


Fitness effects of ecotourism on an endangered carnivore

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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, 2005b; 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, 2005a,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* (Kaijusalo, 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 km² 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

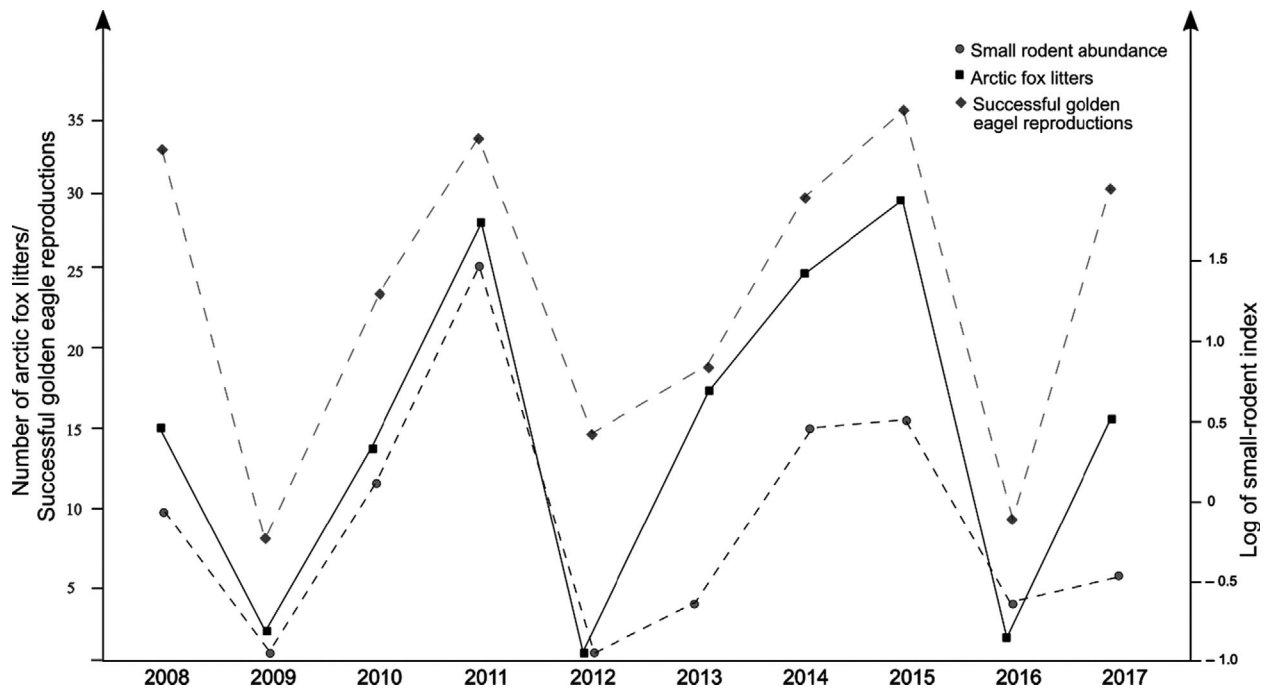


Figure 1 Small-rodent abundance and number of arctic fox litters in the Helagsfjällen area and number of successful of golden eagle reproductions in Jämtland County during the years of the study 2008–2017 (a value of 0.1 was added to the small-rodent trapping values of zero for the plotting).

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],

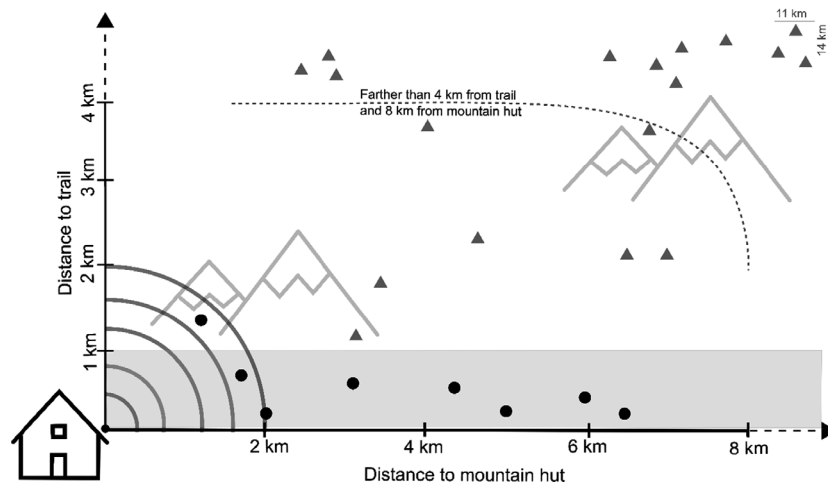


Figure 2 The location of the dens in the study in relation to hiking trails and tourist mountain huts, around which the vast majority of the tourism activity is centered. Dens classified as disturbed by tourism activities (●) are located within 1 km of a trail and within 2 km of a hut and are all within 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 data used in the study along with the small-rodent phase and index as well as golden eagle reproductions for each year

	Year										Total
	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	
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	
<i>n</i> (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

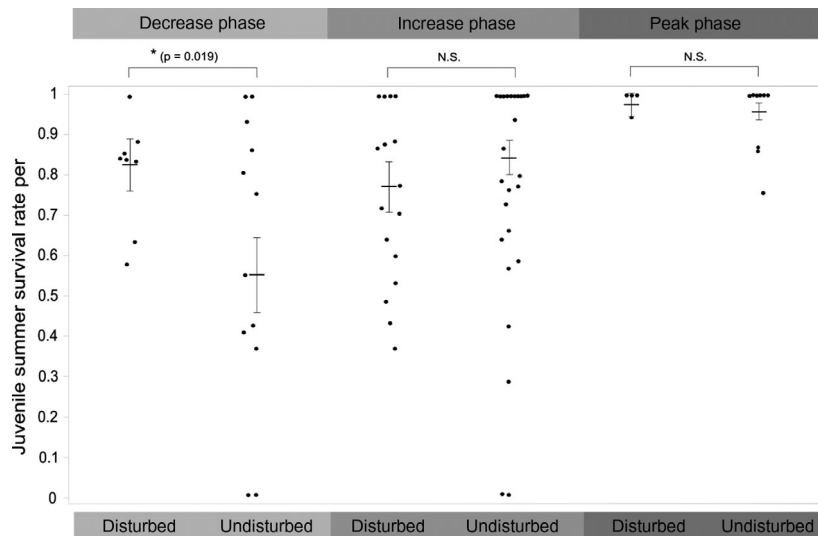


Figure 3 Juvenile summer survival rate per litter (Estimated mean \pm SE) between dens that are classified as disturbed and undisturbed by tourism activities for the different phases of the small-rodent cycle. Juvenile survival was higher at disturbed dens during decrease years, while there was no difference 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, 2005a,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.