory quality. The maternal experience was compared between disturbed and undisturbed den sites using a chi-square test. All analyses were performed using R (R Core Team, 2018), RStudio version 1.1.419 (R

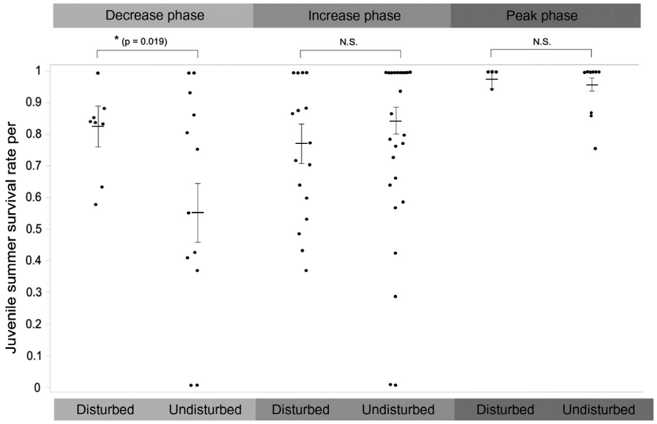

Figure 3 Juvenile arctic fox summer survival rate per litter (Estimated mean ± SE) between dens that are classified as disturbed and undisturbed by tourism activities for the different phases of the small-rodent cycle. Juvenile survival was higher at disturbed dens during decrease years, while there was no difference in survival during increase and peak years. *Indicates significance, N.S. not significant.

Studio, 2017). The survival and physical condition models were fitted using the LME4 package (Bates *et al.*, 2015) and post hoc pairwise comparisons were done using the emmeans package (Lenth *et al.*, 2019).

Results

The summer survival of juvenile arctic foxes varied in a predictable way between the phases of the small-rodent cycle, with exceptionally high survival during the peak phase and lower during the increase and decrease phase ($\chi^2 = 18.67$, $n_{\text{juveniles}} = 553$, $n_{\text{litters}} = 74$, $P > 0.001$, Fig. 3, see full parameter estimates in Supporting Information Table S2). The survival rate was also found to decrease as the summer progressed ($\chi^2 = 9.88$, $n_{\text{juveniles}} = 553$, $n_{\text{litters}} = 74$, $P = 0.002$). During years of decreasing small-rodent abundance, the mean juvenile survival rate increased from 0.56 (CI 95% +0.17/−0.18, $n_{\text{juveniles}} = 78$, $n_{\text{litters}} = 8$) at dens undisturbed by tourism activity to 0.83 (CI 95% +0.09/−0.16, $n_{\text{juveniles}} = 80$, $n_{\text{litters}} = 12$) at disturbed dens, while there was no difference in survival during years of increasing and peak small-rodent abundance (Table 2; Fig. 3). No effect was found of the number of days with researcher presence (likelihood ratio: $\chi^2_{[1]} = 1.37$, $n_{\text{juveniles}} = 553$, $n_{\text{litters}} = 74$, $P = 0.24$).

The physical condition of the juveniles varied neither between small-rodent phases (likelihood ratio: $\chi^2_{[1]} = 4.52$, $n_{\text{juveniles}} = 508$, $n_{\text{litters}} = 102$, $P = 0.1$), nor between disturbed and undisturbed dens (likelihood ratio: $\chi^2_{[1]} = 0.83$, $n_{\text{juveniles}} = 508$, $n_{\text{litters}} = 102$, $P = 0.36$, see Supporting Information Figure S1 and full parameter estimates in Supporting Information Table S3). Furthermore, there were no differences between disturbed and undisturbed den sites in altitude ($t = -0.89$, $n_{\text{dens}} = 26$, $P = 0.39$) or productivity ($t = 0.055$, $n_{\text{dens}} = 26$, $P = 0.96$), nor were there any difference in litter sizes ($n_{\text{litters}} = 74$, $t = 0.12$, $P = 0.9$), indicating that there was no bias between the two groups in territory quality (Supporting Information Figure S2). In a subsample where maternal breeding was known, there was no bias in how experienced and unexperienced females were distributed between disturbed and undisturbed dens (χ^2-test, $n_{\text{litters}} = 47$, $\chi^2 = 0.51$, d.f. = 1, $P = 0.48$).

Table 2. Model estimates of juvenile survival probability for each group and pairwise comparisons between disturbed and undisturbed dens for the different phases of the small-rodent cycle

Small-rodent phase	Tourism disturbance	Survival probability	SE	Lower CI	Upper CI	Pairwise comparisons (*P*)
Decrease	Disturbed	0.831	0.063	0.673	0.922	0.019*
	Undisturbed	0.557	0.092	0.377	0.722	
Increase	Disturbed	0.775	0.061	0.635	0.872	0.272
	Undisturbed	0.851	0.041	0.751	0.915	
Peak	Disturbed	0.976	0.027	0.809	0.997	0.636
	Undisturbed	0.957	0.022	0.887	0.984	

*Indicates significance.

Discussion

The aim of this study was to investigate the effects of tourism activity and researcher presence on summer survival of juvenile arctic foxes. We found the survival to be higher at dens disturbed by tourism activity compared to undisturbed dens, but the effect depended on the phase of the small-rodent cycle (Fig. 1). The difference in survival was only found during small-rodent decrease years (Fig. 3) which is when predation on arctic foxes is presumed to be highest as predators switch to alternative prey when the small rodents decrease (Ims & Fuglei, 2005). As eagles move easily over vast distances, we would expect the golden eagles to be evenly distributed over the relatively small mountain area and the risk of detection to be similar for all observed dens. However, both eagles and the other potential predators of the arctic fox, wolverine and red fox, have been seen to avoid areas with human activity, to a larger extent than the arctic fox (May *et al.*, 2006; Krebs, Lofroth & Parfitt, 2007; Kaisanlahti-Jokimaki *et al.*, 2008; Martin *et al.*, 2011). Thus, a plausible explanation for the higher juvenile survival at disturbed dens could be that the tourism activity creates a predator refuge for the arctic foxes in close proximity of trails and tourist huts but that the effect is only possible to observe when the predation is high. This is in line with the results of Leighton *et al.* (2010), who found decreased nest predation for the critically endangered hawksbill sea turtle *Eretmochelys imbricata* with increasing human activity, as it displaced its main predator, the mongoose *Herpestes javanicus*. Similar effects have also been found for brown bears, where human activity provided subordinate bear groups, like females with cubs, with a refuge from large male bears (Nevin & Gilbert, 2005*a*,*b*).

No differences were found in the physical condition of juveniles between disturbed and undisturbed dens or between phases of the small-rodent cycle, which is in concordance with previous findings that the supplemental feeding reduces variations caused by the fluctuating availability of natural prey (Tannerfeldt *et al.*, 1994). This implies that the juvenile food provisioning was not affected by tourism activity and that the starvation-caused mortality likely was similar between dens and small-rodent phases. Variations in juvenile survival could, however, also be the results of differences in territory quality. As red fox density in the tundra is higher at lower altitudes closer to the forest (Herfindal *et al.*, 2010), altitude can be seen as a proxy of red fox abundance. Higher vegetation productivity may positively affect the local abundance of the herbivorous small rodents within the tundra and thus increase the availability of prey for the arctic foxes. As the arctic foxes in Fennoscandia are too few to be restricted by intra-species competition in their territory occupancy, litter size can also be seen as an indication of the conditions within the territory. However, as neither altitude, productivity (NDVI) nor litter sizes varied between disturbed and undisturbed den sites, we find it unlikely that the difference in juvenile survival between disturbed and undisturbed dens during small-rodent decrease years was due to differences in territory quality. Similarly, differences in maternal breeding experience are also unlikely to cause the difference as there was no bias in how females with previous breeding experience and first-time breeders were distributed between disturbed and undisturbed dens.

In the arctic fox, we have previously documented changes in activity and behavioral patterns in response to tourism activity (Larm, 2015). The foxes at a den regularly visited by guided safari tours changed their activity to be more active at the den during the day when tourists were present compared to control dens. During night, they were instead less present at the den, possibly due to more intensive night time foraging to compensate for lost hunting opportunities at daytime (Larm, 2015). Similar results were found in Svalbard, where arctic foxes in areas with snow mobile traffic fed less from provided reindeer carcasses during the day and more during the night (Fuglei *et al.*, 2017). In this study, tourism activity did not seem to increase the risk of juvenile starvation. However, it was not possible to determine whether that was because food provisioning was not affected by tourism activity or because potential negative effects were compensated for by the supplemental food. Thus, it is possible that tourism could affect juvenile food provisioning if no supplemental food is provided. Impacts on activity and behaviors could compromise the fitness of individual animals, for example by increasing the time they spend vigilant and decreasing the time devoted to activities like foraging and parental care (Frid & Dill, 2002). This suggests that the indirect benefits for the population from a human activity-induced predator refuge could be a trade-off with the fitness of individual animals. A similar trade-off is tourism activities that generate money for conservation. Such activities may cause disturbance and decreased fitness for targeted individuals, while the revenue from them could indirectly benefit the population. As previously suggested in Larm *et al.* (2018), indirect positive effects might compensate for negative effects to a certain degree, but eventually a critical level of negative impact will be reached where it can no longer be compensated for. Thus, it is important to note that these results are for the current level of tourism activity, which is still relatively low and there is likely a point where the disturbance exceeds a certain threshold and negative effects take over.

Another important aspect to consider in a predator-refuge scenario is the impact on the predator species, in this case mainly the golden eagle. In Sweden, it is classified as near threatened (Swedish Red List, 2015) and one aim in the golden eagle management is to decrease disturbance caused by human activities and infrastructure (Swedish Environmental Protection Agency, 2013). Whether the eagles in Fennoscandia suffer any consequences from displacement caused by tourism activities is not yet known, but in Denali National Park, Alaska, predictive models have suggested disturbance from tourism activities to have a potential negative effect on both territory occupancy and reproduction of golden eagles (Martin *et al.*, 2011).

Conclusions and management implications

Our results demonstrate a possible positive effect of nature-based tourism activities and is one among few studies attempting to quantify fitness consequences of tourism (see also: Nevin & Gilbert, 2005b; Griffin *et al.*, 2007; Buckley *et al.*, 2016). For small and endangered populations, empirical knowledge about consequences of tourism have previously been scarce. Together with the results of previous behavioral studies in the same population (Larm, 2015; Larm *et al.*, 2018), it further demonstrates a counter-intuitive and somewhat controversial example of indirect positive effects on a population level potentially compensating for direct disturbance caused to individual animals. Furthermore, the study highlights the importance of context for how animals are affected by disturbance. In this study, the effect was found to be context-dependent, changing with the prey availability and intra-guild interactions. We demonstrate that studying how the effect of tourism activity varies depending on the context could provide opportunities for identifying the mechanisms behind the effects. That can be an important link between the scientific research and the management of wildlife and tourism activities, allowing the management to make informed decisions based on empirical knowledge to ensure that wildlife tourism activities are ecologically sustainable despite the increasing popularity.

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Comparison of juvenile physical condition index between phases of the small rodent cycle and between dens classified as disturbed and undisturbed by tourism activity.

Figure S2. Comparison of potential confounding differences in territory quality.

Table S1. Information for each den on the distance to the nearest trail and tourist mountain hut, which years a litter was included in the study from the den and the number of researcher days (min–max) during those years.

Table S2. Standardized coefficient estimates for the best GLMER model of Juvenile survival.

Table S3. Standardized coefficient estimates for the best LMER model of Juvenile physical condition.

Supporting information, paper III

Table S1. Information for each den on the distance to the nearest trail and tourist mountain hut, which years a litter was included in the study from the den and the number of researcher days (min-max) during those years.

Tourism disturbance	Den ID	Distance to trail (m)	Distance to tourist mountain hut (m)	Number of researcher days (min-max)	Number of litters included in the study
Disturbed	FSZZ009	750	1800	4-6	**4** (-13, -14, -15, -17)
Disturbed	FSZZ012	650	3200	3	**1** (-13)
Disturbed	FSZZ020	250	2000	3-14	**6** (-08, -10, -11, -14, -15, -17)
Disturbed	FSZZ031	1500	1800	3-5	**3** (-08, -11, -14)
Disturbed	FSZZ033	300	5000	3-7	**6** (-08, -10, -11, -13, -14, -17)
Disturbed	FSZZ040	500	6000	6	**1** (-14)
Disturbed	FSZZ042	600	4300	4-7	**5** (-08, -11, -13, -14, -15)
Disturbed	FSZZ066	350	6500	4-5	**3** (-13, -14, -15)
Undisturbed	FSZZ010	7500	7500	5	**1** (-10)
Undisturbed	FSZZ013	7500	14000	4-8	**4** (-08, -10, -11, -13)
Undisturbed	FSZZ014	4000	4000	7	**2** (-10, -11)
Undisturbed	FSZZ015	8300	10200	2-3	**4** (-08, -10, -11, -13)
Undisturbed	FSZZ016	6000	11200	2-5	**3** (-11, -13, -14)
Undisturbed	FSZZ018	4500	7300	2-13	**4** (-08, -10, -11, -14)
Undisturbed	FSZZ019	2500	7300	2-6	**5** (-08, -10, -11, -14, -15)
Undisturbed	FSZZ024	2300	7900	2-11	**6** (-08, -10, -13, -14, -15, -17)
Undisturbed	FSZZ028	6700	6500	6	**1** (-14)
Undisturbed	FSZZ029	1100	3400	3-5	**2** (-10, -14)
Undisturbed	FSZZ030	2300	4500	3	**1** (-13)
Undisturbed	FSZZ032	2000	7000	5-6	**2** (-08, -14)
Undisturbed	FSZZ034	3300	6700	5	**1** (-13)
Undisturbed	FSZZ035	1700	3500	2	**2** (-08, -11)
Undisturbed	FSZZ037	2000	6500	6	**1** (-14)
Undisturbed	FSZZ064	3800	7000	4-5	**3** (-11, -13, -15)
Undisturbed	FSZZ080	10500	11000	7	**1** (-11)
Undisturbed	FSZZ090	8000	7500	3-5	**2** (-08, -14)

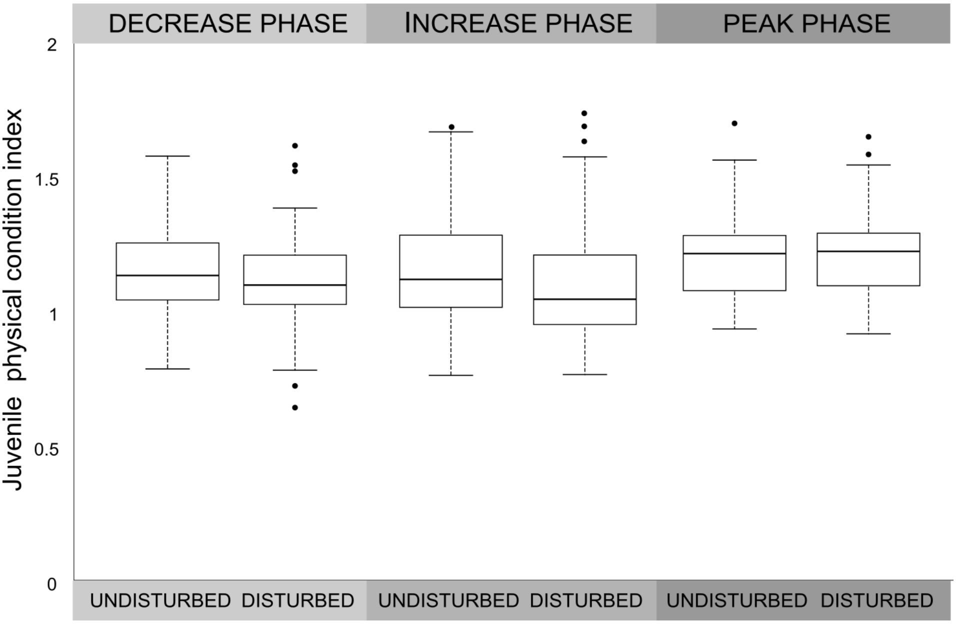


Figure S1. Comparison of juvenile physical condition index between phases of the small rodent cycle and between dens classified as disturbed and undisturbed by tourism activity. The supplemental food provided at all dens in the study have previously been shown to improve the physical condition of the juveniles, especially during years when the abundance of natural food is low, reducing potential variation between dens and years.

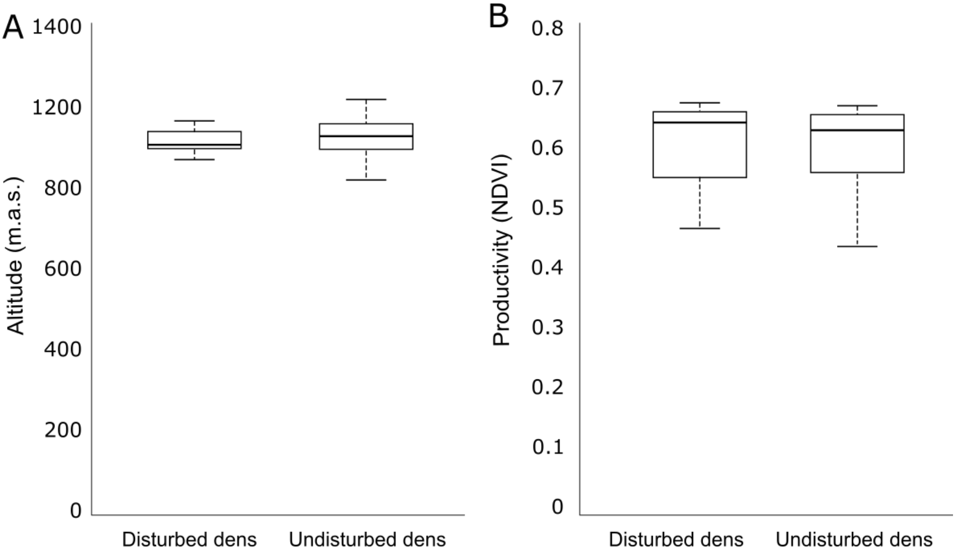


Figure S2. Comparison of potential confounding differences in territory quality. No bias was found in altitude nor productivity (NDVI) between dens classified as disturbed and undisturbed by tourism activity.

Table S2. Standardized coefficient estimates for the best GLMER model of Juvenile survival. Significant effects in bold.

Type II Test of fixed effects

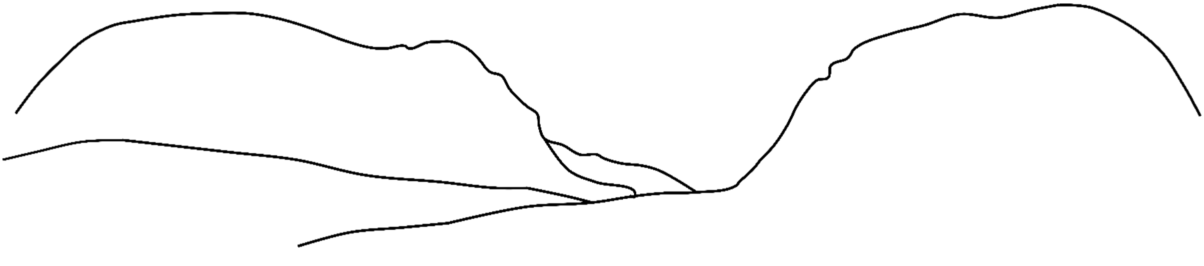
	Estimate	SE	Z value	P value	Lower 95% CI	Upper 95% CI
(Intercept)	**2.678**	0.580	4.618	**<0.001**	1.541	3.814
Week	**-0.645**	0.205	-3.145	**0.002**	-1.046	-0.243
Rodent Peak	2.093	1.226	1.708	0.088	-0.309	4.495
Rodent Increase	-0.360	0.559	-0.643	0.52	-1.455	0.736
Disturbance Undisturbed	**-1.367**	0.582	-2.35	**0.019**	-2.508	-0.227
Rodent Peak : Disturbance Undisturbed	0.778	1.384	0.562	0.574	-1.934	3.489
Rodent Increase : Disturbance Undisturbed	**1.871**	0.747	2.504	**0.012**	0.406	3.335

Table S3. Standardized coefficient estimates for the best LMER model of Juvenile physical condition. There were no significant effects of rodent phase or tourism disturbance on the juvenile physical condition.

Type II Test of fixed effects

	Estimate	SE	T value	Lower 95% CI	Upper 95% CI
(Intercept)	1.135	0.041	27.591	1.054	1.215
Rodent Peak	0.098	0.071	1.373	-0.042	0.238
Rodent Increase	-0.033	0.051	-0.647	-0.133	0.067
Disturbance Undisturbed	0.018	0.052	0.036	-0.080	0.117
Rodent Peak : Disturbance Undisturbed	-0.051	0.086	-0.595	-0.221	0.118
Rodent Increase : Disturbance Undisturbed	0.025	0.064	0.397	-0.099	0.150

IV



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The role of wildlife tourism in conservation of endangered species: Implications of safari tourism for conservation of the Arctic fox in Sweden

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ABSTRACT

There are both positive and negative impacts on wildlife associated with wildlife tourism. In Sweden, the endangered Arctic fox is subject to a growing tourist interest. In the Helags mountain region there are guided Arctic fox safari tours that provide visitors with information about the Arctic fox. A survey of five separate groups of visitors in the region revealed that knowledge about the status of Arctic foxes and awareness of the behavioral guidelines for Arctic fox encounters improved after participation in a safari tour and with increasing Arctic fox interaction. We propose a schematic model summarizing the diverse ways in which wildlife tourism affects wildlife and their relative importance for conservation. The Arctic fox population in Sweden is small and sensitive to disturbance, but the positive impacts of Arctic fox tourism seem to compensate for the negative and contribute to their conservation under the current level of tourism pressure.

KEYWORDS

Wildlife tourism; tourism impact; conservation; endangered; Arctic fox

Introduction

Interest in wildlife tourism is growing rapidly (Cong, Wu, Morrison, Shu, & Wang, 2014; Snyder, 2007) and the variety of experiences offered is constantly expanding to include new areas, species and ways of interacting with the wildlife (Higginbottom, 2004; Snyder, 2007). Wildlife tourism activities are often located in pristine environments of high conservation value and are generally claimed to be ecologically and socially sustainable (Weaver, 2002). Despite these claims, many such activities are likely to cause disturbance to the viewed animals and environments to some extent (Higginbottom, 2004; Knight & Cole, 1991; UNEP, 2001). Rare and endangered species that often are subject to tourist interest (Reynolds & Braithwaith, 2001) are especially vulnerable to disturbance since even small negative effects might have a significant impact on the viability of the population (Gill, 2007). Considering the inherent sensitivity of protected areas and species and the high abundance of visitors, it has been argued that nature-based tourism could have a larger negative impact than activities in already developed areas (Higham & Lück, 2007; Weaver, 2002). Recreational activities such as wildlife tourism have even been identified as

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one major cause of species endangerment (Czech, Krausman, & Devers, 2000). Since the tourism business is dependent on the existence of pristine environments and the wild animals that inhabit them, it is sensitive to overexploitation (Higginbottom, Tribe, & Booth, 2003). Ensuring ecological sustainability is critical for the future of the viewed species and environments, as well as for the tourism business (Meltofte, 2013).

Wildlife tourism can generate positive economic contributions that in many cases are crucial for conservation (Buckley, Castley, Pegas, Mossaz, & Steven, 2012; Higginbottom, Northrope, & Green, 2001; Schänzel & McIntosh, 2000; Steven, Castley, & Buckley, 2013). For many regions and communities, tourism is an essential source of income and, as such, provides an incentive for protecting species and habitats (Higginbottom et al., 2003; Schänzel & McIntosh, 2000) as well as compelling arguments against more exploitative land uses with less potential for reversal (Buckley, Morrison, & Castley, 2016; Schänzel & McIntosh, 2000; Wilson & Tisdell, 2003). The possibility of encountering an animal in its natural environment also poses a strong incentive for conservation (Higginbottom et al., 2003; Krüger, 2005). Wildlife tourism has the potential to affect knowledge, attitudes and behaviors of participants in the activities, with indirect benefits for animals and habitats (Ballantyne, Packer, & Sutherland, 2011; Orams, 1997; Waylen, McGowan, & Milner-Gulland, 2009; Zeppel & Muloin, 2008). Impacts of human disturbance on prey, predators or competitor species of the viewed animal can also have a substantial effect (Griffiths & Van Schaik, 1993; Higginbottom et al., 2001; Nellemann et al., 2001).

Managing wildlife tourists

Various management strategies have been used to influence the behavior of visitors. These can be either direct regulating strategies such as restricting legislation, rules and physical barriers or indirect strategies such as economic motivations and education to promote the desired behavior (Kuo, 2002; Orams, 1996). When regulations are explained visitors can develop an understanding of the reasons behind those regulations, as well as the effects on the wildlife, if they are ignored (Granquist & Nilsson, 2016; Kuo, 2002). For activities taking place in nature where there are limited opportunities to enforce regulations, education is essential in motivating visitors to voluntarily follow regulations such as behavioral guidelines or codes of conduct for wildlife encounters (Granquist & Sigurjonsdottir, 2014; Kuo, 2002; Marschall, Granquist, & Burns, 2017; Orams, 1996). Interpretive education is likely to enhance the experience of the visitors, and thereby increase the support for management strategies (Kuo, 2002; Marschall et al., 2017; Moscardo, 1996; Orams, 1996; Powell & Ham, 2008). Though behavioral guidelines and codes of conduct are voluntary, they can work well as a complement to formal regulations (Garrod & Fennel, 2004). Other advantages are that they generally are easier and quicker to introduce than formal regulations and often contain more information and arguments for following the regulations (Garrod & Fennel, 2004).

Knowledge, attitudes and behaviors

A common belief is that a nature experience itself creates increased awareness and appreciation for the environment and results in improved environmental attitudes and behaviors in humans participating in wildlife tourism (Russel, 1994). However, for those effects to be reached there often needs to be more to the experience than simply being in nature (Orams, 1994). For nature-based tourism to be an effective tool in managing human–nature interactions increased knowledge and awareness of visitors is often not enough, there needs to be a change in attitudes and ultimately behaviors (Ballantyne et al., 2011; Buckley, 2009; Orams, 1994).

The relationship between knowledge, attitudes and behaviors is complex and though improved environmental knowledge and attitudes are often followed by intentions of behavioral changes, they are not reliable predictors of actual pro-environmental behaviors (Heberlein, 2012; Hughes, 2013; Kollmuss & Agyeman, 2002; Tubb, 2003). Attitudes are often based on a few salient beliefs that will vary from visitor to visitor, depending on previous knowledge and experiences (Ajzen, 1991; Ham, 2007). To change an attitude these underlying beliefs need to be altered (Ajzen, 1991; Apps, Dimmock, & Lloyd, 2015; Ham, 2007). Attitudes, in conjunction with motivations to action, will form behavioral intentions. The likelihood of these intentions translating into actual behavior depends on the opportunities of carrying them out and the associated cost of doing so. (Ajzen, 1991; Orams, 1996). Generally, the greater the environmental benefit of a behavior, the larger the cost and the motivation to perform it needs to be stronger (Diekmann & Preisendoerfer, 1992 in Kollmuss & Agyeman, 2002). A pro-environmental attitude can often be enough to change "low-cost" environmental behaviors like recycling and willingness to accept political pro-environmental changes, while "high-cost" behaviors like cutting down on driving or flying require strong motivations (Diekmann & Preisendoerfer, 1992 in Kollmuss & Agyeman, 2002).

Without knowing the individual salient beliefs and motivations, the probability of changing visitors' attitudes and behaviors is reduced (Ham, 2007; Orams, 1996). Such a change can be facilitated by an interpretative approach, rather than only passively providing information (Ham, 2007). Evoking emotions in visitors and giving examples of specific attitudinal and behavioral changes that are easy to implement can also increase the possibilities (Ballantyne, Packer, Hughes, & Dierking, 2007; Kuo, 2002; Orams, 1997; Schänzel & McIntosh, 2000). Common interpretative approaches are interactive displays, first-hand experience of animals and guided tours (Kuo, 2002). A tour guide has the potential to impact visitors both through mediation of knowledge and as a role model for attitudes and behaviors (Apps et al., 2015; Littlefair & Buckley, 2008).

Specific attitudes and behaviors connected to the particular animals or environment that is viewed are easier to impact than general environmental attitudes and behaviors (Beaumont, 2001; Kim, Airey, & Szivas, 2011; Tubb, 2003; Zeppel & Muloin, 2008). Taylor and Knight (2003) found that recreationists assumed they could keep a shorter distance to the wildlife without disturbing the animals than that which was appropriate according to empirical data from the same study. People tended to blame other groups and activities for causing disturbance, while underestimating and justifying their own impact (Taylor & Knight, 2003). Realizing one's own impact and keeping an appropriate distance when approaching wildlife are examples of specific attitudes and behaviors where a change could reduce disturbance to wildlife (Taylor & Knight, 2003). Motivations for specific attitudinal and behavioral changes can be gained from a single experience, while general environmental attitudes and behaviors need to be continuously reinforced (Beaumont, 2001). A nature tourism experience could thus contribute to maintaining or improving environmental attitudes and behaviors in those who are already initiated (Ballantyne et al., 2011;

Beaumont, 2001), but could also be a first step towards more environmentally friendly attitudes and behaviors for those who are not (Ballantyne et al., 2011; Beaumont, 2001; Schänzel & McIntosh, 2000; Zeppel & Muloin, 2008).

The case of Arctic fox tourism in Sweden

In Scandinavia the endangered Arctic fox (*Vulpes lagopus)* (Swedish Red List, 2015) is subject to a growing tourist interest. During the early 20th century, the Arctic foxes in Scandinavia were subject to extensive hunting for their valuable fur. The number of Arctic foxes was heavily reduced and despite receiving legal protection in Sweden 1928 and in Norway 1930, the population did not recover (Angerbjörn, Meijer, Eide, Henttonen, & Norén, 2008). Today, one large threat to the Scandinavian Arctic fox population is expansion of the dominant competitor red fox (*Vulpes vulpes)* into the mountain and tundra regions which the Arctic fox inhabits (Elmhagen et al., 2017). They also suffer food shortage due to disruptions in the cyclic dynamic of voles and lemmings with long periods of low small rodent availability, likely caused by altered snow conditions due to climate change. (Elmhagen, Hellström, Angerbjörn, & Kindberg, 2011; Ims, Henden, & Killengreen, 2008). However, more than 15 years of successful conservation actions, such as supplementary feeding and hunting of red foxes, have resulted in a population growth and the red list status for the Fennoscandian Arctic fox has improved from critically endangered (CR) to endangered (EN) (Swedish Red List, 2015).

Today one of the largest Arctic fox populations in Scandinavia is found in the mountain region of Helags in Sweden (Angerbjörn et al., 2013), with 29 litters in the summer of 2015 (Figure 1) (Swedish Arctic fox project, 2015). The region is also a popular location for recreational outdoor activities during both summer and winter, and the Swedish Tourist Association (STF) runs several mountain stations and huts in the areas that are connected by a large network of hiking and skiing trails. STF accommodates approximately 60 000 (2014) stays per year in the area (Jämtland Härjedalen Turism, 2015). At the STF Helags Mountain station there is a substantial focus on the Arctic fox. The station uses the Arctic fox in their profile and marketing, and easily accessible information about Arctic foxes is provided on information signs, boards, in brochures and in a children's movie. For six years, the station has also operated guided Arctic fox safari tours to an inhabited den site during summer. The revenue from the tours is donated to the Arctic fox conservation program and is used to purchase dog food, which is needed for summer supplementary feeding. The number of participants has increased rapidly from 35 at the start in 2011 to over 120 in the peak summer of 2015, and the funds donated to Arctic fox conservation have increased so much that it covers approximately 60–70% of the food cost for the area (Larm, 2015a). Although the disturbance from the tours has been shown to affect the diurnal activity pattern of the Arctic foxes at the den visited during the safari tours (Larm, 2015b), no negative impact has been observed on their breeding success or survival rate. In addition, there has been no indication of the foxes abandoning the den site during the years that the tours have been running. Thus, the direct negative impact of the safari tours seems low (i.e., there is some impact on individual foxes and den sites, but it does not extend to affect the population) (Larm, 2015b). Another aspect that is likely to be important in the case of the Arctic foxes in Sweden is the indirect effect human disturbance has on predators and

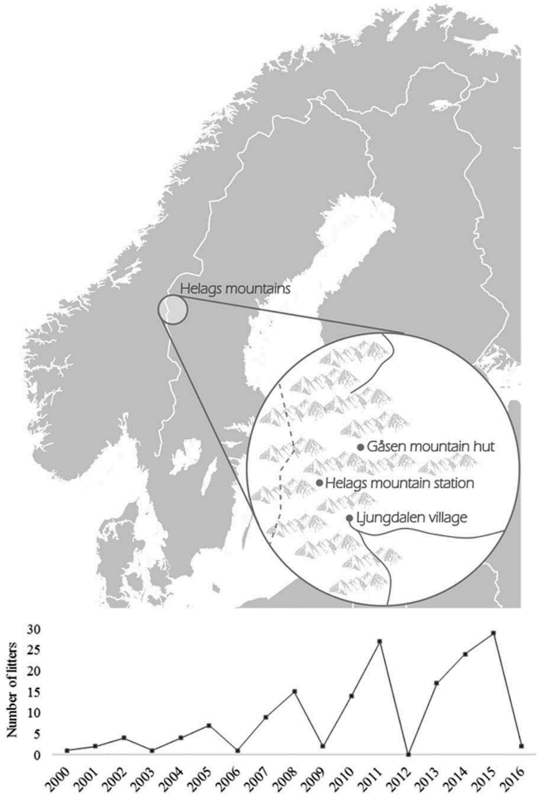

Figure 1. A map of Scandinavia and the Helags mountain region. Groups A-C participated in the survey at Helags mountain station, group D at Gåsen mountain hut and group E in the village Ljungdalen. The graph shows the number of Arctic fox litters in the Helags mountain region between 2000 and 2016.

competitors of the Arctic fox. Previous studies propose that the red fox benefits from human infrastructure such as cabins, roads, and power lines due to increased food availability (Killengren et al., 2011; Selås, Johnsen, & Eide, 2010). However, the red fox is more easily disturbed by human activity in the wild than the Arctic fox; the Sami name for Arctic fox means the fearless and the foolhardy (Østbye & Pedersen, 1990). The other main predators and competitors of the Arctic fox–golden eagle (*Aquila chrysaetos*), white-tailed eagle (*Haliaeetus albicilla*) and wolverine (*Gulo gulo*) (Tannerfeldt & Angerbjörn, 1996)–also avoid areas with human activity (Kaisanlahti-Jokimaki et al., 2008; May, Landa, Van Dijk, Linnell, & Andersen, 2006). Human disturbance to species posing a threat to Arctic foxes could provide a refuge, leading to human activity benefitting Arctic foxes.

The tours in Helags were the first regularly operated Arctic fox safari tours in Sweden, but a small number of other operators have already followed and include similar experiences in their activities. The legal regulations in Sweden regarding Arctic foxes state that there should be no disturbance at occupied Arctic fox dens. All organized Arctic fox tourism activities require a permit from the County Administration Board with regulations regarding the time, number and length of the tours, number of participants and the distance kept to the den site (Länsstyrelsen Jämtlands län in Eide, 2015). There are also guidelines for the general public on how to behave when encountering an Arctic fox or a den site in order to minimize the disturbance, with a recommended distance to keep of 300 meters, based on estimations by the County Administration Board (Länsstyrelsen Jämtlands län in Eide, 2015; Norwegian Environment Agency, 2015). Given the success of the safari tours and the overall increase in tourism to the mountain areas in Sweden (Heberlien, Fredman, & Vuorio 2002; Wall-Reinius & Bäck, 2011), it is likely that the Arctic fox safari tour operation will continue to grow and expand to other mountain regions and operators in the near future.

This article sought to investigate the impact of Arctic fox information provided in different contexts and environments on visitors' knowledge, awareness and attitudes about the Arctic fox situation and related conservation work. This was tested using a survey distributed to five groups of visitors to the Helags mountain region. Given that the Arctic fox safari tour experience is highly interactive, with an expert guide and close encounters with the animals, it was predicted that the information provided to tour participants will improve their knowledge, awareness and attitudes. The Arctic fox information provided at Helags mountain station was also predicted to improve knowledge and awareness, though not to the same extent as the safari tours, while impacts on attitudes are predicted to be small. We further sought to put these potential impacts in relation to other impacts of tourism on Arctic foxes. To do this we developed a schematic model summarizing the factors contributing to the total impact of tourism on wildlife and evaluate their relative importance for Arctic fox conservation.

Methods

Study area and respondent groups

The survey was distributed to five separate groups of visitors at three locations in or close to the Helags mountain region in central Sweden (Groups A-E, Figure 1). The groups were ranked by degree of "Arctic fox interaction" based on (a) how close the location was to the Arctic fox habitat and the possibility of Arctic fox encounter, (b) availability of information about the Arctic fox and behavioral guidelines and (c) how that information

Table 1. Group characters of the five survey groups in order of increasing "Arctic fox interaction" and the number of respondents in each group in 2015 and 2016 respectively.

Group characters						Survey respondents		
Group	Location	Within arctic fox habitat	Possibility for arctic fox encounters	Information availability	Information mediation	2015	2016	Total
E	Ljungdalen village	No	No	Low	None	58	28	86
D	Gåsen mountain hut	Yes	Yes	Low	None		156	156
C	Helags mountain station	Yes	Yes	High	Displays	85	78	163
B	Helags mountain station	Yes	Yes	High	Displays	46	25	71
A	Helags mountain station	Yes	Yes	High	Guide	57	19	76
						246	306	552

was mediated to the groups (Table 1). The “Arctic fox interaction” increased from group E to group A. Three groups of visitors responded to the survey at STF Helags mountain station (groups A-C). All Helags groups had the opportunity to access the Arctic fox information provided at the station. Groups A (*n* = 76) and B (*n* = 71) participated in an Arctic fox safari tour. Group A responded after the tour, while group B responded before the tour. As a control, visitors at the mountain station that did not participate in a tour constituted a third group (group C, *n* = 163). For comparison, visitors to other locations were also included. The fourth group were visitors to STF Gåsen mountain hut (group D, *n* = 156, only from 2016), which is located in the mountains, but does not provide the extensive and easily accessible Arctic fox information that is available at the Helags mountain station. The fifth group were visitors at a hostel in Ljungdalen (group E, *n* = 86), a nearby village located in the boreal forest outside the mountains and the only of the three locations that is accessible by car. Little or no information about the Arctic fox is provided at the hostel. While all groups A-D were visiting Arctic fox habitat and they all had the possibility to encounter an arctic fox, only group A and B deliberately sought out Arctic fox encounters. Since random Arctic fox encounters are rare, only the visitors who have already been on a tour (group A), were likely to actually have seen an Arctic fox when responding to the survey.

Survey

The survey was performed during the summers of 2015 and 2016. A total of 246 people responded in 2015 and 306 people in 2016. The survey consisted of questions on both personal information and environmental values of the respondents and of Arctic fox specific questions. The information needed to answer the questions in the survey was provided by the guide during the safari tours and was easily accessible on information boards and in brochures at Helags mountain station. Most questions were multiple-choice questions with closed-ended answers, while some had open-ended follow-up questions for the respondents to elaborate their answers further. The answers to the free text questions were evaluated as either correct or not correct. In 2016, two Arctic fox specific questions were added to the survey (Sample sizes: A = 8, B = 16, C = 35 and D = 130), but apart from that, there were similar questions in both years. The survey distributed in Ljungdalen (group E) in 2016 was not the extended version, but the same as in 2015. All safari tour participants (groups A and B) were asked to respond to the survey, while for the remaining groups (groups C-E), surveys were provided in public areas at each of the locations and were open to everyone who wanted to participate. The survey was in Swedish as the great majority of respondents came from Sweden, though some Swedish speaking international visitors also participated. There were no significant differences in the demographic information or general environmental values between the groups. Surveys where the respondent only finished the first of the two pages were excluded, while surveys with only a few questions not answered were used in the analysis. The safari tour participants also filled out an evaluation of their experience of the tour, with questions on what they thought was positive/negative about the tour and the guide, whether they believed it was worth its price and whether they would talk about and recommend the tour to others.

Data analysis

A Spearman's rank correlation test was used to test for correlations between degree of "Arctic fox interaction" and (a) knowledge and awareness of the Arctic fox situation and conservation; (b) attitude towards Arctic fox conservation; (c) knowledge of behavioral guidelines on how to behave when encountering Arctic foxes; and (d) beliefs about human disturbance as a reason for the Arctic foxes endangerment. Knowledge and awareness were analyzed using Pearson's χ^2-tests between adjacent groups to determine where the difference was. The results from the tour evaluation were only treated as descriptive statistics.

Tourism impact model

A schematic model of the various factors contributing to the total impact of tourism on wildlife was developed. The positive and negative impact factors attributed to wildlife tourism in the model are well established and supported by previous research (Beale & Monaghan, 2005; Buckley et al., 2012; Green & Higginbottom, 2001; Griffin, Valois, Taper, & Mills, 2007; Griffiths & Van Schaik, 1993; Higginbottom et al., 2001; Higginbottom, 2004; Higham & Shelton, 2011; Knight & Cole, 1991; Orams, 1997; Powell & Ham, 2008; Selås et al., 2010; Steven et al., 2013; Nellemann et al., 2001; Waylen et al., 2009; Zeppel & Muloin, 2008).

Results

Survey

Knowledge and awareness of the Arctic foxes' situation and the conservation actions taken to preserve them was positively correlated with increasing "Arctic fox interaction" (Figure 2A, $p < .001$, $rho = .25$). As expected, the largest increase was found after participation in an Arctic fox safari tour with a significant knowledge difference between the groups that responded before and after a tour (groups A & B, $p < .001$, $\chi^2 = 1.97$). Even after removing the group that responded after a tour (group A) from the analysis the correlation was significant ($p = .01$, $rho = .11$). However, for these four remaining groups (groups B-E) there were no significant differences between adjacent groups but rather a gradual knowledge increase.

The support for protecting Arctic foxes in Sweden was very high among all responding groups and no significant attitudinal differences were found between groups (Figure 2B). The awareness of the behavioral guidelines for Arctic fox encounters was also positively correlated with increasing "Arctic fox interaction" (Figure 2C, $p < .001$, $rho = .36$). All who responded after participation in a tour knew about the distance recommended, indicating that they had encountered the behavioral guidelines. Only 2% of all respondents believed that a shorter distance (100 m) than the recommended 300 meters was appropriate. The number of respondents that stated human disturbance or exploitation as reasons why the Arctic foxes are endangered was negatively correlated with increasing "Arctic fox interaction" (Figure 2D, $p = .01$, $rho = -.10$).

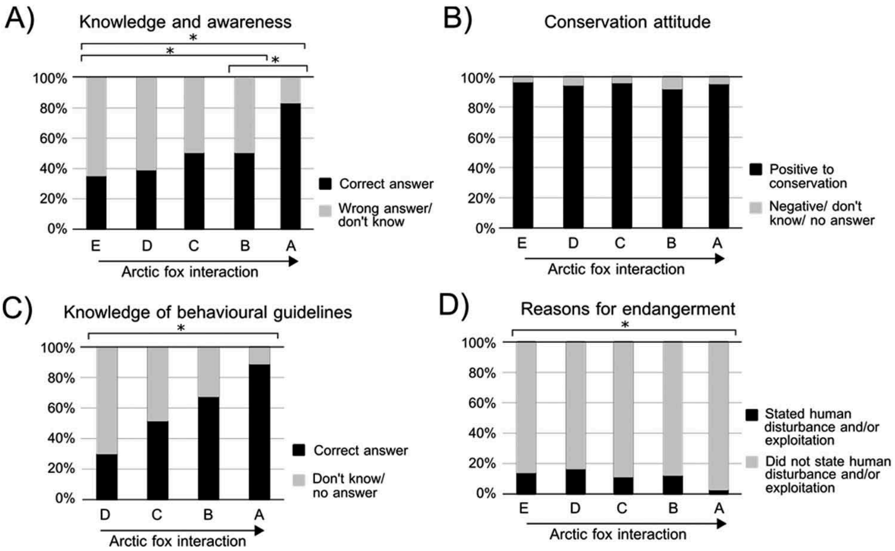

Figure 2. The survey results for: A) knowledge and awareness about the reasons to why the Arctic fox is endangered and what is done to preserve it in Sweden. B) Attitude towards preserving the Arctic fox in Sweden. C) Knowledge about the behavioral guidelines on how to behave when encountering Arctic foxes or an Arctic fox den. D) The number of respondents that stated human disturbance and/or exploitation as a reason to why the Arctic fox is endangered in Sweden. * marks significant results. See Table 1 for group descriptions.

Tour evaluation

Of the participants on the guided Arctic fox safari tours in Helags, 97% said that they were going to talk about the experience and recommend the tour to their friends and family and some respondents stated that they did in fact participate in the safari tour after recommendation from someone who had previously been on a tour. Eighty-four percent found the tour to be worth its price and several respondents specifically stated that they thought so because the money contributed to the conservation of the foxes. Only 3% thought it was too expensive and the remaining 13% didn't know or didn't answer. When asked what the greatest benefit of being on a guided tour was, the answers were that without a guide they would not have been able to find and see the foxes or their den, information about the foxes and the environment and the possibility to ask questions.

Tourism impact model

To view the results of this study in perspective of the total impact of tourism on wildlife, we propose a schematic model summarizing the contributing factors and their relative importance for conservation (Figure 3). Positive and negative impacts are shown on separate axes since they are not always additive or synergistic, but can be rather compensatory to each other (Buckley, 2009). Positive impacts can compensate for negative impacts to some extent and for a tourism activity to contribute to conservation the

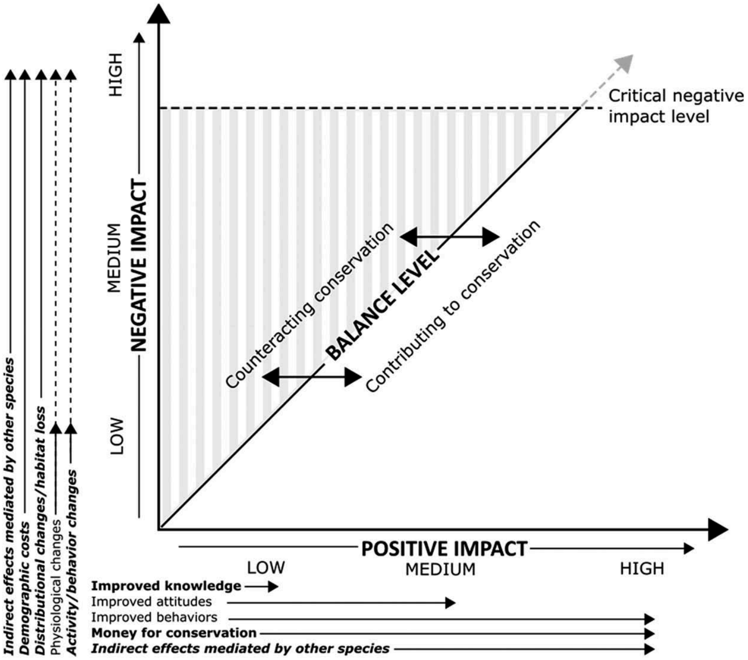

Figure 3. A schematic model of the overall impact of tourism on wildlife and the relative importance of each contributing factor. Positive and negative impacts are shown on separate axes since they are not additive or synergistic, but rather compensatory to each other. The factors in bold are within the scope of this study, while factors in bold italic have been covered for the Arctic fox in previous studies. The solid lines show impacts on the animal population level, while the dashed lines show impacts only on individual animals.

positive impacts need to exceed the negative. Eventually, a critical level is reached where they are too extensive to be compensated for (Buckley et al., 2016; Krüger, 2005; Reynolds & Braithwaite, 2001). The higher vulnerability of small and endangered populations would correspond to a lowered critical level for negative impacts. The model further visualizes the complexity of evaluating the combined impact, especially for the positive factors that often are indirect (Buckley, 2009; Higginbottom, 2004). Examples of positive impact are improved knowledge, attitudes and behaviors of visitors (Higginbottom, 2004; Orams, 1997; Powell & Ham, 2008; Waylen et al., 2009; Zeppel & Muloin, 2008), money raised for conservation (Buckley et al., 2012; Higginbottom et al., 2003; Steven et al., 2013) and indirect positive effects mediated by predator, competitor or prey species (Griffiths & Van Schaik, 1993; Higginbottom et al., 2001; Nellemann et al., 2001). Examples of negative impact are activity and behavioral changes in the viewed animals (Green & Higginbottom, 2001; Griffin et al., 2007; Knight & Cole, 1991), physiological changes (Higginbottom, 2004; Higham & Shelton, 2011; Shutt et al., 2014), distributional changes or habitat loss (Knight & Cole, 1991; Nellemann et al., 2001), demographic costs (Beale & Monaghan, 2005; Griffin et al., 2007) and indirect negative effects mediated by predator, competitor or prey species (Griffiths & Van Schaik, 1993; Selås et al., 2010).

Discussion

As predicted, the knowledge and awareness about the Arctic foxes' situation, as well as of the behavioral guidelines for Arctic fox encounters, improved with increasing "Arctic fox interaction". Though having participated in an Arctic fox safari tour had the strongest effect, the correlation was still significant without the after tour group (group A), indicating that being in the Arctic foxes' habitat and studying the provided information also had a positive effect. Improved knowledge and awareness could potentially generate a more positive attitude towards political pro-environmental decisions, tolerance for nature and wildlife preservation and increased willingness to donate money for conservation (Diekmann & Preisendoerfer, 1992 in Kollmuss & Agyeman, 2002). Impact on the specific knowledge regarding the behavioral guidelines along with the economic contributions is likely to have the largest positive effect for the foxes in this study. Though improved general environmental attitudes and behaviors can benefit other species and environments as well, specific attitude and behavior changes in accordance with the behavioral guidelines are likely to have a larger and more direct impact for the viewed animals themselves. An essential part of most codes of conduct and behavioral guidelines is the distance observers are recommended to keep away from an animal or a den site. Awareness of the behavioral guidelines increased steadily with increasing "Arctic fox interaction". Over 50% of respondents at Helags mountain station (groups A-C) knew the recommended distance and could give examples of other actions to take in order to decrease their disturbance when encountering Arctic foxes, indicating that they were aware of the behavioral guidelines. Whether that resulted in actual attitude or behavior changes was not covered in this study, but as shown in previous studies, people are more likely to adapt smaller, more specific changes related to the content of the experience (Beaumont, 2001; Kim et al., 2011; Tubb, 2003). Given that the improved knowledge resulted in attitudinal changes and behavioral intentions, there would be good opportunities for carrying out the actual behavior (Ajzen, 1991; Kollmuss & Agyeman, 2002). Studies of the actual behaviors carried out by visitors as a complement to the survey responses would be an interesting future follow-up study.

The importance of environment and interpretation was demonstrated by the positive correlation between "Arctic fox interaction" and knowledge and awareness. The strongest increase in knowledge and awareness occurred after participation in a safari tour. Since the comparison was made between tour participants before and after a safari tour (groups A and B), the knowledge difference was not caused by a generally larger prior knowledge of tour participants, but was actually an effect of the tour. Further, as indicated by the evaluations of the safari tours, the participants found the information to be an important part of the experience and they were likely to share their knowledge and experience with friends and family, which in turn might affect the awareness of these people and could recruit future tour participants. Since the survey was open to all who wanted to participate for the groups who did not participate in a tour (group C, D and E), it likely attracted people who were already interested in the subject. Since that was the case for all responding groups, it should not have affected the differences between the groups.

That the survey mostly attracted people with prior interest could also be a part of the reason that all groups showed such a strong desire to preserve the Arctic fox in Sweden. With surveys there is always the risk that the answer does not represent the true opinion of the respondent, but what people know they are "supposed" to reply. However, the Arctic fox is generally regarded as a charismatic and uncontroversial animal in Sweden, suggesting that the support is likely to be high. It is possible that the survey questions regarding attitudes were too general and need to be more specific in order to detect subtler attitudinal differences. The number of respondents that sited human disturbance and exploitation as reasons why the Arctic fox is endangered decreased with increasing "Arctic fox interaction" and as the knowledge and awareness improved. Possible explanations for the decrease could be that people re-evaluate their beliefs as they perceive the disturbance as lower than they previously thought or as a way of justifying the disturbance they cause by visiting the area or participating in a safari tour (Taylor & Knight, 2003). It could also be interpreted as an example of an, as previously discussed, subtler attitudinal change. The lack of major differences in attitudes among the groups is thus not necessarily showing that there are no impacts of tourism activities on attitudes.

Applying the proposed schematic model (Figure 3) on the results of this and previous studies on tourism impact on the Arctic fox we reveal that, for the tourism pressure in the Helags region today, the positive impact seems to outweigh the negative. Positive impact factors associated with wildlife tourism that have been either demonstrated or strongly indicated for the Arctic fox are improved knowledge and awareness (present study), money for conservation (Larm, 2015a) and indirect effects mediated by other species (Larm, 2015b). Several factors of negative impact from tourism on Arctic foxes have been studied, but the only confirmed impact is effects on the activity of individual foxes (Larm, 2015b), which is suggested to have a high impact on the disturbed individual or den site, but low impact on a population level as long as it does not cause demographic costs. The impacts of wildlife tourism activities on wildlife are strongly context dependent, varying between species, population and individuals as well as with food availability, presence of predators and other factors affecting the animals' condition (Beale & Monaghan, 2004; Gill, Norris, & Sutherland, 2001; Higham & Shelton, 2011). Given the high between-year variation in living conditions for the Arctic fox due to fluctuating access to small rodents (Elmhagen et al., 2011), the degree to which the disturbance affects them is also likely to vary between years. Such variations make it difficult to ensure that the required compensatory relationship between positive and negative impacts is sustained. It will be important to keep monitoring the breeding success, survival rate and distribution of the Arctic foxes as well as the development of the tourism in the area. That would allow us to study potential long-term effects as well as other dimensions in the study of human impact.

Conclusions and conservation implications

Though disturbance to individual animals or family groups is of course undesirable, the positive impacts of tourism often exceed the negative and may be favorable for the entire population. However, for small and/or endangered populations the tolerance for disturbance may be low and consequently the critical level for negative impact may be quickly reached. For each specific case of wildlife tourism, monitoring is essential in order to determine a tolerable degree of impact, for individual animals, the animal population and the environment. However, it is still important to remember that, regardless of the extent; positive impacts can compensate but never undo negative impacts. As wildlife tourism activities are becoming increasingly popular, strategies are needed for keeping wildlife tourism businesses ecologically sustainable.

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1906. Nils Holmgren: Studien über südamerikanische Termiten.

1907. Lännart Ribbing: Die distale Armmuskulatur der Amphibien, Reptilien und Säugetiere.

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1914. John Runnström: Etudes sur la morphologie et la physiologie cellulaire du développement de l'oursin.

1918. Olof Hammarsten: Beitrag zur Embryonalentwicklung des *Malacobdella grossa*.

1920. Bertil Hanström: Zur Kenntnis des centralen Nervensystems der Arachnoiden und Pantopoden.

1921. Axel Palmgren: Embryological and morphological studies on the mid-brain and cerebellum of vertebrates.

1922. Torsten Pehrson: Some points in the cranial development of teleostomian fishes.

Gertie Söderberg: Contributions to the fore-brain morphology in Amphibians.

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Gert Bonnier: Contributions to the knowledge of intra- and inter-specific relationships in *Drosophila*.

Hialmar Rendahl: Embryologische und morphologische Studien über das Zwischenhirn beim Huhn.

1928. Sven Hörstadius: Über die Determination des Keimes bei Echinodermen.

1932. Harry Bergqvist: Zur Morphologie des Zwischenhirns bei niederen Wirbeltieren.

Gösta Johansson-Kvenne: Beiträge zur Kenntnis der Morphologie und Entwicklung des Gehirns von *Limulus polyphemus*.

Mois Koffmann: Die Mikrofauna des Bodens, ihr Verhältnis zu anderen Mikroorganismen und ihre Rolle bei den mikrobiologischen Vorgänge im Boden.

1936. Eric Lindahl: Zur Kenntnis der physiologischen Grundlagen der Determination im Seeigelkeim.

1937. Figge Hammarberg: Zur Kenntnis der ontogenetischen Entwicklung des Schädels von *Lepisosteus osseus*.

Märtha Kindahl: Zur Entwicklung der Exkretionsorgane von Dipnoern und Amphibien.

1942. Egron Vallén: Beiträge zur Kenntnis der Ontogenie und der vergleichenden Anatomie des Schildkrötenpanzers.

1945. Birger Rudebeck: Contribution to fore-brain morphology in Dipnoi.

1948. Gösta Notini: Biologiska undersökningar över grävling.

Alf G. Johnels: On the development and morphology of the skeleton of the head of *Petromyzon*.

1949. Thorolf Lindström: On the cranial nerves of the cyclostomes with special reference to N. trigeminus.

Bertil Lekander: The sensory line system and the external bones in the head of some Ostariophysi.

1958. Ragnar Olsson: The subcommisural organ.

1959. Gunnar Bertmar: On the ontogeny of the chondral skull in Characidae, with a discussion on the chondrocranial base and the visceral chondrocranium in fishes.

1961. Armin Lindquist: Über die Morphologie und Biologie von *Limnocalanus* im Ostseebecken.

1963. Gunnar Fridberg: Morphological studies on the caudal neurosecretory system in teleosts and elasmobranchs.

Kjell Engström: Studies on teleostean visual cells.

1964. Valdek Jürisoo: Agro-ecological studies on leafhoppers (Auchenorrhynca, Homoptera) and bugs (Heteroptera) at Ekensgård farm in the province of Hälsingland, Sweden.

1965. Hubertus Eidmann: Ökologische und physiologische Studien über die Lärchen-miniermot (*Coleophora laricella* HBN).

1968. Bengt-Owe Jansson: Studies on the ecology of the interstitial fauna of marine sandy beaches.

1970. Göran Malmberg: The excretory systems and the marginal hooks as a basis for the systematics of *Gyrodactylus* (Monogenoa, Trematoda).

Perarvid Skoog: The food of the Swedish badger (*Meles meles* L.)

Yngve Espmark: Mother-young relations and development of behaviour in roe-deer (*Capreolus capreolus* L.).

Bo Ingemar Hjort: Reproductive behaviour in Tetraonidae with special reference to males.

Jan Karl Englund: Population dynamics of the Swedish red fox, *Vulpes vulpes* (L.).

1971. Björn Ganning: Studies on Baltic rockpool ecosystems.

Lars Westin: Studies on the biology and ecology of fourhorn sculpin, *Myoxocephalus quadricornis* (L.).

Hans Ackefors: Studies on the ecology of the zooplankton fauna in the Baltic proper.

Lars Wilsson: Observations and experiments on the ethology of the European beaver (*Castor fiber* L.). A study in the development of phylogenetically adapted behaviour in a highly specialized mammal.

1972. Bo Fernholm: Pituitary and ovary of the Atlantic hagfish. An endocrinological investigation.

Anders Bjärvall: Nest-exodus behaviour and nest-site selection of the mallard.

Kaj Holmberg: The retina and responses to light in hagfish.

1973. Björn Sohlenius: Growth, reproduction and population dynamics in some bacterial feeding soil nematodes.

1974. Lars-Olof Hagelin: Studies on the development of the membranous labyrinth in lampreys, *Lampetra fluviatilis* Linné, *Lampetra planeri* Bloch and *Petromyzon marinus* Linné.

Birgitta Weman: The adenohypophysis of the mink, *Mustela vison*.

AnnMari Jansson: Community structure, modelling and simulation of the *Cladophora* ecosystem in the Baltic Sea.

Arnold Stenmark: Studies on the pea moth (*Laspeyresia nigricana* Steph) in central Sweden.

1975. Erik Neuman: The dynamics of the coastal fish fauna in the Baltic with special reference to temperature.

Tommy Radesäter: Ethological studies on the triumph ceremony of the Canada goose (*Branta canadensis* L.) - with special reference to ontogeny and causation.

Christer Wiklund: Ecological and evolutionary aspects on the host plant biology of *Papilio machaon* L.

Christer Solbreck: Flight habits and environment of a seed bug, *Lygaeus equestris* (L.) (Heteroptera, Lygaeidae).

Finn Sandegren: Social behaviour in the Steller sea lion (*Eumetopias jubatus*) and northern elephant seal (*Miroungas angustirostris*).

Bo Ekengren: Structural aspects of the Hypothalamo-Hypophysial complex of the roach, *Leuciscus rutilus.*

Inga-Britt Ahlbert: Organization of the cone cells in the retinae of some teleosts in relation to their feeding habits.

1976. Per Haage: Studies on the Baltic *Fucus* macrofauna.

Laila Winbladh: Endocrine pancreas in cyclostomes.

Ragnar Elmgren: Baltic benthos communities and the role of the meiofauna.

1977. Eva Norman: Studies on the ecology of the marine woodboring molluscs on the Swedish west coast with special reference to the degradation of wood.

Sven Ankar: The soft bottom ecosystem of the northern Baltic proper with special reference to the macrofauna.

Olle Lindén: Effects of oils and dispersants on the early development of Baltic herring and some invertebrates from the Baltic Sea.

Thorsten Klint: Factors contributing to mate selection in female mallards (*Anas platyrhynchos* L.) - with particular emphasis on the role of the male nuptial plumage.

Otto Kugelberg: Food relations of a seed feeding insect, *Lygaeus equestris* (L.) (Heteroptera, Lygaeidae).

Sverre Sjölander: Reproductive behaviour of the divers (Gaviidae).

Peter Öhman: Structure and function of the river lamprey (*Lampetra fluviatilis*) retina.

Mats Olsson: Mercury, DDT and PCB in aquatic test organisms. Baseline and monitoring studies, field studies on biomagnification substances harmful to the Swedish environment.

Lars Hernroth: Studies on the population dynamics of zooplankton in the Baltic.

1978. Gunnel Skoog: Aspects on the biology and ecology of *Theodoxus fluviatilis* (L.) and *Lymnea peregra* (O. F. Müller) (Gastropoda) in the northern Baltic.

Fredrik Wulff: Ecological studies on Baltic rock pools.

Greta Ågren: Sociosexual behaviour in the Mongolian gerbil *Meriones unguiculatus*. Interactions between gonadal hormones and social relationships.

1979. Gunnar Aneer: On the ecology of the Baltic herring with special reference to the Askö-Landsort area.

Hans Cederwall: Energy flow and fluctuations of deeper soft bottom macrofauna communities in the Baltic Sea.

1980. Hans Lundberg: Ecology of bumblebees (Hymenoptera Apidae) in a subalpine/alpine area with special reference to food plant and habitat utilization.

Stig Sjöberg: Modelling, simulation, and analysis of pelagic ecosystems with special reference to the Baltic Sea.

Hans Ahnlund: Aspects of the population dynamics of the badger (*Meles meles* L.).

Annikki Lappalainen: On the ecology of shallow sandy bottoms in the Baltic Sea with special reference to mud snails (Hydrobiidae).

Stellan Hedgren: Ecological aspects of the breeding biology of the guillemot *Uria aalge* in the Baltic Sea.

Bengt Lindlöf: Some aspects of ecology in hares.

Jan Landin: Habitats, life histories, migration and dispersal by flight in water beetles (Hydrophilidae and Hydraenidae).

Åke Pehrson: Intake and utilization of winter food in the mountain hare (*Lepus timidus* L.).

1981. Nils Kautsky: On the role of the blue mussel, *Mytilus edulis* L. , in the Baltic ecosystems.

Göran Cederlund: Some aspects of roe deer (*Capreolus capreolus* L.) winter ecology in Sweden.

1982. Erik Lindström: Population ecology of the red fox (*Vulpes vulpes* L.) in relation to food supply.

Olavi Grönwall: Aspects of the food ecology of the red squirrel (*Sqiurus vulgaris* L.).

Tjelvar Odsjö: Eggshell thickness and levels of DDT, PCB and mercury in eggs of osprey (*Pandion haliaetus* (L.)) and marsh harrier (*Circus aeruginosus* (L.)) in relation to their breeding success and population status in Sweden.

Göran Nordlander: Systematics and phylogeny of an interrelated group of genera within the family Eucoilidae (Insecta: Hymenoptera, Cynipoidea).

Birgitta Sillén-Tullberg: Behavioural ecology and population dynamics of an aposematic seed bug, *Lygaeus equestris* L. (Heteroptera, Lygaeidae).

1983. Björn Helander: Reproduction of the white-tailed sea eagle *Haliaetus albicilla* (L) in Sweden, in relation to food and residue levels of organochlorine and mercury compounds in the eggs.

Sven O. Kullander: Taxonomic studies on the percoid freshwater fish family Cichlidae in South America.

1984. Per-Olov Larsson: Some characteristics of the Baltic salmon, *Salmo sala*r L., population.

Torbjörn Järvi: On the evolution of inter- and intraspecific communication through natural and sexual selection.

Magnus Enquist: Game theory studies on aggressive behaviour.

Nils-Ove Hilldén: Behavioural ecology of the labrid fishes (Teleostei: Labridae) at Tjärnö on the Swedish west coast.

Helena Obermüller-Wilén: Neuroendocrine studies in the brain of the lancelet, *Branchiostoma lanceolatum* (Cephalochordata).

Paula Kankaala: On the ecology and productivity of zooplankton in the northern Baltic.

Lars-Åke Janzon: Taxonomical and biological studies of *Tephritis* species (Diptera) and their parasitoids (Hymenoptera).

1986. Kenneth Lindahl: Endocrinological studies on the young salmon, *Salmo sala*r L., with special reference to smoltification.

Anders Angerbjörn: Population dynamics of mountain hares (*Lepus timidus* L.) on islands.

Ulf Larsson: The pelagic microheterotrophic food web in the Baltic Sea: Bacteria and their dependence on phytoplankton.

Anders Fernö: Aggressive behaviour between territorial cichlid fish and its regulation.

Staffan Tamm: Behavioural energetics: Acquisition and use of energy by hummingbirds.

1987. Per-Olof Wickman: Mate searching behaviour of Satyrine butterflies.

Erkki Schwanck: Reproductive behaviour of a monogamous cichlid fish *Tilapia mariae*.

Vidar Øresland: Life cycle feeding of the chaetognaths *Sagitta setosa* and *S. elegans* in European shelf waters.

Odd Lindahl: Plankton community dynamics in relation to water exchange in the Gullmar fjord, Sweden.

Sven Jakobsson: Male behaviour in conflicts over mates and territories.

1988. Hans Temrin: Polyterritorial behaviour and polygyny in the wood warbler (*Phylloscopus sibilatrix* Bechst).

Bertil Widbom: The benthic meiofauna of three coastal areas: Structure, seasonal dynamics and response to environmental perturbations.

Johan Forsberg: Reproductive biology of some pierid butterflies.

Hans Kautsky: Factors structuring phytobenthic communities in the Baltic Sea.

Sven Boström: Morphological and systematic studies of the family Cephalobidae (Nematoda, Rhabditida).

Lars G. Rudstam: Patterns of zooplanktivory in a coastal area of the northern Baltic proper.

Sture Nellbring: Quantitative and qualitative studies of fish in shallow water, northern Baltic proper.

Olof Leimar: Evolutionary analysis of animal fighting.

Lena Svärd: Mating strategies of male butterflies in relation to female fecundity and polyandry.

Gunnar Fredriksson: Thyroid-like systems in endostyles: A study on morphology, function and evolution in "primitive" chordates.

1989. Magnus Rydevik: Smoltification and early sexual maturation in the Baltic salmon, *Salmo salar* L.

Bengt Karlsson: Fecundity in butterflies: Adaptations and constraints.

Rolf Gydemo: Studies on reproduction and growth in the noble crayfish, *Astacus astacus* L.

Sture Hansson: Biotic interactions in fish and mysid communities, studies in two Baltic coastal areas.

Brita Sundelin: Ecological effect assessment of pollutants using Baltic benthic organisms.

Fredrik Pleijel: Taxonomy of the Phyllodocidae (Polychaeta).

1990. Lennart Edsman: Territoriality and competition in wall lizards.

Dag Broman: Transport and fate of hydrophobic organic compounds in the Baltic aquatic environment - Polycyclic aromatic hydrocarbons, polychlorinated dibenzodioxins and dibenzofurans.

Michael Tedengren: Ecophysiology and pollution sensitivity of Baltic Sea invertebrates.

1991. Sören Nylin: Butterfly life-history adaptations in seasonal environments.

Mats Amundin: Sound production in Odontocetes with emphasis on the harbour porpoise, *Phocoena phocoena*.

Kerstin Holmberg: Mallard ducks, mate choice and breeding success.

Erland Dannelid: Dental morphology in eurasian shrews of the genus *Sorex* - aspects on taxonomy, evolution and ecology.

Catherine Hill: Mechanisms influencing the growth, reproduction and mortality of two co-occurring amphipod species in the Baltic sea.

1992. Sif Johansson: Regulating factors for coastal zooplankton community structure in the northern Baltic proper.

Carl André: Settlement of bivalve larvae: the role of larval behaviour predation and hydrodynamics.

Tomas Bollner: Regeneration and development of the nervous system in the ascidian *Ciona intestinalis* (L.).

Eva Andersson: Neuroendocrine control of reproduction in the three-spined stickleback, *Gasterosteus aculeatus* (L.).

Thorleifur Eiriksson: Female response and male singing strategies in two orthopteran species.

1993. Nina Wedell: Evolution of nuptial gifts in bushcrickets.

Björn Forkman: The gathering and use of information in foraging.

C. Tomas Lundquist: Localization and chemical properties of peptides related to galanin and tachykinins in the blowfly nervous system.

1994. Tom Arnbom: Maternal investment in male and female offspring in the southern elephant seal.

Anders Brodin: Time aspects on food hoarding in the willow tit - an evolutionary perspective.

Gisela Holm: The tree-spined stickleback, *Gasterosteus aculeatus* L. in ecotoxicological test systems.

Cecilia Lindblad: Perturbation of functions in shallow benthic ecosystems.

1995. Ulrik Kautsky: Ecosystem processes in coastal areas of the Baltic Sea.

Kjell Wahlström: Natal dispersal in roe deer - an evolutionary perspective.

Per Berggren: Stocks, status and survival of harbour porpoises in swedish waters.

Anders Modig: Social behaviour and reproductive success in southern elephant seal (*Mirounga leonina*).

1996. Michael Gilek: Bioaccumulation and cycling of hydrophobic organic contaminants by Baltic Sea blue mussels.

Elin Sigvaldadottir: Systrematics of Spionidae and *Prionospio* (Polychaeta).

Anders Silfvergrip: A systematic revision of the neotropical catfish genus *Rhamdia* (Teleostei, Pimelodidae).

Agneta Johansson: Territorial dynamics and marking behaviour in male roe deer.

Eric Muren: Tachykinin-related neuropeptides in the Madeira cockroach: structures distributions and actions.

1997. Niklas S. Mattson: Fish production and ecology in african small water bodies with emphasis on *Tilapia*.

Thord Fransson: Time and energy in long distance bird migration.

Birgitta Johansson: Oxygen deficiency and the ecology of Baltic macrobenthos.

Johan Axelman: Biological, physico-chemical and biogeochemical dynamics of hydrophobic organic compounds.

Marie Arnér: Organisms and food webs in rock pools: Responses to environmental stress and trophic manipulation.

Pete Hurd: Game theoretical perspectives on conflict and biological communication.

Erik Wilsson: Maternal effects on behaviour of juvenile and adult dogs.

Magnus Tannerfeldt: Population fluctuations and life history consequences in the arctic fox.

Kristjan Lilliendahl: Fattening strategies in wintering passerines.

Björn Birgersson: Maternal investment in male and female offspring in the fallow deer.

Bohdan Sklepkovych: Kinship and conflict: resource competition in a proto-cooperative species: The Siberian Jay.

1998. Simon G.M. Ndaro: Ecological aspects of soft bottom meiofauna in Eastern Africa.

Efthimia Antonopoulou: Feedback control of reproduction in Atlantic salmon, *Salmo salar,* male parr.

Petra Wallberg: Distribution and fate of polychlorinated biphenyls within the pelagic microbial food web.

Carl Rolff: Stable isotope studies of contaminant and material transport in Baltic pelagic food-webs.

Marcus Öhman: Aspects of habitat and disturbance effects on tropical reef-fish communities.

Cecilia Kullberg: Behaviour under predation risk in birds.

Thomas Lyrholm: Sperm whales: Social organization and global genetic structure.

Min-Yung Kim: Neuropeptides related to tachykinins and leucokinins in the developing nervous system of insects.

Salim M. Mohammed: Nutrient dynamics and exchanges between a mangrove forest and a coastal embayment: Chwaka Bay, Zanzibar.

Gunilla Ejdung: Predatory processes in Baltic benthos.

Virpi Sjöberg-Lindfors: Butterfly life history and mating systems.

1999. Karl Gotthard: Life history analysis of growth strategies in temperate butterflies.

Niklas Janz: Ecology and evolution of butterfly host plant range.

Staffan Jakobsson: Target organs for androgens in two teleost fishes, Atlantic salmon, *Salmo salar*, and three-spined stickleback, *Gasterosteus aculeatus*.

Anna Thessing: Genetic and environmental factors influencing growth and survival in willow tits *Parus montanus*.

Kenneth Ekvall: Alloparental care and social dynamics in the fallow deer (*Dama dama*).

Gunilla Ericson: 32P-postlabelling analysis of DNA adducts in fish as a biomarker of genotoxic exposure.

Karin Maria Björkman: Nutrient dynamics in the North Pacific subtropical gyre: Phosphorus fluxes in the upper oligotrophic ocean.

2000. Olle Israelsson: *Xenoturbella*.

Carl-Adam Wachtmeister: The evolution of courtship rituals.

Cecilia Bornestaf: Mechanisms in the photoperiodic control of reproduction in the three-spined stickleback, *Gasterosteus aculeatus*.

Olle Brick: Risk assessement and contest behaviour in the Cichlid fish, *Nannacara anomala*.

Gabriella Gamberale-Stille: On the evolution and function of aposematic coloration.

Helene Modig: Responses of Baltic soft-bottom invertebrates to settled organic material.

2001. Tomislav Vladic: Gonad and ejaculate allocation in alternative reproductive tactics of Salmon and Trout with reference to sperm competition.

Susanne Stenius: Cooperation and conflict during reproduction in polyterritorial wood warblers (*Phylloscopus sibilatrix*).

Ruben Tastàs-Duque: Studies of Cecidomyiidae (Diptera).

Sven Burreau: On the uptake and biomagnification of PCBs and PBDEs in fish and aquatic food chains.

Åsa Winther: Distribution and actions of insect tachykinin-related peptides.

Fang Fang Kullander: Phylogeny and species diversity of the South and Southeast Asian cyprinid genus *Danio* Hamilton (Teleostei, Cyprinidae).

Magnus G. S. Persson: Distribution and modulatory action of neuropeptides in the insect ventral nerve cord.

Minna Miettinen: Egg carrying in the golden egg bug.

Stefano Gihrlanda: Towards a theory of stimulus control.

Annkristin H. Axén: Behaviour of Lycaenid butterfly larvae in their mutualistic interactions with ants.

2002. Patrik Lindenfors: Phylogenetic analyses of sexual size dimorphism.

Patrik Börjesson: Geographical variation and resource use in harbour porpoises.

Michael Norén: Phylogeny and classification of prolecithophoran flatworms.

Johan Liljeblad: Phylogeny and evolution of gall wasps (Hymenoptera: Cynipidae)

Ulf S. Johansson: Clades in the "higher land bird assemblage"

2003. Ulf Norberg: Evolution of dispersal and habitat exploration in butterflies.

Johan Lind: Adaptive body regulation in the life history of birds.

Olle Karlsson: Population structure, movements and site fidelity of grey seals in the Baltic Sea.

Helena A D Johard: Neuropeptide signaling in insects: peptide binding sites, tachykinin receptors and SNAP-25

Bodil Elmhagen: Interference competition between arctic and red foxes.

Henrik Lange: Social dominance and agonistic communication in the great tit.

Anna Hellqvist: The brain-pituitary-gonadal axis and gonadotropic hormones in the three-spined stickleback, *Gasterosteus acculeatus*.

Anders Bignert: Biological aspects and statistical methods to improve assessments in environmental monitoring.

Julia Carlström: Bycatch, conservation and echolocation of harbour porpoises.

Kenth Svartberg: Personality in dogs.

Susanna Hall: Moult strategies in relation to migration in long-distance migrants

Miklós Páll: Role of 11-ketotestosterone and prolaction in the control of reproductive behaviour in the male three-spined stickleback, *Gasterosteus aculeatus*.

Bo Delling: Species diversity and phylogeny of *Salmo* with emphasis on southern trouts (Teleostei, Salmonidae).

Karolina Westlund: On post-confilict affiliation in humans and other primates - methodological considerations.

Malin Ah-King: Phylogenetic analyses of parental care evolution.

2004. Jonas Bergström: The evolution of mating rates in *Pieris napi*

Jörgen Ullberg: Dispersal in free-living, marine, benthic nematodes: passive or active processes?

Eva Stensland: Behavioural ecology of Indo-Pacific bottlenose and humpback dolphins.

Helena Strömberg: Benthic cryptofauna and internal bioeroders on coral reefs.

Liselotte Jansson: Evolution of signal form.

Martin Irestedt: Molecular systematics of the antbird-ovenbird comples. (Aves: Furnariida)

Jesper Nyström: Predator - prey interactions of raptors in an arctic community.

Ola Svensson: Sexual selection in *Pomatoschistus* - nests, sperm competition, and paternal care.

2005. Anders Bergström: Oviposition strategies in butterflies and consequences for conservation.

Helena Elofsson: Speerm motility in Gasterosteiform fishes. The role of salinity and ovarian fluid.

Fredrik Stjernholm: Allocation of body resources to reproduction in butterflies.

Fredrik Dalerum: Sociality in a solitary carnivore, the wolverine.

Ana Beramendi: Morphological and functional studies on the *Drosophila* neuromuscular system during postembryonic stages.

Georg H. Nygren: Latitudinal patterns in butterfly life history and host plant choice.

Love Dalén: Distribution and abundance of genetic variation in the arctic fox.

Ulrika Kaby: Attacking predators and fleeing prey: detection, escape and targeting behaviour in birds.

2006. Yasutaka Hamasaka: Multiple neurotransmitter inputs modulate circadian clock neurons in *Drosophila*.

Rasmus Hovmöller: Molecular phylogenetics and taxonomic issues in dragonfly systematics (Insecta: Odonata)

Adrian Vallin: On the protective value of conspicuous eyespots in Lepidoptera.

Ryan Tyge Birse: Tachykinin-related peptide signaling and its role in metabolic stress in *Drosophila.*

Maria Lissåker: Paternal care, filial cannibalism and sexual conflict in the sand goby, *Pomatoschistus minutus.*

2007. Ulrika Alm Bergvall: Food choice in fallow deer - experimental studies of selectivity.

Petra Souter: Causes and consequences of spatial genetic variation in two species of scleractinian coral in East Africa.

Hanne Løvlie: Pre- and post-copulatory sexual selection in the fowl, *Gallus gallus.*

Kajsa Garpe: Effects of habitat structure on tropical fish assemblages.

Erica Sjölin: Tubificids with trifid chaetae: morphology and phylogeny of *Heterodrilus* (Clitellata, Annelida)

2008. Karin Enfjäll: Mobility and emigration in butterflies.

David Berger: Body size evolution in butterflies.

Reihaneh Dehghani: Aspects of carnivoran evolution in Africa.

I. Jan Ohlson: Molecular phylogeny of tyrant flycatchers, cotingas, manakins and their allies (Aves: Tyrannida)

Elisabeth Weingartner: Phylogenetic perspective on host plant use, colonization and speciation in butterflies.

Kerstin Mehnert: Circadian plasticity in the neuromuscular junction of *Drosophila melanogaster.*

Lena Larsson: disentangling small genetic differences in large Atlantic herring populations: comparing genetic markers and statistical poweer.

2009. Carlos Pena: Evolutionary history of the butterfly subfamily Satyrinae (Lepidoptera: Nymphalidae).

Maria Almbro: Excape flight in butterflies.

Stefan Hallgren: Aromatase in the guppy, *Poecilia reticulata* Distribution, control and role in behaviour.

Augustine Mwandaya: Fish community patterns in Tanzanian mangrove creeks.

Ida Envall: Evolutionary Perspectives on Naidinae (Annelida, Clitellata, Naididae): Molecular and Morphological Revelations.

Ian Henshaw: Avian migration: the role of geomagnetic cues.

Alexandra Balogh: Predator psychology and mimicry evolution - a theoretical analysis.

Ullasa Kodandaramaiah: The dispersal-vicariance pendulum and butterfly biogeography.

Marina Dimitrova: Life at stake when playing hide and seek.

Magne Friberg: The evolutionary ecology of niche separation.

Dan Wilhelmsson: Aspects of offshore renewable energy and the alterations of marine habitats.

2010. Omar Amir: Biology, ecology and anthropogenic threats of Indo-Pacific bottlenose dolphins in east Africa.

Tobias Malm: Climbing the Trichoptera Tree - Investigations of Branches and Leaves.

Veronica Nyström: Studies of declining populations - temporal genetic analyses of two arctic mammals.

Marianne Espeland: Diversification on an ancient Darwinian island.

Lily Kahsai Tesfai: Distribution and modulatory roles of neuropeptides and neurotransmitters in the *Drosophila* brain.

Anna Palmé: Assessing and monitoring genetic patterns for conservation purposes with special emphasis on Scandinavia.

Te-Yu Liao: A phylogenetic analysis of rasborin fishes (Teleostei, Cyprinidae).

Karin Norén: Genetic structure in the North - population connectivity and social organization in the Arctic fox.

2011. Mathias Andersson: Offshore wind farms - ecological effects of noise and habitat alteration on fish.

Martin Bergman: The evolution of territoriality in butterflies.

Lina Enell: Chemical signalling in the *Drosophila* brain.

Hanna Aronsson: On sexual imprinting in humans.

Agata Kolodziejczyk: Chemical circuitry in the visual system of the fruitfly, *Drosophila melanogaster*.

Anna Särnblad Hansson: Ecology and genetic population structure of Indo-Pacific bottlenose dolphins in East Africa.

Saleh Yahya: Habitat structure, degradation and management effects on coral reef fish communities.

Jeannette Söderberg: Neuropeptides and GABA in control of insulin producing cells in *Drosophila*.

Aleksandra Johansen: Seasonal change in defensive coloration in a shieldbug.

Johan Charlier: Monitoring gene level biodiversity - aspects and considerations in the context of conservation.

Tobias Kånneby: Gastrotricha of Sweden - Biodiversity and Phylogeny.

2012. Lina Söderlind: Life history consequences of host plant choice in the comma butterfly.

Magnus Gelang: Babblers, Biogeography and Bayesian Reasoning.

Jessica Slove Davidson: The plasticity and geography of host use and the diversification of butterflies.

Marianne Aronsson: Colour patterns in warning displays.

Yi Ta Shao: The brain-pituitary-gonadal axis of the three-spined stickleback, *Gasterosteus aculeatus*.

Neval Kapan: Regulation of insulin producing cells, stress responses and metabolism in *Drosophila*.

Helena Larsdotter Mellström: Life history evolution in a bivoltine butterfly.

2013 Tomas Meijer: To survive and reproduce in a cyclic environment - demography and conservation of the Arctic fox in Scandinavia.

Martin Olofsson: Antipredator defence in butterflies.

Julia Stigenberg: Hidden Creatures - systematics of the Euphorinae (Hymenoptera).

Emma Lind: Genetic responce to pollution in sticklebacks; natural selection in the wild.

Oskar Henriksson: Genetic connectivity of fish in the Western Indian Ocean.

George Sangster: Integravite taxonomy of birds: Studies into the nature, origin and delimitation of species.

Jiangnan Luo: Regulation of insulin signaling and its developmental and functional roles on peptidergic neurons in the Drosophila central nervous system.

2014 Mija Jansson: Assessing inbreeding and loss of genetic variation in canids, domestic dog (*Canis familiaris*) and wolf (*Canis lupus*), using pedigree data.

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Peter Hellström: Predator responses to non-stationary rodent cycles.

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2015 Karolina Tegélaar: Dynamics of the aphid-ant mutualism.

Diana Posledovich: Effects of climate on phenological synchrony between butterflies and their host plants.

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Hélène Audusseau: Effect of climate and land use on niche utilization and distribution of nettle-feeding butterflies.

Johanna Hedlund: Climate change effects on migratory birds and on the ecology and behaviour of the willow warbler (*Phylloscopus trochilus*).

2016 Kristin Löwenborg Di Marino: Nesting ecology of the grass snake (*Natrix natrix*) and its implications for conservation.

Yiting Liu: Morphological and functional effects of insulin signaling and the bHLH transcription factor Dimmed on different neuron types in *Drosophila.*

Robert Stach: Migratory routes and stopover behaviour in avian migration.

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Sandra M. Granquist: Ecology, tourism and management of harbour seals (*Phoca vitulina*).

2017 Jeanette Stålstedt: Phylogeny, taxonomy and species delimitation of water mites and velvet mites.

Anna Favati: The relationship between personality and social dominance in the domestic fowl – a critical perspective.

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Alyssa Woronik: A functional genomic investigation of an alternative life history strategy - The Alba polymorphism in *Colias croceus*.

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Alberto Corral López: The link between brain size, cognitive ability, mate choice and sexual behaviour in the guppy (*Poecilia reticulata*).

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