Stockholm University

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

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

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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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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).

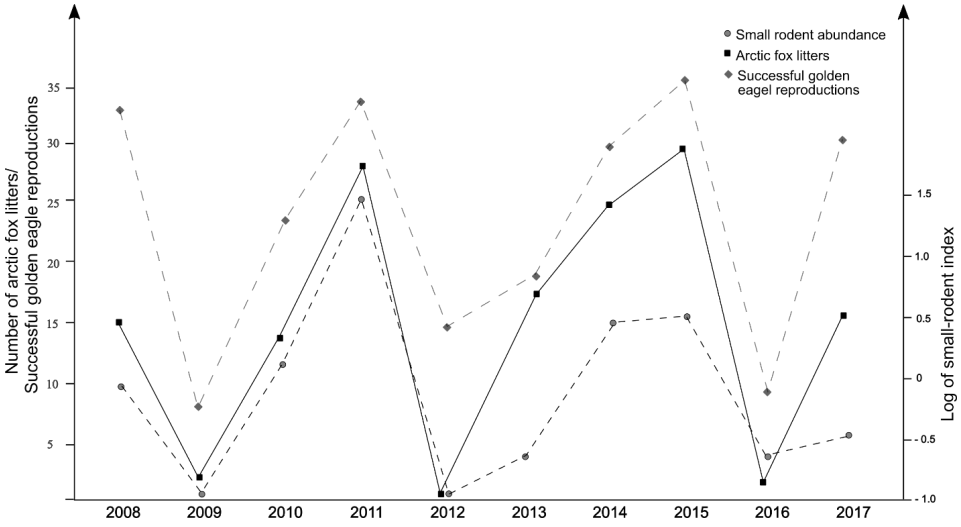

Figure 3. Rodent abundance and number of arctic fox litters in the Helagsfjällen area during 2008-2017, and successful golden eagle breeding in Jämtland County for the same period. (Larm et. al. 2020b).

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.

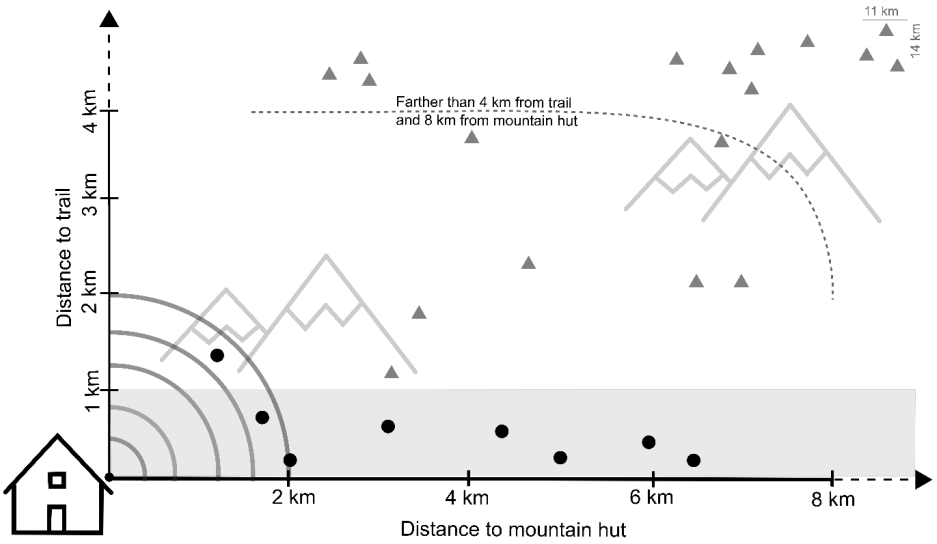

Figure 4. The location of the arctic fox dens included in the study in relation to hiking trails and tourist mountain cabins, around which the vast majority of the tourism activity is centered. Dens classified as disturbed by tourism activities (●) are located within 1 km of a trail and within 2 km of 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).

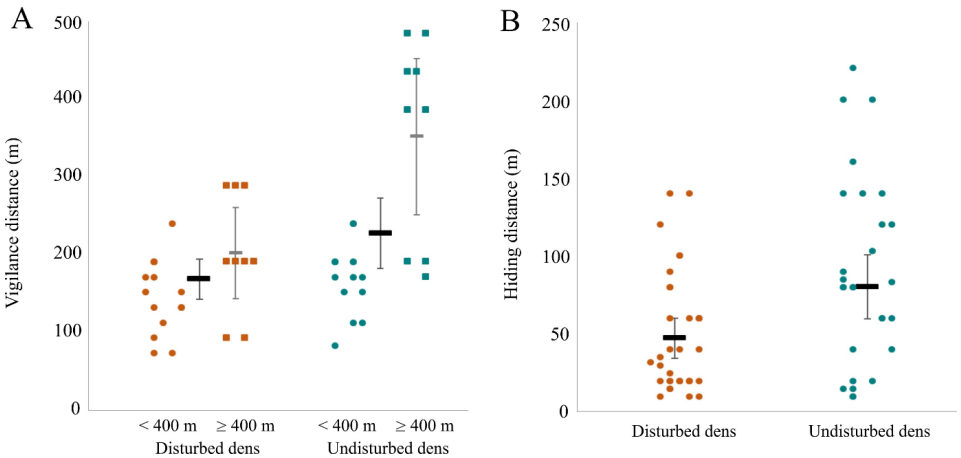

Figure 5. (A) Vigilance distance for arctic foxes at disturbed dens (● <400 m, ■ ≥400 m) and undisturbed dens (● <400 m, ■ ≥400 m), with approaches starting at <400 m on the left and ≥400 m to the right. Mean and error bars to the left (black) represent all approaches and to the right (grey) only approaches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

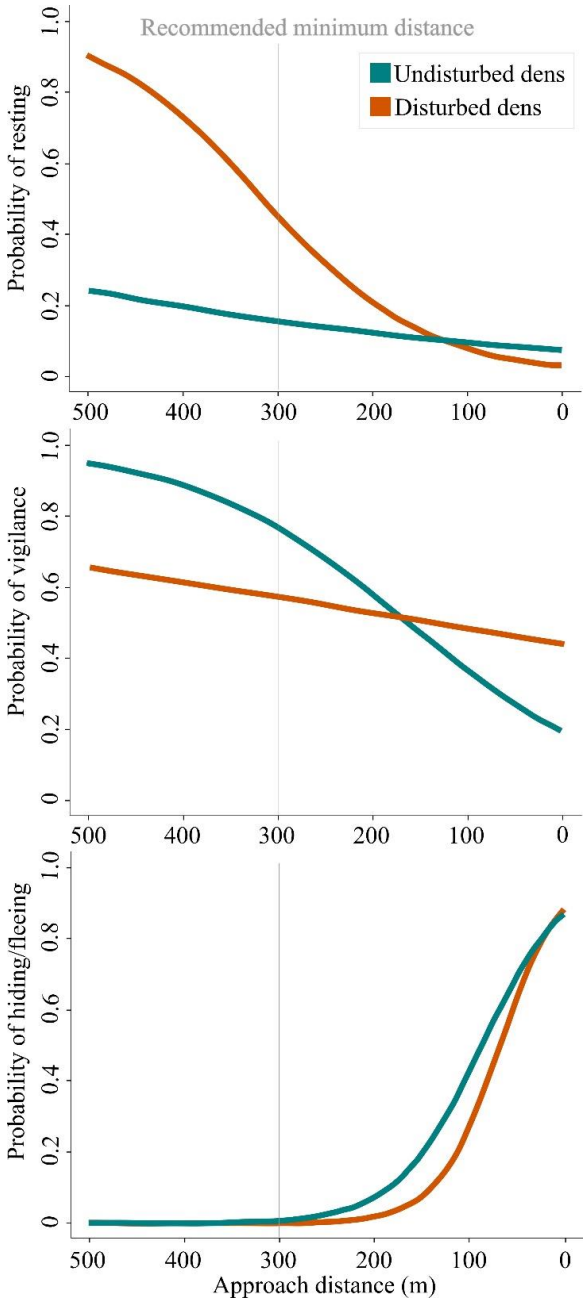

Figure 6. Probability of an arctic fox resting, being vigilant, or hiding or fleeing at decreasing approach distances for disturbed and undisturbed dens, as predicted by the generalized linear models. The grey vertical line marks the current recommended minimum distance (300m). (Larm et al., 2020a).

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).

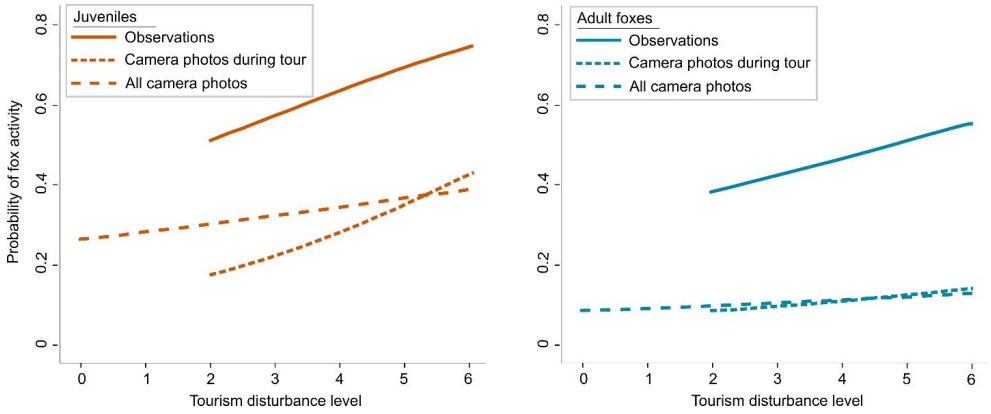

Figure 7. Three different probability estimates of adult and juvenile arctic fox activity with increasing disturbance level of the tour group during 13 guided tours in 2015. Solid lines are based on observation during the tour, short dotted lines (from 2 to 6) are based on camera photos taken during 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).

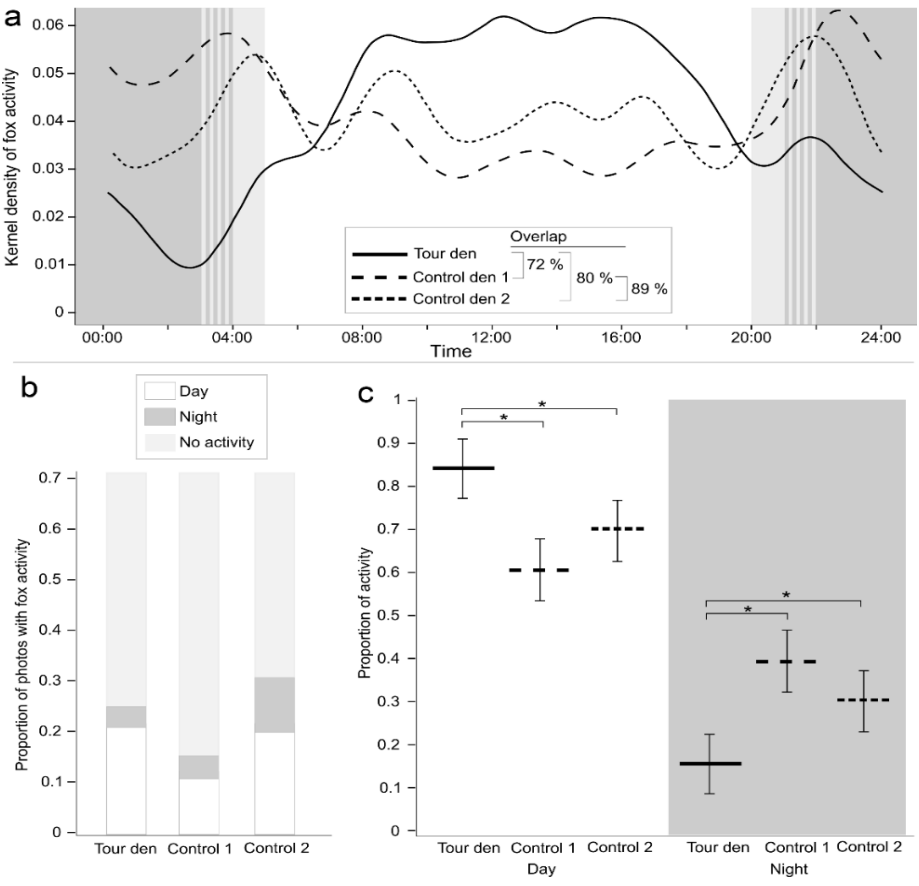

Figure 8. a) Comparison of diurnal activity distribution between the arctic fox den visited during the guided tours (solid line) and two undisturbed control dens (dotted lines). White background represents time with daylight, dark grey nighttime and light grey dawn and dusk. b) The proportion of photos 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.

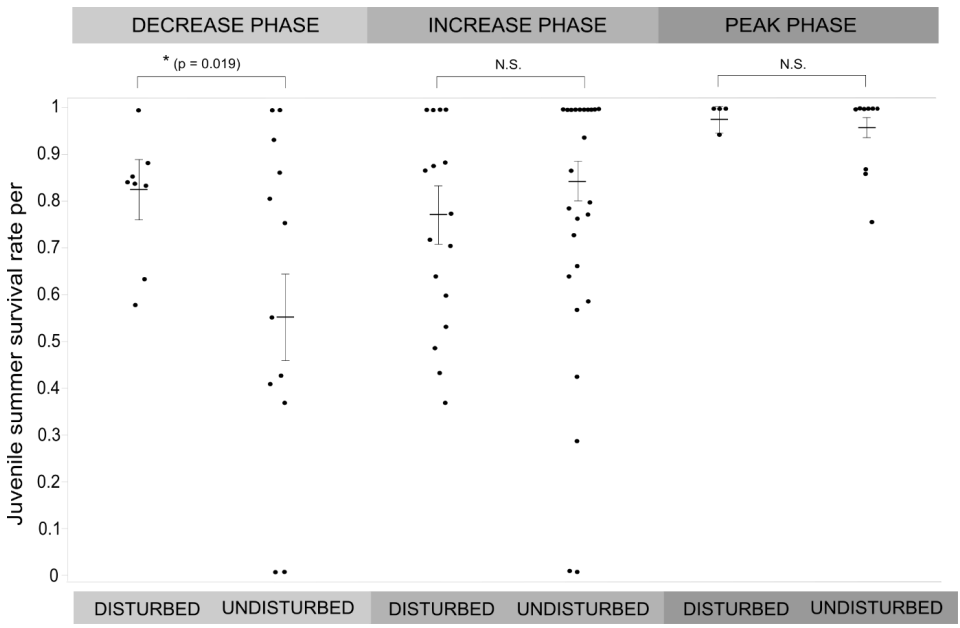

Figure 9. Differences in juvenile summer survival between dens that are disturbed and undisturbed by tourism activities for the different phases of the small-rodent cycle. The juvenile survival was higher at disturbed dens during decrease years, while there was no difference in survival during increase 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.

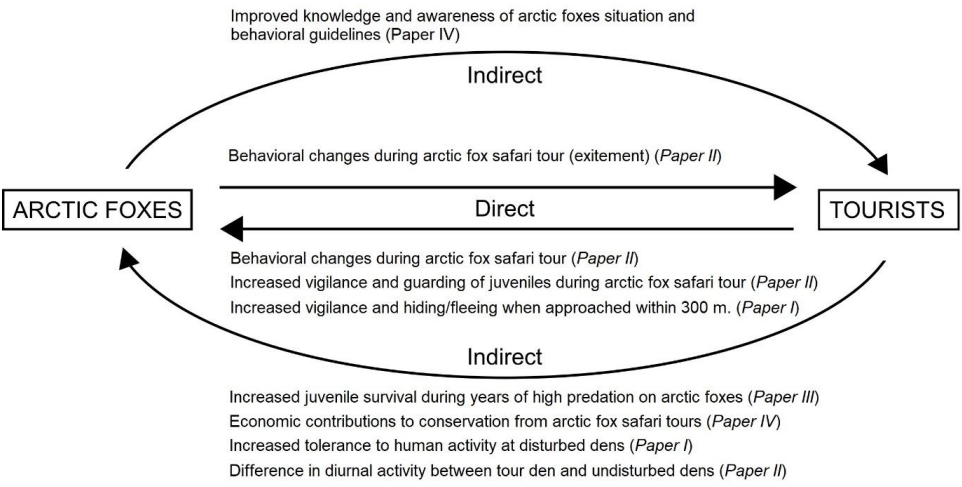

Figure 10. Schematic model summarizing the different direct and indirect effects on both arctic foxes and tourists identified in the studies included in this thesis.

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.