Research Article

Use of Supplementary Feeding Dispensers by Arctic Foxes in Norway

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ABSTRACT Supplementary feeding is often used as a conservation tool to reverse the decline of food-limited populations. The arctic fox (*Vulpes lagopus*) is one of the most endangered mammals in Norway and has been the target of several conservation initiatives for almost 3 decades, including supplementary feeding. To measure and improve the efficiency of supplementary feeding as a conservation action, we used passive integrated transponder (PIT)-tags in arctic foxes and 6 feeding stations equipped with PIT-tag readers to monitor individual use of supplemental food between 2013 and 2018. We tested hypotheses about the potential influence of temporal and spatial patterns, individual characteristics (i.e., age, sex, reproductive status), and food abundance (abundance of small rodents and amount of food filled) on the frequency and intensity of use of supplementary feeding stations by arctic foxes. The feeding stations were visited ≥1 time by 196 PIT-tagged individuals. We detected 54% of juveniles born in the study area between 2013 and 2017 at the feeding stations. More arctic foxes used the feeding stations during the pre-breeding period than during the other seasons, and the visits occurred mostly at night. The closest feeding station to each natal den was systematically used by the established pair and by the juveniles born at this den. Juveniles did not use the feeding stations more than adult foxes. Older foxes, and breeding adults, visited the feeding stations more than younger and non-breeding adults. Foxes used feeding stations more intensively when prey was scarce and with greater amounts of supplemental food. This study highlights that supplemental feeding is important for breeding adults, especially in periods of low prey abundance. Understanding the use of feeding stations will contribute to the optimization of supplemental feeding as a conservation action and help wildlife managers to carefully plan and manage its discontinuation. © 2020 The Authors. *Journal of Wildlife Management* published by Wiley Periodicals, Inc. on behalf of The Wildlife Society.

KEY WORDS arctic fox, conservation, food limitation, monitoring, Norway, PIT-tag, supplementary feeding, *Vulpes lagopus*.

Biodiversity is declining globally; species persistence and ecosystem functioning and services are threatened as a result of human-mediated environmental degradation (Pimm et al. 2014, Brondizio et al. 2019). Within the range of actions to protect and restore wildlife species in their natural habitat, supplementary feeding is often used to reverse the decline of food-limited populations (Boutin 1990, López-Bao et al. 2008, Ewen et al. 2015, Murray et al. 2016). Supplementary

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feeding can have positive effects on several life-history traits, such as body condition (Boutin 1990, Banks and Dickman 2000, Isaac et al. 2004), growth, survival, or reproductive success (Angerbjörn et al. 1991, Tannerfeldt et al. 1994, Newey et al. 2010, Johnsen et al. 2017), and hence on population dynamics (Banks and Dickman 2000, López-Bao et al. 2010, Johnsen et al. 2017). Supplemental feeding may also affect individuals' movements and habitat choices (van Beest et al. 2010, Sahlsten et al. 2010, Bannister et al. 2016), including those of non-targeted species (Lambert and Demarais 2001, Kubasiewicz et al. 2016).

A prerequisite to supplementary feeding as a conservation action is that it is meant as a transitory measure, applied over a short period (Boutin 1990), and should allow for evaluation of the needs, benefits, risks, and actual use by the target species (Inslerman et al. 2006, Ewen et al. 2015). Given this, wildlife managers should minimize any undesired effects of

supplementary feeding, in particular the reduced ability of individuals to efficiently exploit wild prey (López-Bao et al. 2008). Necessary precautions should be taken to reduce potential harm to imperiled species because small populations could be most at risk of unforeseen negative consequences of supplementary feeding such as the transmission of infectious diseases (Tollington et al. 2015). Most studies on the effects of supplementary feeding have focused on comparing areas with and without supplementary feeding sites (Desy and Thompson 1983, Banks and Dickman 2000, Angerbjörn et al. 2013, Bannister et al. 2016, Johnsen et al. 2017). A small number of researchers examined the behavior of individuals under conditions of supplemental food (Boutin 1990), quantifying how individual characteristics, including sex, reproductive status, or age class, may affect the use of supplementary feeding in mammals (Isaac et al. 2004, Kenward et al. 2005, López-Bao et al. 2009, Newey et al. 2010, Ossi et al. 2017). Most of these analyses generally assume that all individuals have access to and use the food equally; however, it is not always the case (Newey et al. 2009). The logistical difficulties of assessing individual responses to supplemental food, particularly for cryptic or nocturnal species, has contributed to the inconclusiveness of supplementary feeding studies (Newey et al. 2009). Data should be collected and analyzed to better understand how individual animals use the supplied food and whether this use is constant over space and time to carefully plan supplementary feeding and its discontinuation. The knowledge gained will also be relevant to assess the costs and benefits of supplementary feeding as a conservation action.

The management of the arctic fox (*Vulpes lagopus*) in Scandinavia is an ideal study system to explore supplementary feeding. Supplementary feeding has been part of arctic fox conservation programs in Scandinavia for almost 3 decades (Angerbjörn et al. 1991). This small homeothermic carnivore with nocturnal habits has a circumpolar distribution across tundra above tree line. It can also be found in coastal areas, on arctic islands, and even in the open drift ice (Audet et al. 2002). Although still an abundant species in most of its distribution range, the arctic fox is listed as critically endangered in Norway (Wiig et al. 2015) and endangered in Sweden (Angerbjörn 2015). The Fennoscandian population was close to extinction in 2000, with only 40–60 adult animals left in the whole population, despite being fully protected since the 1930s (Angerbjörn et al. 2013).

The main hypothesis explaining the drastic decline involves extensive hunting in the late 1800s and early 1900s (Hersteinsson et al. 1989), whereas the lack of recovery is explained by low population size (Loison et al. 2001), decline and collapse of small rodent cycles (Henden et al. 2008, Ims et al. 2008, Kausrud et al. 2008), and increased competition with red fox (*Vulpes vulpes*; Tannerfeldt et al. 2002, Frafjord 2003). Considered as an opportunistic predator and scavenger (Frafjord 1993), the arctic fox is, in most inland areas, strongly dependent on fluctuating rodent populations such as lemmings (*Lemmus* spp.; Angerbjörn et al. 1995, Elmhagen et al. 2011, Meijer et al. 2013). In Scandinavia, the species reproduces almost exclusively in the increase and peak phase

of the lemming cycle (Ims et al. 2008, Meijer et al. 2013). Rodent cycles, however, have changed during the past decades, passing from large outbreaks every 3–5 years to a dampening of the cycle with irregular amplitudes (Ims et al. 2008, Kausrud et al. 2008, Cornulier et al. 2013), likely limiting the probability for arctic foxes to breed.

A combination of large-scale conservation actions has been implemented in Scandinavia to save the arctic fox from extinction since 1999, including supplementary feeding, red fox culling, and captive breeding and release (Angerbjörn et al. 2013; Landa et al. 2017a, b). This combination of actions has contributed to the partial recovery of the arctic fox population in Scandinavia (Angerbjörn et al. 2013), with an estimated minimum population of 304 adults in 2018 (Ulvund and Wallén 2018). The first attempts of supplementary feeding and red fox culling started in 1998 (Angerbjörn et al. 2013). The captive-breeding and release program, established in Norway in 2005, with the first releases in 2006 (Landa et al. 2017b), has released >400 arctic fox juveniles in 6 subpopulations in Norway (Landa et al. 2017a).

The captive-breeding and release program designed and built feeding dispensers to be exclusive to the arctic fox. The objective of the feeding dispensers is to reduce intra-guild competition for food with other carnivores, especially the red fox (Landa et al. 2017b), by increasing food availability during summer and winter. Energy requirements of arctic foxes are lower during winter than during summer (Audet et al. 2002) because of reduced activity and basal metabolic rate (Fuglei and Øritsland 1999, Fuglesteg et al. 2006) and high fur insulation in winter (Scholander et al. 1950), but food is scarcer and more difficult to find during winter. Feeding dispensers stand in areas with high density of arctic fox den sites to benefit adult and juvenile foxes. Juveniles are considerably less efficient hunters than the adults when foraging on their own, and may need comparatively more accessible, supplemental food than adults. High availability of supplemental food, however, might trigger hoarding behavior in arctic foxes (Careau et al. 2008); breeding adults are territorial (Landa et al. 1998), with older foxes dominate over younger individuals (Kullberg and Angerbjörn 1992). Considering the challenge of assessing individual use of supplementary feeding, the importance of evaluating feeding efficiency (Ewen et al. 2015), and the need to assess the cost efficiency of supplementary feeding as a conservation action, the captive-breeding program also developed an automated technique to strictly monitor the use of feeding dispensers by arctic foxes, using passive integrated transponder (PIT)-tag technology.

The main purpose of this descriptive study was to investigate the use of supplemental feeding dispensers by arctic foxes in central Norway. Our objectives were to test whether arctic fox visits to feeding dispensers were constant among seasons (pre-breeding, breeding, and post-breeding) and daily time periods (growing light, declining light, and night) and over space (distance to den); to evaluate how animals used the supplied food depending on individual characteristics (age, reproductive status, sex); and to investigate whether use of supplemental food was influenced by varying food abundance (small rodent abundance and amount of

food filled in each feeding station). We tested 4 hypotheses associated with season and time of day, spatial patterns, individual characteristics, and food abundance on the frequency and intensity of use of supplementary feeding stations by arctic foxes. We consider these hypotheses not to be mutually exclusive. Our predictions are built upon the assumptions that each detection of an arctic fox at a feeding dispenser is representative of an individual feeding on the supplemental food, and that the frequency of visits is proportional to the intake of supplemental food.

First, we evaluated the hypothesis that season and time of day would influence the use of feeding stations by arctic foxes. We predicted that the use of feeding dispensers is higher during winter (pre- and post-breeding periods) than during summer (breeding period), and that most visits at feeding stations occur at night. Second, we tested the hypothesis that the location of feeding dispensers would affect the use of feeding dispensers by arctic foxes. We predicted that juveniles and breeding adults would use mostly the closest feeding stations to their natal or active den. Third, we examined the hypothesis that individual characteristics, namely age, breeding status, and sex, would influence arctic fox use of supplementary feeding stations. We expected juveniles would use feeding stations more than adults, older foxes more than younger adults, and breeding individuals more than non-breeding foxes. We did not expect any difference in the use of feeding stations between males and females. Fourth, we tested the hypothesis that food abundance, namely the abundance of small rodents in the study area and the amount of food added to a feeding dispenser during a given period, influenced the use of feeding dispensers by arctic foxes. We predicted that foxes would use the supplemental feeders more when small rodent abundance was low and with increased amounts of supplemental food added.

STUDY AREA

We conducted the study in Norway between 2013 and 2018 in 1 core area of the current Scandinavian arctic fox population where the number of arctic foxes has been increasing because of the release of captive-bred juveniles combined with supplemental feeding (Angerbjörn et al. 2013, Landa et al. 2017b, Ulvund et al. 2018). The study area was located on the Dovrefjell Mountain plateau, within Dovrefjell-Sunndalsfjella National Park (1,693 km²; 62°21′00″N9°6′00″E) and in the eastern part of adjacent Knutshø (Fig. 1). The main activities in the area included hiking, cross-country skiing, reindeer hunting, and sheep grazing.

The region consists of mountain plateaus of an average altitude of 1,300 m, with peaks ≤2,200 m, separated by narrow and deep forested valleys. Above the tree line (~900–1,000 m), the vegetation was dominated by alpine meadow and lichen-heath communities up to about 1,500 m, above which there was little vegetation. Terrestrial mammals inhabiting the alpine tundra ecosystem of the study area included wild reindeer (*Rangifer tarandus*), wolverine (*Gulo gulo*), introduced muskox (*Ovibos moschatus*), arctic fox, and Norwegian lemming (*Lemmus lemmus*). The continental climate of the study area is characterized by long

winters, with ground usually covered by snow for 150–225 days from November to April with an average temperature of −6.2°C (1961–1990), and short summers, with a short growing season of 110–120 days from May to September (Framstad 2017) and an average temperature of 7.2°C (1961–1990). The area received an average of 400 mm of precipitation annually (The Norwegian Meteorological Institute 2018). Weather during the study period was similar to the long-term trends recorded in the study area, apart from a wetter and warmer summer in 2014 (The Norwegian Meteorological Institute 2018). We distinguish 3 periods based on arctic fox biology: the pre-breeding period followed by the mating period (Jan–May), the breeding period between June (birth of the litter) and the end of September (when the arctic fox juveniles leave the den), and the post-breeding period (early winter: Oct–Dec), when the juveniles are dispersing from the natal den.

METHODS

We carried out this study in accordance with the Norwegian animal welfare act and the regulation on the use of animals in research. Capture and marking of free-ranging arctic foxes was approved by the institutional animal welfare unit, the Norwegian Animal Research Authority (FOTS ID 8946), and the Norwegian Environmental Agency (2013/2412, 2015/5402). Marking of arctic foxes performed at Sæterfjellet captive breeding station is regarded part of the management procedures of the approved animal research facility (Unit number 150).

Feeding Stations

Food dispensers, or feeding stations, consist of 3 120-L inter-connected polyester barrels, with a 125-mm-diameter entrance tube (Fig. 2). The entrance tube restricts larger species (red fox and wolverine) from entering the device (Landa et al. 2017b). Feeding dispensers are refilled with commercial dog food pellets (Troll Elite Tørrfôr, Troll Hunderfôr AS, Trondheim, Norway). Between 2013 and 2017, local mountain rangers filled an average of 3,386 kg of dog food per year in all 31 feeding stations located within the study area. Out of these 31 feeding stations, 6 were equipped with a Biomark PIT-tag circular antenna and reader (FS-2001, Biomark, Boise, ID, USA), together with a solar panel and a set of batteries. The 6 feeding dispensers were located in the low and middle alpine tundra in areas with high densities of arctic fox den sites.

The antenna of the PIT-tag reader is installed between the entrance tube and the first standing barrel of the food dispenser, with a maximum detection distance of 15–20 cm. The reader continuously scanned for PIT-tags and logged the presence of any PIT-tag along with date and time, apart from some winter periods because of lack of battery power (limited sunlight) or because of equipment maintenance. Local mountain rangers checked the information stored on the reader each time they maintained and filled a feeding station (i.e., at a regular interval of 4–5 weeks). They provided an average of 159 kg of food per year in each of the
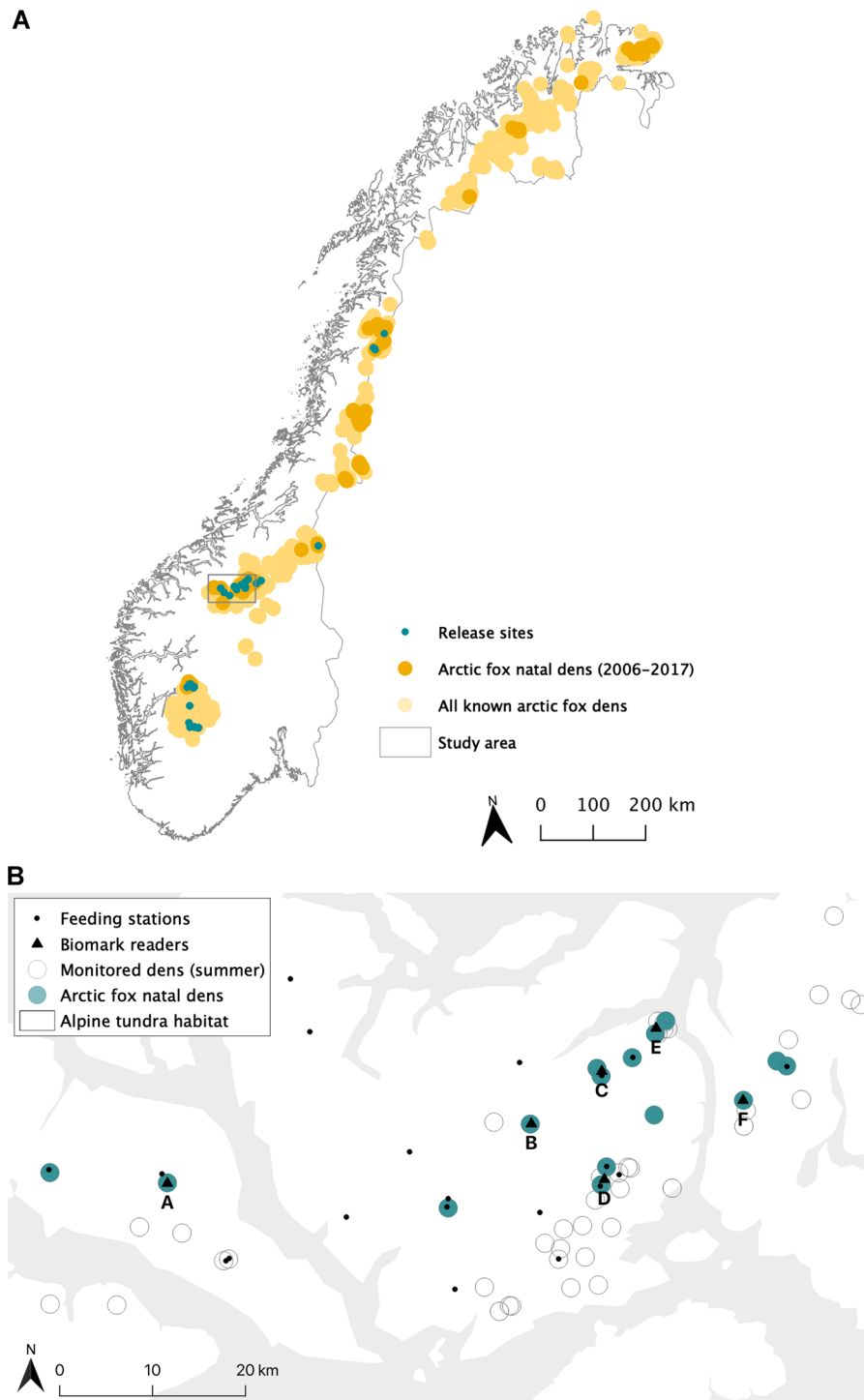
Figure 1. All known arctic fox dens in Norway and core areas of the population in Norway (A) and an overview of monitored arctic fox dens, feeding stations, and Biomark passive integrated transponder (PIT)-tag readers in Dovrefjell and Knutshø regions, Norway, summer 2013 to spring 2018 (B). The mountain landscape, the local names, and the national park boundaries are not shown because the localization of arctic fox dens is shielded from public access (https://sensitive-artsdata.miljodirektoratet.no/, accessed 1 Jul 2019).

6 feeding stations equipped with a PIT-tag reader in the study area.

Passive Integrated Transponders
The PIT-tags consist of a passive electronic microchip encased in biocompatible glass, and are commonly used in wildlife research, including to study feeding behavior (Isaac et al. 2004, Kenward et al. 2005, Newey et al. 2009). If a tag is present, the reader generates a close-range, electromagnetic field that causes the tag to transmit a unique alphanumeric code, which is read and stored by the reader. Testing the detection distance confirmed that PIT-tags are only detected when a fox or a test chip passes through the loop antenna of the PIT-tag reader, and are not detected outside of the feeding stations.

Figure 2. A feeding station in Dovrefjell, Norway designed by T. Sandal, later modified by R. D. Meås for exclusive use by arctic foxes monitored between summer 2013 and spring 2018 with entrance tube of the feeder (a), entrance barrel (b), access to food (c), solar panel to supply the battery (d), food barrel (e), and depot barrel to store food, batteries, and Biomark reader (f). The Biomark loop antenna is located between the entrance barrel (b) and the first standing barrel (c).

We captured juvenile arctic foxes in the study area between 2008 and 2017 and marked each with a PIT-tag. We used baited Tomahawk live traps (model SLDG DR, 6 kg, 81 cm long, 24 cm wide, and 30 cm high; Tomahawk, Hazelhurst, WI, USA) at den sites between July and August. We marked pups weighing >700 g and adults with PIT-tags. We injected arctic foxes released in the study area through the captive-breeding and release program between 2006 and 2017 with a PIT-tag before their release. We injected Biomark tags (HPT12, 12.5 mm in length, biocompatible glass, 134.2 kHz FDX-B, ISO 11784/11785 compliant) subcutaneously between the shoulder blades to provide a reliable lifetime barcode for each tagged fox. We weighed all foxes with a spring scale to the nearest 50 g (Pesola spring scale 5 kg, Pesola, Schindellegi, Switzerland) and identified sex.

Data Handling

We identified all arctic fox individuals detected at the 6 feeding dispensers of Dovrefjell and Knutshø between January 2013 and May 2018. Readers operated from 18 January to 19 December. Readers were active on average 63, 71, and 27 days during the pre-breeding, breeding, and post-breeding periods, respectively.

We considered an individual to be detectable during a given time period if it was marked with a PIT-tag during the time period; it was detected on ≥1 occasion during the time period; or it was marked in a previous time period, was not detected during the time period, and was detected during a later time period. We excluded arctic foxes born at the captive-breeding station and released in the study ($n = 10$ captive-bred and released foxes out of 196 different detected foxes) from the analyses. We also excluded periods when the PIT-tag readers were not working (limited battery power or maintenance).

For each detectable fox, for each site and each season, we computed a binary variable indicating whether a fox was never detected (0) or detected on ≥1 occasion (1), to calculate the proportion of detected foxes. We also estimated the visitation rate as the number of days a detectable fox was detected per site per period out of the number of days it could have been detected, based on the date the fox was marked and the number of days the reader was active.

We categorized individuals as juveniles and adults based on the year of birth, with foxes first registered as during the pre-breeding season following the birth. We classified adult males and females as breeders if they were observed, captured, or recorded with cameras or DNA samples at a den with pups between June and September; otherwise, we considered them non-breeders. Arctic fox dens are monitored in winter and summer through the arctic fox national monitoring program, and the probability of not detecting a breeding event is low in the study region (Ulvund et al. 2018). We also recorded the distance between active dens and feeding stations equipped with Biomark readers. Small rodent abundance was categorized as low, intermediate, or high based on the number of rodents trapped per 100 trap-nights collected by the terrestrial ecosystem monitoring program (TOV) in Norway (Framstad 2017). Low rodent abundance corresponds to the low phase, when rodents are at the lowest densities (trap index = 0.3 ± 0.5 [SD], $n = 4$, TOV data at Åmotsdalen, Dovrefjell, Norway, 2005–2017). Intermediate rodent abundance corresponds to the increase phase (i.e., increasing rodent density over the summer, trap index = 3.0 ± 1.9, $n = 4$), followed by a year with relatively high rodent abundance (i.e., peak phase, trap index = 28.3 ± 25.8, $n = 4$). We calculated the amount of supplemental food (kg of dog food) added to each feeder per period as supplied by field personnel.

To better understand the use of the feeding stations by arctic fox throughout the day, we defined 1 hourly visit as 1 individual detected at 1 locality at a given hour. To analyze time patterns of activity, we defined 3 periods using the ephemerides of Oppdal, Sør-Trøndelag (The Norwegian Meteorological Institute 2018) and the hourly visits of foxes: the growing light when the detection occurred between sunrise and meridian, declining light for detections between the meridian and the sunset, and night.

Statistical Analysis

We carried out all statistical analyses in R (R version 3.6.0, www.r-project.org, accessed 6 Jun 2019). To study arctic fox use of the feeding stations, we focused on whether and how often each detectable individual was detected per period per feeding station. We built a generalized linear mixed model [GLMM] with the glmer function from the package lme4 (Bates et al. 2015) with a binomial distribution and a logit function to test the fixed effects of season, age, sex, small rodent abundance, and amount of supplemental food on the proportion of detected foxes (response variable: 1 = detectable and detected versus 0 = detectable and not detected). We fitted a GLMM with a binomial distribution and a logit function to test the fixed effects of season, age, sex, small rodent abundance, and amount of supplemental food on the visitation rate of arctic foxes at the feeding dispensers (response variable: number of detections per fox per site per season versus number of occurrences where it could have been detected).

We used GLMMs with a binomial distribution to test the fixed effects of age class, sex, season, small rodent abundance, and amount of supplemental food for all wild-born PIT-tagged foxes; the fixed effects of age, sex, season, small rodent abundance, amount of supplemental food, and reproductive status for adult foxes; the fixed effects of age, sex, season, small rodent abundance, amount of supplemental food and distance to the breeding den for adult breeders only; and the fixed effects of sex, season, small rodent abundance, amount of supplemental food, and distance to natal den for juvenile foxes only. We mean-centered distance to active dens and amount of refilled food by subtracting their means and dividing by their standard deviations. We fitted a GLMM with a Poisson distribution to test the fixed effect of time of day on the number of detections of detectable arctic foxes per season per site.

All models included random, intercept-only terms for fox identity and site. Because of the limited number of covariates, we ran global models, and only simplified in cases of convergence, overdispersion, or singularity issues. In such cases, we present the most complex appropriate model. We obtained overall effects of the different fixed parameters with the package car (Package car, ftp://mirrors.ucr.ac.cr/CRAN/web/packages/car/car.pdf, accessed 6 Dec 2017). We obtained confidence intervals of fixed effect parameter estimates using the profile likelihood method implemented in the confint.merMod function of the lme4 package, and back-transformed using the plogis function. We used the r.squaredGLMM function from the MuMIn package (Bartoń 2017) to estimate marginal and conditional R^2 values. Marginal R^2 (R^2_m) values represent variance explained by fixed factors, and conditional R^2 (R^2_c) values give information about the variance explained by the complete model (Nakagawa and Schielzeth 2013). We used the ggpredict function (Package ggeffects, https://cran.r-project.org/web/packages/ggeffects/index.html, accessed 6 May 2019) to plot the fixed effects.

RESULTS

Tagged Foxes and Visits to Feeding Stations
We captured and injected 325 juvenile arctic foxes with PIT-tags at den sites between 2010 and 2017 (Table 1), and released 94 captive-bred arctic foxes marked with a PIT-tag in the study between 2006 and 2017. We recorded 69,568 detections of PIT-tags at the 6 feeding stations equipped with PIT-tag readers in the study area between 2013 and 2018. We recorded an average of 3.2 active dens within a 10-km radius of a feeding stations equipped with a PIT-tag reader between 2013 and 2017 (Fig. 1B; Table 2).

During the study period, the feeding stations were visited at least once by 196 PIT-tagged individuals (93 females and 103 males, 10 captive-bred and 186 wild-born foxes, on average 27 ± 11 [SE] adults [range = 10–39] and 36 ± 35 juveniles [range = 7–104] per calendar year; Appendix A). The number of arctic foxes detected (Fig. 3B) varied between localities (Appendix B), ranging from 2 to 45, with a sex ratio (male/female) of detected foxes of 1.4 ± 1.2 (range = 0.3–7). Two detected foxes were not expected: a fox born in captivity in 2011 and released in southern Norway (Finse) on 1 February 2012, around 400 km away from Knutshø, was detected using the feeding station of Vårstigdalen and a fox that escaped the captive-breeding station in 2012 and was not detected by any technique (DNA, camera trap, observation) before it bred in 2014.

Temporal and Spatial Patterns of Activity
Wild-born PIT-tagged arctic foxes used the feeding stations more during the pre-breeding period than during the other seasons (proportion of detected foxes, $P < 0.001$; Table 3; Fig. 4). Arctic foxes used the feeding station mostly at night (Fig. 5; $P < 0.001$). We identified 5,122 visits during growing light (27.9%), 1,434 during declining light (7.8%), and 11,807 at night (64.3%).

Arctic foxes used all 6 feeding stations and some individuals visited >1 feeding station, indicating that there was movement between areas despite the distance between the sites. On average there was 9 km between 2 Biomark stations, ranging from 7 km to 9 km, with 1 outlier 39 km away from the other closest feeding station equipped with a reader.

The distance between a given feeding station and an active den was known for only breeding adults and juveniles. The established pair and the juveniles born at the den systematically used the closest feeding station to each natal den (1 fox also fed at another feeding station equipped with a PIT-tag reader located 7 km away from its den). We detected breeding adults

Table 1. Monitoring effort and status of the arctic fox population in Dovrefjell and Knutshø regions, Norway, summer 2013 to spring 2018.

	2013	2014	2015	2016	2017	2018
Number of monitored dens[a]	75	72	79	78	85	
Estimated minimum population size (spring)[a]	32	41	25	24	44	49
Number of natal dens[a]	15	16	1	9	16	
Minimum number of juveniles born[a]	103	133	4	31	90	
Number of juveniles PIT[b]-tagged in Jul–Aug	102	125	0	25	68	
Number of feeding dispensers[a]	31	31	32	35	35	35
Number of feeding dispensers with a PIT-tag reader	6	6	4	4	5	5
Abundance of small rodents[a,c]	High	High	Low	Intermediate	High	Low

[a] Information extracted from Rovbase, Norwegian Environmental Agency, the yearly reports of the national monitoring program on arctic foxes (Ulvund et al. 2018).
[b] Passive integrated transponder.
[c] Low rodent abundance corresponds to the low phase, when rodents are at the lowest densities. Intermediate rodent abundance corresponds to the increase phase, followed by a year with high rodent abundance.

	Site						
	Avlsstasjonen	**Åmotsdalen**	**Slettehø høy**	**Tjønnglupen**	**Vangsvatnet**	**Vårstigdalen**	
Mountain area	Dovrefjell	Dovrefjell	Dovrefjell	Dovrefjell	Dovrefjell	Knutshø	
Number of natal dens within 1-km radius (2013–2017)	1.3 (1–2)	0.8 (0–1)	1.0 (0–2)	1.5 (0–2)	1	0.8 (0–1)	1.1
Number of natal dens within 10-km radius (2013–2017)	5.0 (3–6)	3.4 (0–5)	3.8 (0–5)	4.5 (0–7)	1	1.8 (0–4)	3.2
Number of natal dens within 20-km radius (2013–2017)	11.3 (10–13)	8.2 (0–12)	8.3 (0–13)	7.8 (0–13)	2	7.5 (0–12)	7.5
Number of days with arctic fox detections (2013–2018)	15.3 (9–21)	27.7 (8–39)	31.2 (8–69)	20.5 (7–28)	15.7 (11–20)	7.8 (2–20)	19.7
Number of days the readers were active (2013–2018)	109 (0–230)	121 (62–151)	99 (0–204)	100 (6–235)	66 (0–171)	95 (19–196)	98

on average 1.7 ± 2.2 km (range = 0.1–7.3) away from the active den during the breeding period, 4.8 ± 4.9 (range = 0.1–14.9) before the breeding period, and 4.6 ± 6.5 (range = 0.1–17.5) after the breeding period. Breeding adults used the feeding stations closest to the natal dens ($P < 0.001$; Table 4; Fig. 6). An estimated 99.0% (95% CI = 79.3–100) of detectable breeders were detected at a feeding station if the natal den was located within 1 km of the feeding station, versus 97.0% (95% CI = 64.4–99.8) if the natal den was within a distance of 40 km. Juveniles were detected on average 1.3 ± 3.0 km (range = 0.1–18.3) away from their natal den during the breeding period, and 3.4 ± 5.8 km (range = 0.1–30.4) away during the post-breeding period. The distance to the natal den had a major influence on the proportion of detected wild-born juvenile foxes and on their visitation rates at feeding stations ($P < 0.001$; Table 5). In the areas with the highest den density, juveniles from different dens (≤ 7 different dens) shared the feeding stations.

Individual Characteristics

We recorded 47 litters, for which 98% of the parentage was known, in the study area between 2013 and 2017. We marked 318 juveniles between 2013 and 2017 and detected 143 (45%) of them at the feeding stations during their first year of life. Some foxes were not detected as juveniles but used the feeding stations later in life. A total of 172 (54%) of the 318 marked juveniles were detected using a feeding station on at least 1 occasion. Juveniles did not use the feeding stations more than adult foxes ($P = 0.320$; Table 3). Out of the 64 identified breeding adults (92 when summing the number of litters of each individual during the study period), 37 individuals were potentially detectable by a PIT-tag reader (51 from 34 different pairs), and 20 (54%) were detected using the feeding stations of Dovrefjell and Knutshø (23 of 18 different pairs). Every year, we detected the majority of the detectable breeders (57–100%), versus 36–77% of the detectable non-breeders. On average, 42 ± 23 non-breeding foxes were not detected out of 93 ± 45 available for detection. Breeding adults visited the feeding stations significantly more than the non-breeding adults (visitation rate, $P \leq 0.001$; Table 6). Age had a positive effect on the proportion of detected adult foxes and on their visitation rates ($P = 0.019$ and $P < 0.001$, respectively; Table 6). Sex did not affect the detection and visitation rates of adult ($P = 0.262$, $P = 0.446$,
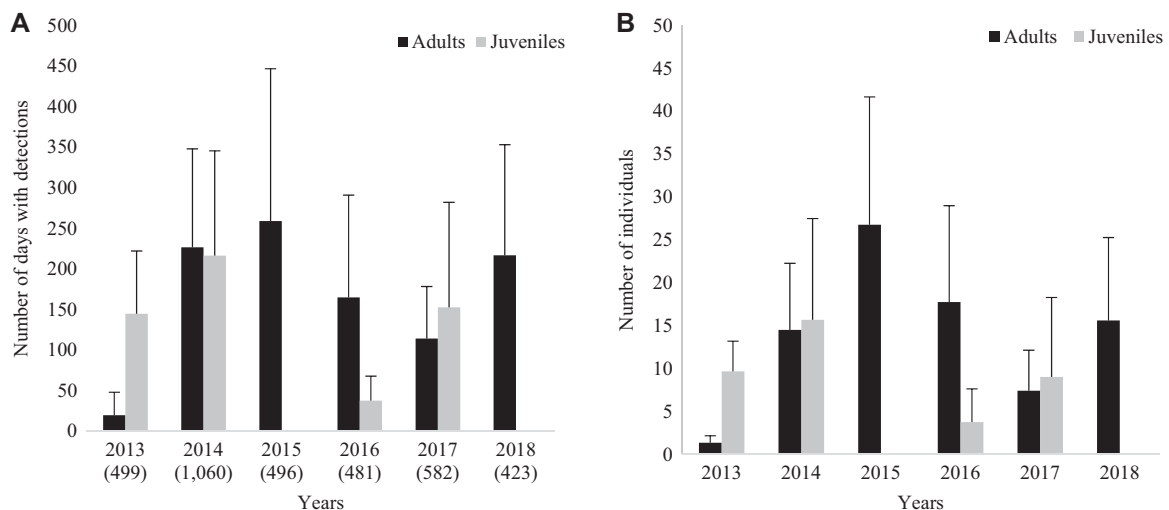

Figure 3. Average number of days with detections of arctic fox juveniles and adults per site (A) for each year in Dovrefjell and Knutshø regions, Norway, summer 2013 to spring 2018 (the number of days that the readers were active are shown in parentheses) and average number of arctic fox individuals per site for each year of the study (B).

Table 3. Results from a generalized mixed effects model (GLMM) testing the effects of season, age class, small rodent abundance, and amount of supplemental food, on the proportion of detected arctic foxes at supplementary feeding stations fitted with Biomark passive integrated transponder (PIT)-tag readers in Dovrefjell and Knutshø regions, Norway, summer 2013 and spring 2018. We calculated parameters using GLMM with a binomial distribution, with fox identity and site included as random intercept-only terms, and with pre-breeding period, juvenile age class, and high abundance of small rodents as reference levels. We excluded sex from the model because of convergence failure of the full model. We obtained 4,055 observations of 325 individuals at 6 sites. There was no valid model for the visitation rate data.

Parameter	Estimate	2.5% CI	97.5% CI	Z	P
Proportion of detected foxes[a]					
Intercept	−1.508	−1.990	−1.026	−6.13	≤0.001
Breeding period	−0.904	−1.192	−0.614	−6.12	≤0.001
Post-breeding period	−0.582	−0.955	−0.210	−3.06	0.002
Sex		Excluded from model (convergence failure)			
Age class	−0.140	−0.416	0.136	−1.00	0.320
Intermediate abundance of small rodents	0.344	0.024	0.665	2.10	0.035
Low abundance of small rodents	0.502	0.263	0.741	4.12	≤0.001
Food (scaled)	0.520	−0.054	0.215	1.17	0.243

[a] $R_m^2 = 0.077$, $R_c^2 = 0.196$, overdispersion ratio = 0.917.

respectively; Table 6) and juvenile foxes (proportion of detected foxes: $P = 0.947$; Table 5).

Food Abundance

We detected the highest proportion of wild-born PIT-tagged arctic foxes at feeding stations during periods of low small rodent abundance ($P < 0.001$; Table 3; Fig. 4). This was also observed for adults ($P = 0.029$; Table 6) and juveniles separately ($P = 0.001$; Table 5). Of the juveniles born within a distance of 1 km of a feeding station with a PIT-tag reader, 90.9% were detected during the breeding season of a period of low abundance of small rodents, versus 48.6% for intermediate, and 68.5% for high abundance (Table 5; Fig. 7). The visitation rates of adult and juvenile foxes increased with higher amounts of supplemental food ($P < 0.001$; Tables 5 and 6).

DISCUSSION

In our study, 143 juvenile and 113 adult arctic foxes visited the 6 feeding stations equipped with PIT-tag readers in Dovrefjell

and Knutshø between 2013 and 2018. Considering the map of all active feeding stations of the area (Fig. 1B), we assumed that the whole population had access to supplemental food.

Temporal and Spatial Patterns of Activity at Feeding Stations

The proportion of detected foxes at feeding stations was significantly higher during the pre-breeding period than during the post-breeding period, and during the post-breeding period than during the breeding period, as predicted (Fig. 4). It seems that arctic foxes used feeding stations highly opportunistically in response to lower food availability during winter, when food is scarce. A study from Sweden on radio-collared foxes born between 1986 and 2001 reported that all adult mortality occurred between October and May, during winter months, although the cause of deaths could not be established (Angerbjörn et al. 2004). Fat stores of arctic foxes decrease mostly during March and April, following the harshest winter period, concomitantly to increased energetic requirements related to reproduction (Prestrud and Nilssen 1995). Moreover, most of the detections of arctic foxes at feeding stations occurred at night, which is consistent with the nocturnal habits of the species
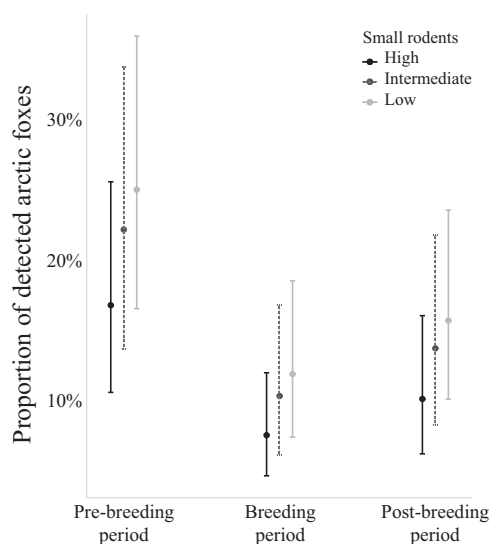

Figure 4. Predicted probabilities of arctic fox detections at supplementary feeding stations equipped with Biomark passive integrated transponder (PIT)-tag readers depending on abundance of small rodents and season in Dovrefjell and Knutshø regions, Norway, summer 2013 to spring 2018.
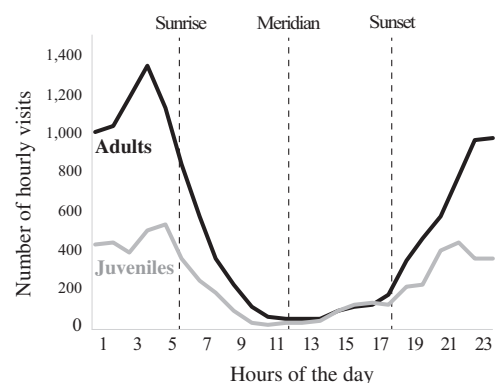

Figure 5. Number of visits of arctic fox adults and juveniles per hour of the day in Dovrefjell and Knutshø regions, Norway, summer 2013 to spring 2018 ($n = 18,363$ visits, 196 individuals). Dotted lines show from left to right the average hour of sunrise (0510), meridian (1121), and sunset (1732) in Oppdal, Norway.

Table 4. Results from generalized mixed effects models (GLMM) testing the effects of season, sex, age, small rodent abundance, amount of supplemental food, and distance to breeding den on the proportion of detected arctic fox breeding adults and on their visitation rates at supplementary feeding stations fitted with Biomark passive integrated transponder (PIT)-tag readers in Dovrefjell and Knutshø regions, Norway between summer 2013 and spring 2018. We calculated parameters using GLMM with a binomial distribution, with fox identity and site included as random intercept-only terms, and with pre-breeding period, female sex, and high abundance of small rodents as reference levels. We excluded 2 covariates from each model because of convergence failures. We obtained 201 observations of 14 individuals at 6 sites.

Parameter	Estimate	2.5% CI	97.5% CI	Z	P
Proportion of detected breeding adults[a]					
Intercept	−7.079	−9.940	−4.217	−4.85	≤0.001
Breeding period	−1.261	−2.926	0.403	−1.49	0.138
Post-breeding period	−0.576	−2.528	1.377	−0.58	0.564
Small rodent abundance		Excluded from model (convergence failure)			
Sex	−0.704	−2.512	1.032	−0.82	0.413
Distance to breeding den (scaled)	−10.362	−14.820	−5.903	−4.56	≤0.001
Age		Excluded from model (convergence failure)			
Food (scaled)	0.277	−0.557	1.111	0.65	0.515
Visitation rate of breeding adults[b]					
Intercept	−15.066	−17.699	−12.432	−11.21	≤0.001
Breeding period	−0.709	−1.000	−0.418	−4.78	≤0.001
Post-breeding period	−2.106	−2.803	−1.401	−5.92	≤0.001
Intermediate abundance of small rodents	−1.491	−2.171	−0.811	−4.30	≤0.001
Low abundance of small rodents	2.372	1.484	3.260	5.24	≤0.001
Sex		Excluded from model (convergence failure)			
Age	0.900	0.564	1.236	5.25	≤0.001
Food (scaled)		Excluded from model (convergence failure)			
Distance to breeding den (scaled)	−12.743	−14.493	−10.994	−14.28	≤0.001

[a] $R_m^2 = 0.964$, $R_c^2 = 0.971$, overdispersion ratio = 3.188.
[b] $R_m^2 = 0.947$, $R_c^2 = 0.980$.

(Audet et al. 2002) and was also confirmed by analyzing camera trap data in the same study area (Bouchetard-Aubus 2017). This is consistent with the hypothesis that time would influence the use of feeding stations by arctic foxes. The nocturnal activity peak is likely linked to predator avoidance; the arctic fox is described as less nocturnal in regions like Svalbard where it is not exposed to other mesocarnivore competitors (Fuglei et al. 2017).

When the distance between a given fox's den location and a feeding station was known, GLMMs revealed a strong effect of the distance to the active den on the proportion of detected foxes and the visitation rates at feeding stations as predicted. This indicates that the traveling distance to a feeding dispenser is a very important predictor of whether and how often foxes actually have access to supplemental food. A careful geographical
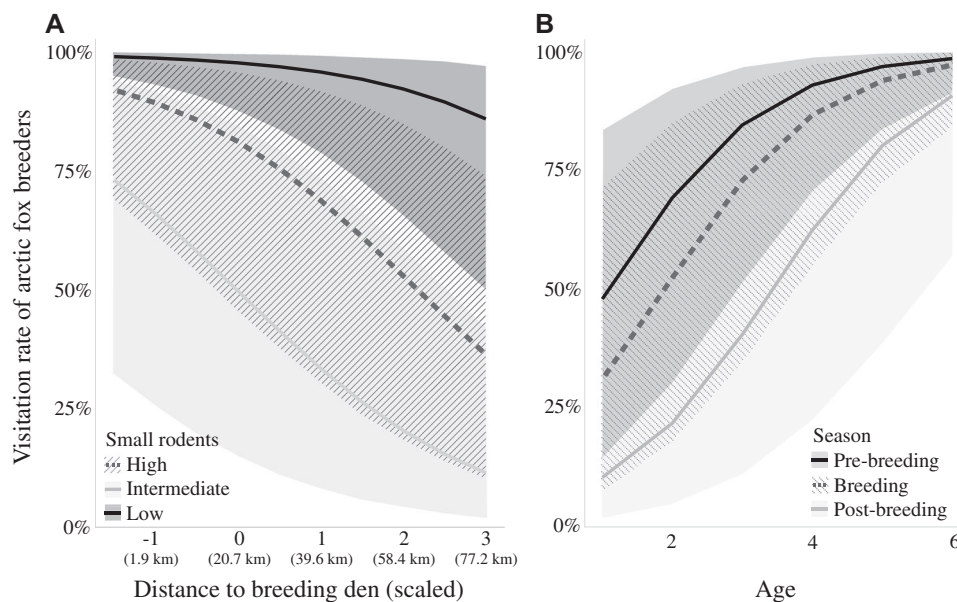

Figure 6. Predicted visitation rates of arctic fox breeders at supplementary feeding stations equipped with Biomark passive integrated transponder (PIT)-tag readers depending on distance to natal den and abundance of small rodents (A), and age and season (B) in Dovrefjell and Knutshø regions, Norway, summer 2013 to spring 2018.

Table 5. Results from generalized mixed effects models (GLMM) testing the effects of season, sex, small rodent abundance, amount of supplemental food, and distance to natal den on the proportion of detected arctic fox juveniles and on their visitation rates at supplementary feeding stations fitted with Biomark passive integrated transponder (PIT)-tag readers in Dovrefjell and Knutshø regions, Norway between summer 2013 and spring 2018. We calculated parameters using GLMM with a binomial distribution, with fox identity and site included as random effects, and with breeding period, female sex, and high abundance of small rodents as reference levels. We excluded sex from the visitation rate model because of convergence failure. We obtained 2,153 observations from 318 individuals at 6 sites.

Parameter	Estimate	2.5% CI	97.5% CI	Z	P
Proportion of detected juveniles[a]					
Intercept	−8.579	−9.925	−7.233	−12.49	≤0.001
Post-breeding period	0.599	−0.121	1.318	1.63	0.103
Intermediate abundance of small rodents	−0.834	−1.836	0.167	−1.63	0.103
Low abundance of small rodents	1.522	0.610	2.434	3.27	0.001
Sex	0.015	−0.437	0.468	0.07	0.947
Food (scaled)	0.135	−0.216	0.486	0.75	0.450
Distance to natal den (scaled)	−7.804	−8.986	−6.621	−12.94	≤0.001
Visitation rate of juveniles[b]					
Intercept	−14.371	−15.194	−13.547	−34.21	≤0.001
Post-breeding period		Excluded from model (convergence failure)			
Intermediate abundance of small rodents	−0.877	−1.342	−0.412	−3.69	≤0.001
Low abundance of small rodents	1.322	1.130	1.515	13.46	≤0.001
Sex		Excluded from model (convergence failure)			
Food (scaled)	0.298	0.201	0.395	6.00	≤0.001
Distance to natal den (scaled)	−9.934	−10.490	−9.380	−35.06	≤0.001

[a] $R_m^2 = 0.938$, $R_c^2 = 0.949$, overdispersion ratio = 7.706.
[b] $R_m^2 = 0.907$, $R_c^2 = 0.969$.

distribution of feeding dispensers around known active dens will likely maximize the efficiency of the feeding dispensers.

Effects of Prey Abundance and Availability of Supplemental Food

Juvenile and adult arctic foxes visited the feeding stations more during periods of low rodent abundance in the study area, consistent with the hypothesis that food abundance influenced the use of feeding dispensers by arctic foxes. Small rodents, and especially lemmings, are key species of the alpine tundra ecosystem in that the existence of many other species depends on their occurrence (Krebs et al. 2003), especially the arctic fox. Arctic fox reproductive effort fluctuates with small rodent abundance, with the maximum number of litters and the biggest litters during peaks in small

Table 6. Results of generalized mixed effects models (GLMM) testing the effects of season, breeding status, sex, age, small rodent abundance, and amount of supplemental food, on the proportion of detected adult arctic foxes and on their visitation rates at supplementary feeding stations fitted with Biomark passive integrated transponder (PIT)-tag readers in Dovrefjell and Knutshø regions, Norway between summer 2013 and spring 2018. We calculated parameters using GLMM with a binomial distribution, with fox identity and site included as random intercept-only terms, and with pre-breeding period, active breeding status, female sex, and high abundance of small rodents as reference levels. We excluded amount of supplemental food from the proportion of detected foxes model because of convergence failure. We obtained 1,902 observations from 95 individuals at 6 sites.

Parameter	Estimate	2.5% CI	97.5% CI	Z	P
Proportion of detected adults[a]					
Intercept	−1.911	−2.726	−1.095	−4.59	≤0.001
Breeding period	−0.827	−1.119	−0.535	−5.55	≤0.001
Post-breeding period	−1.084	−1.463	−0.704	−5.59	≤0.001
Breeding status	0.133	−0.367	0.634	0.52	0.601
Sex	0.221	−0.165	0.607	1.12	0.262
Age	0.133	0.022	0.244	2.34	0.019
Intermediate abundance of small rodents	0.317	−0.079	0.713	1.57	0.117
Low abundance of small rodents	0.331	0.034	0.629	2.18	0.029
Food (scaled)		Excluded from model (convergence failure)			
Visitation rate of adults[b]					
Intercept	−3.289	−3.710	−2.869	−15.32	≤0.001
Breeding period	−0.329	−0.413	−0.246	−7.72	≤0.001
Post-breeding period	0.118	−0.026	0.263	1.60	0.109
Intermediate abundance of small rodents	−0.201	−0.318	−0.085	−3.39	≤0.001
Low abundance of small rodents	0.039	−0.060	0.137	0.77	0.443
Sex	−0.185	−0.684	0.313	−0.73	0.446
Breeding status	−0.601	−0.726	−0.475	−9.38	≤0.001
Age	0.215	0.178	0.252	11.50	≤0.001
Food (scaled)	0.150	0.102	0.198	6.17	≤0.001

[a] $R_m^2 = 0.069$, $R_c^2 = 0.269$, overdispersion ratio = 0.961.
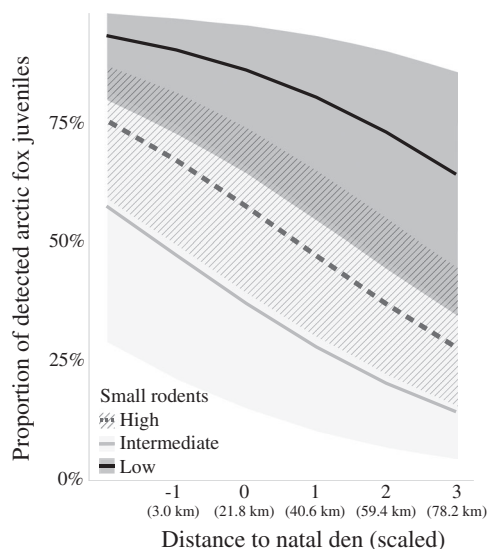[b] $R_m^2 = 0.040$, $R_c^2 = 0.339$.

Figure 7. Predicted visitation rates of arctic fox juveniles at supplementary feeding stations equipped with Biomark passive integrated transponder (PIT)-tag readers depending on distance to natal den and abundance of small rodents in Dovrefjell and Knutshø regions, Norway, summer 2013 to spring 2018.

rodents (Angerbjörn et al. 1999, Meijer et al. 2013). The variation in the use of supplementary feeding dispensers during the rodent cycle was also documented by wildlife cameras in the same study area (Bouchetard-Aubus 2017). Bouchetard-Aubus (2017) reported arctic fox presence at the feeding dispensers also varied with maintenance of feeding stations, season, and occurrence of competing red foxes and wolverines.

The amount of food refilled in each feeding station varied through the year because of the accessibility of feeders, with difficult access during challenging winter weather and light conditions. The visitation rates of adults and juveniles at feeding stations were positively correlated with the amount of supplemental food, as expected. Empty feeders had lower visitation rates, and could be out of use for long periods if not refilled. The methods, however, do not allow us to distinguish whether foxes visited more often because there was more supplemental food added to the feeding dispensers, or if more food was added because foxes visited the feeding dispensers more often. High availability of supplemental food could also trigger hoarding behavior (Sklepkovych and Montevecchi 1996, Careau et al. 2008). At the Sæterfjellet arctic fox captive-breeding station, foxes have been observed hoarding food for later use, and males filling their mouths with dog pellets to bring to the denning female (A. M. Landa, Norsk institutt for natur-forskning, personal observation).

Of foxes born in the study area between 2013 and 2017, 54% were detected as juveniles at ≥1 feeding station equipped with PIT-tag readers. This is surprisingly high because only 6 of the 31 feeding dispensers had a PIT-tag reader, and 4 of them were relatively spatially concentrated (Fig. 1B). We have not yet explored survival patterns related to the use of supplemental food in arctic fox juveniles, but starvation is an important cause of mortality during some

years, particularly for juveniles (Tannerfeldt et al. 1994). Survival has been estimated as 0.44 for arctic fox juveniles released in the study area between 2006 and 2013 (Landa et al. 2017a). The fact that juvenile foxes use the feeding dispensers almost twice as much under low abundance of small rodents highlights the importance of supplementary feeding as a conservation action for arctic fox juvenile survival.

Effects of Age, Reproductive Status, and Sex

As expected, we detected a higher proportion of older foxes at feeding stations than younger adult foxes, out of all detectable foxes. It appears that juveniles did not use the feeding stations more than the adults, contrary to our predictions. We did not record a significant difference in feeding station use between males and females. The basic social unit of the arctic fox is the breeding pair, and both parents take an active part in rearing the pups (Angerbjörn et al. 2004, Eide et al. 2004). Arctic foxes are normally territorial when breeding (i.e., during summer; Angerbjörn et al. 1997). They usually defend a territory around their den where they remain resident even in years with low abundance of rodents, when they do not breed (Strand et al. 2000). Foxes defend territory directly by chasing and mobbing, and indirectly via scent-marking and vocalizations (Kullberg and Angerbjörn 1992). Natal dens are generally used by only 1 family group, and the home range of adults varies from 6 km^2 to 60 km^2 in Norway (Landa et al. 1998). Increasing overlap of home ranges has been described with increasing prey availability (Eide et al. 2004, Elmhagen et al. 2014). Our study shows we detected breeding adults using the feeding stations significantly more than non-breeding adults, and that pairs that were established close to feeding stations used them significantly more than pairs established farther away. This could explain why many of the non-breeding adults marked with PIT-tags were not detected at all: dominant animals could have scent-marked or aggressively defended feeding stations, deterring other individuals from entering. Further use of low-light video footage at feeding stations from camera traps could help understand this behavior.

Juveniles from unrelated litters used the same feeding stations and sometimes at the same time, suggesting that breeding pairs seemed to allow the juveniles from other litters at the dispensers within their territory. Temporal variation in food availability may allow a breeding pair to tolerate additional individuals in its territory at times when food abundance is high, as described in Svalbard (Eide et al. 2004), Canada (Lai et al. 2017), Sweden, and Iceland (Elmhagen et al. 2014). It could also be that these unrelated juveniles were only visiting the feeding dispensers sporadically while dispersing, during a period when adults were less territorial. Because pedigree information is available from the Norwegian arctic fox monitoring program and the Norwegian arctic fox captive breeding program, avoidance or tolerance of non-related individuals at feeding dispensers could be explored accurately using a relatedness index. Our results indicate that the feeding stations are efficient for

juveniles from the entire area and provide benefit to the litters closest to the food dispensers.

MANAGEMENT IMPLICATIONS

The PIT-tag system offers a simple, robust, and automated method to assess individual use and potentially the individual-level effects of food supplementation. It also allows managers to quantify the proportion of a target population that actually uses supplementary food, with limited handling of animals (single capture event). Our results emphasize the importance of regular maintenance of feeding dispensers during winter months before reproduction (Jan–May) and during low rodent years; the need for refilling the feeding stations is lower following years of low reproductive success.

ACKNOWLEDGMENTS

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APPENDIX A. DETECTION SUMMARY

Table A1. Number of arctic foxes detected at each site per age class, reproductive status, and sex (±SD [range]/yr) in Dovrefjell and Knutshø regions, Norway, summer 2013 to spring 2018.

	Site						
	Avlsstasjonen	**Åmotsdalen**	**Sletthø høy**	**Tjønnglupen**	**Vangsvatnet**	**Vårstigdalen**	$\bar{x}^a$
Mountain area	Dovrefjell	Dovrefjell	Dovrefjell	Dovrefjell	Dovrefjell	Knutshø	
Age class							
Adults	6.6 ± 3.6	15.8 ± 9.8	16.6 ± 11.1	13.8 ± 8.0	3.7 ± 3.1	2.8 ± 2.6	113
	(3–11)	(3–31)	(1–26)	(2–25)	(1–7)	(1–8)	
Juveniles	4.6 ± 4.4	6.7 ± 6.8	6.4 ± 11.1	4.0 ± 5.8	5.7 ± 3.2	3.2 ± 4.1	143
	(0–10)	(0–15)	(0–26)	(0–14)	(2–8)	(0–10)	
Reproductive status							
Breeding adults	1.6 ± 0.9	1.0 ± 1.1	1.2 ± 2.2	1.5 ± 2.3	0	0.3 ± 0.5	20
	(0–2)	(0–3)	(0–5)	(0–6)		(0–1)	
Non-breeding adults	5.0 ± 4.2	14.8 ± 10.5	15.4 ± 11.1	12.3 ± 8.5	3.7 ± 3.1	2.5 ± 2.9	110
	(1–10)	(2–31)	(1–26)	(2–25)	(1–7)	(0–8)	
Sex							
Males	5.8 ± 2.4	13.2 ± 4.5	13.4 ± 9.3	10.7 ± 4.6	3.3 ± 2.3	3.0 ± 2.6	103
	(2–8)	(5–18)	(3–27)	(6–17)	(2–6)	(1–10)	
Females	5.4 ± 3.9	9.6 ± 6.3	9.6 ± 6.3	7.2 ± 4.8	6.0 ± 2.6	3.0 ± 2.6	93
	(1–10)	(2–18)	(2–18)	(1–14)	(3–8)	(1–8)	

[a] Some individuals were detected at several feeding stations.
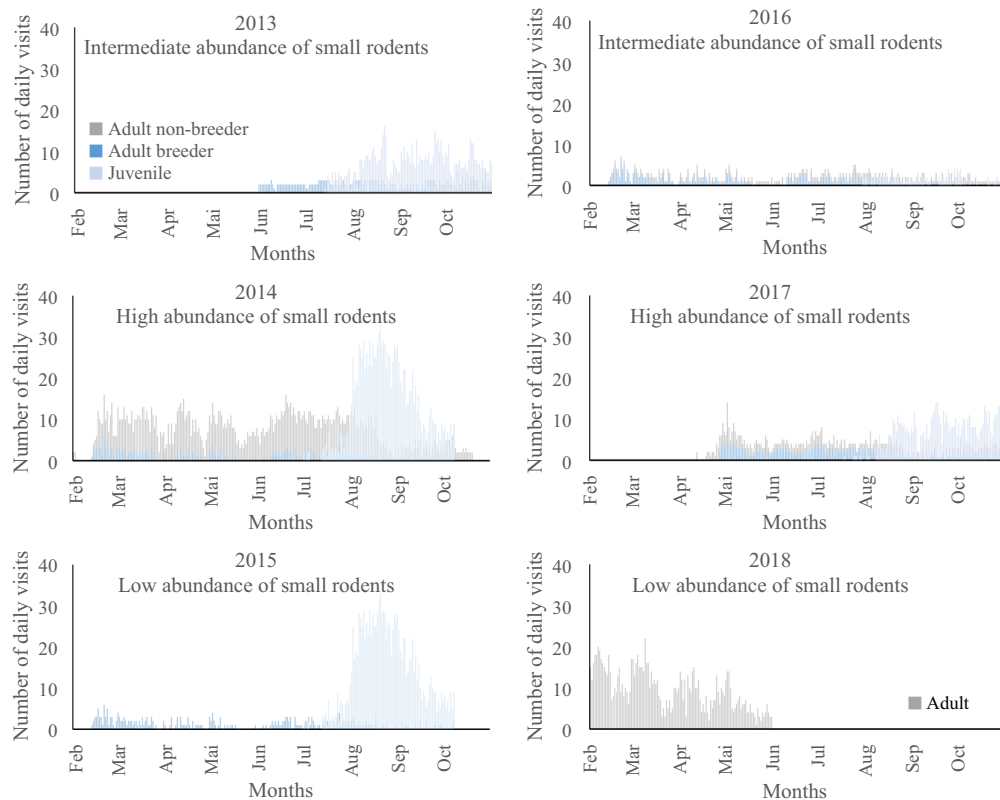
APPENDIX B. VISITS TO EACH SITE

Figure B1. Average number of daily visits of adult and juvenile arctic foxes for each year of the study period (*n* = 9,914 visits of adult and juvenile foxes) at supplementary feeding stations equipped with passive integrated transponder (PIT)-tag readers in Dovrefjell and Knutshø regions, Norway, 2013–2018.