European Journal of Wildlife Research (2024) 70:74
https://doi.org/10.1007/s10344-024-01824-0

RESEARCH

Invasion in cold: weather effects on winter activity of an alien mesopredator at its northern range

Vesa Selonen[1] · **Pyry Toivonen**[1] · **Elina Tuomikoski**[1]

Received: 15 February 2024 / Revised: 5 June 2024 / Accepted: 23 June 2024

Abstract

Whether an invasive species thrives in cold ecosystems depends on its response to winter weather. A potential threat to these ecosystems in Europe is the invasive raccoon dog (*Nyctereutes procyonoides*). The survival of this mesopredator is supported in cold weather, because it can periodically use winter sleep, but its winter activity levels compared to native mesopredators remain unclear. We investigated the winter behaviour of raccoon dogs in Finland, near the edge of their invasion front, and compared their activity to native red foxes and badgers. Using wildlife cameras, we found that raccoon dogs do reduce activity during the coldest months, but camera observations did not strongly correlate with temperature perhaps due to feeding at camera sites. That is, artificial food sources may have increased raccoon dogs' winter activity. Nevertheless, they responded more clearly to temperature drops than red foxes, but were more active than badgers that were mostly dormant and thus absent from our data. GPS-tracked raccoon dogs remained at some level active through winter, even near subarctic regions, but the cold and snowy weather clearly decreased activity and individuals stayed close to their nests during the coldest periods. Overall, these findings suggest that raccoon dogs can maintain some winter activity even in extremely cold environments, and they readily exploit human-provided resources. This potential ability to thrive in cold regions highlights the invasive potential of raccoon dogs. As winters become milder due to climate change, their numbers could increase significantly within cold-adapted ecosystems, impacting native species and posing conservation challenges.

Keywords Invasive species · Mesopredators · Conservation · Winter sleep · Climate change

Introduction

Warming weather in northern ecosystems increases primary production and enhances winter survival. This allows new species to move their range northwards towards arctic or uphill in mountainous regions (Walther et al. 2002; Callaghan et al. 2004; Parmesan 2006). The arrival of newcomers can cause problems for the species adapted to cold ecosystems, even when it is the native boreal species expanding its geographical distribution northwards. Such as, the expansion of red fox (*Vulpes vulpes*) to the north threatens the artic fox (*V. lagopus*; Killengreen et al. 2007; Elmhagen et al. 2017). However, especially problematic is when non-native invasive species reach northern sensitive ecosystems (Walther et al. 2009; Bellard et al. 2013).

The most common invasive mesopredator in Europe with a still ongoing expansion process is the raccoon dog (*Nyctereutes procyonoides*; Kauhala and Kowalczyk 2011). It is an important predator of ground nesting birds (Holopainen et al. 2021; Jaatinen et al. 2022) and amphibians (Tuomikoski et al. 2024). Thus, the invasion of northern regions by raccoon dogs may create extra costs for these populations (Hof et al. 2012). The expansion of raccoon dogs is also problematic from the perspective of spread of zoonotic diseases and parasites (Kauhala and Kowalczyk 2011; Mustonen and Nieminen 2018). The raccoon dog spread to Finland from former Soviet Union in the 1950s, where it was introduced for fur production. The current European range of the species is expanding mainly consisting Eastern and Northern Europe, Germany and Denmark. In Finland, raccoon dog distribution covers most of the country excluding northern parts in Lapland (Kauhala and Kowalczyk 2011).

✉ Vesa Selonen
vessel@utu.fi

[1] Department of Biology, University of Turku, Turku FI-20014, Finland

The ability to survive in winter plays a central role behind the expansion into northern areas (Kauhala and Kowalczyk 2011; Cunze and Klimpel 2022). The raccoon dog is the only canid species that has potential to exhibit passive overwintering by winter sleep (Kauhala and Kowalczyk 2011), which enhance this species ability to survive in cold environments. The wintering strategy of raccoon dog includes alternating periods of physical activity and passivity (Mustonen et al. 2012; Mustonen and Nieminen 2018). This strategy is intermediate between actively wintering carnivores and those that sleep most winter in northern regions (Mustonen and Nieminen 2018). The winter sleep of raccoon dogs typically occurs in underground burrows or dens under barns, cottages, rocks, rootstalks or inside hollow trees (Kowalczyk and Zalewski 2011). The raccoon dog does not need winter sleep in central Europe, but at some level uses it in northern Europe as a wintering strategy (Kauhala and Kowalczyk 2011; Mustonen et al. 2012; Zoller and Drygala 2013). However, it is unclear how active the species is during the winter months in northern regions. In other words, how much it needs to sleep to survive in very cold climates.

Due to lack of major competition and predators in invaded areas, the dispersal potential of the raccoon dog is likely to depend to a large extent on climatic factors (Melis et al. 2007; Fløjgaard et al. 2009; Mustonen et al. 2012). In its native Asian range, the species is known to live in wide variety of habitats and ecological circumstances, with apparent adaptations to varying climates, habitats and diets (Kauhala and Saeki 2004). Recent studies there have focused on genetics and distribution (e.g. Hong et al. 2018; Van Pham et al. 2023), but for comparison of the ecology of European and Japanese raccoon dogs, see Kauhala and Saeki (2004). Within the native range, six subspecies have been identified (Hong et al. 2018). Individuals introduced to Europe originated from the northernmost subspecies. This subspecies can tolerate the cold climates of southeast Siberia and can use winter sleep, while southern raccoon dogs do not need to do that (Novikov 1962; Kauhala and Kowalczyk 2011). However, raccoon dogs' native range does not extend as far north, as it does in invaded area in northern Europe (Kauhala and Kowalczyk 2011). Some earlier studies have failed to predict the species invasion range within the northern Europe due to inadequate data on the species responses to cold weather (Kochmann et al. 2021). Thus, better information on species winter activity and response to cold weather are needed to forecast the possible expansion of the species in changing climate. Comparing the activity patterns of the newcomer to ecologically similar native species, also gives information on expected changes in the ecosystem.

In this study, we investigate how weather conditions affect the winter activity of raccoon dogs at their northern range and at the invasion front. We hypothesize that (i) colder temperature and deeper snow decrease activity of raccoon dogs observed in wildlife-camera data and GPS-tracking data during winter; and (ii) the activity level lower in the north with longer periods of winter sleep, due to harsh winter. We also compare raccoon dog observations in wildlife cameras in winter to those of native mesopredators, the red fox and the badger (*Meles meles*). Our findings will help to understand the role of weather as a limiting factor behind the potential of raccoon dogs to expand their range. This information is essential for predicting where and when raccoon dogs are most likely to expand their range, and how they might interact in winter with native species in these newly invaded areas.

Materials and methods

Study species and study areas

The raccoon dog is an omnivorous canid that weighs typically 5 kg in early summer and about 9 kg in autumn before winter sleep (Kauhala 1993). It is monogamous denning in pairs. In Finland, the ecologically similar native species are the red fox and the badger. The red fox weighs typically 5–8 kg. It dens solitarily, in pairs or in family groups, depending on food resources (Lindström 1989). It is active the whole winter, but decreases activity levels during cold months. The badger is also an omnivorous mesopredator with mean weight from 9 to 12 kg (according to the season; Macdonald and Barrett 1993). It dens in family groups in large burrows, which it digs itself and uses the year round, but the badger also shares its burrows with raccoon dogs especially in winter (Kowalczyk et al. 2008). In Finland, badgers mostly sleep during winter, between November and March (Lindström 1989).

The study was carried out in boreal managed forest landscape. The wildlife-camera data originates from southern and central Finland and the GPS data from southern and northern Finland (at the invasion front near the Arctic Circle; Fig. 1). The landscape in these areas is dominated by mainly managed coniferous and mixed forests, the main tree species being the scots pine (*Pinus sylvestris*), the Norway spruce (*Picea abies*), and the birch (*Betula* sp). The bodies of water and agricultural areas fragment the forest landscape. Agricultural areas and urban areas are found more in southwestern and southern Finland, but occur sparsely within the whole country.

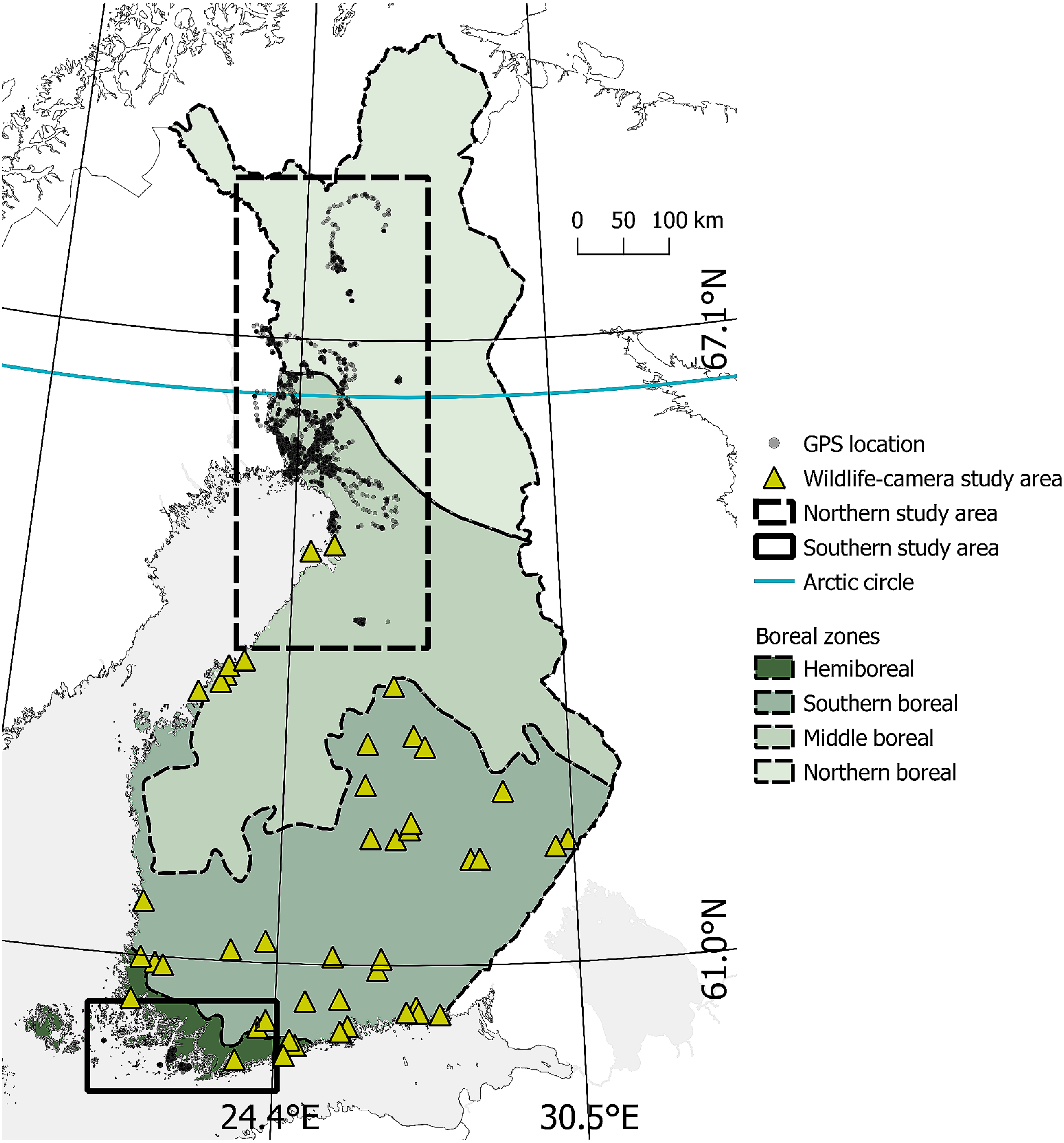

Fig. 1 Location of study areas: yellow triangles are sites where wildlife-camera data was collected and squares indicate where GPS-tracked raccoon dogs were in southern and northern study region. Blue line indicates the Arctic Circle

Wildlife-camera data

We had wildlife-camera data from 45 study areas and 175 cameras from winter 2021/2022. The study areas were located in forests or in agricultural fields or in other open areas surrounding wetlands important for waterfowl conservation in southern and middle Finland (Fig. 1). The wildlife cameras were used in hunting, that is, the aim was to remove the observed raccoon dogs from the areas. Thus, the location of study areas was not random but determined by the location of wetlands important for waterfowl and the hunting areas surrounding these wetlands. The hunting of mesopredators was part of a project by Finnish Ministry of Agriculture and Forestry aiming for improving the conservation of endangered waterfowl. The size of the hunting areas was large (on average 63 ± 52 km^2) and the number of used wildlife cameras was low (on average 4 ± 2 per hunting area) ensuring that observations in each camera were independent from each other. The cameras were 5–10 m from a feeder or carcass, which was used to attract predators to the site. Within this distance, the mesopredator species visiting the site were easy to identify. The feeders typically included grain, apples or dog pellets. The carcasses were usually leftovers form hunted deer or moose. The lack of effect of the type of these attractants on observed results can be seen in Supplement Table 2.

The removal of mesopredators affect the wildlife-camera observations in this study, likely decreasing observations in time. Both raccoon dogs and red foxes were hunted in these sites, but likely the previous more than the latter. However, we use data from the beginning of the removal project, as the camera survey and hunting started in winter 2021/2022, and very clear effects cannot be observed in the data (see observations in time in Supplement Table 1). Most of the camera data came from January – March with fewer data in November and December (Supplement Table 1). Camera photos were checked for approximately one-week period each month, but for longer period in November (Supplement Table 1). The length of observation period was selected to be able to manage the large photo numbers produced and was controlled while analyzing the data. There were two observation periods for January because we wanted to increase data from midwinter (Supplement Table 1). Number of mesopredator photos (the badger, the raccoon dog, and the red fox) within the observation period were counted, including only photos separated by 30 min (following earlier studies, e.g. Holopainen et al. 2021; Selonen et al. 2022b). However, the badger observations were so few that we had to omit it from the analyses (Supplement Table 1).

GPS-tracked raccoon dogs

We used data from GPS-tracked raccoon dogs from two study areas (Fig. 1), the first located in northern Finland near Rovaniemi and Tornio (31 individuals) and the second located in southern Finland around Kemiö and Lohja (12 individuals). Raccoon dogs were tracked with Followit Ultra Light GSM/GPRS GPS collars that weighed 211 g, which is less than 5% of the weight of the animal.

We used location data from winter months (November-March). The hunting of raccoon dogs influences the data. That is, tracking often ended in mortality of an individual. In addition, partner removal of the tracked individuals may have increased their movement activity (the raccoon dog is mostly monogamous). We had data for occurrence of this partner removal in southern Finland, but only for part of data from northern Finland. The mean tracking interval was around 6 h, but tracking was set to be mainly during nighttime, with usually 0–2 daytime location attempts (the raccoon dog is mostly active at night, but often is also active at daytime). The attempts of the collard to have connection to satellites varied between 1 and 10 attempts per 24 h (Supplement Table 1).

Based on how many of the fix attempts produced coordinates (the GPS got satellite contact) we calculated activity of the tracked individual. The assumption here is that if the individual was in the nest, which is in Finland typically underground or under rocks or buildings, the collar could not reach satellites and produce location information. Sometimes this may happen also if the animal is outside the nest, but in a location without satellite contact. However, in general the proportion of fixes that produced location information from all location attempts gives an index of activity level of the individual.

We calculated the *activity index*, as “fixes with coordinates” / ”all fix attempts per 24 h”. In addition, we calculated the length of *inactivity periods* ≥ 2 days, that is, length of gaps without any fixes with coordinates, indicating periods that the individual was in winter sleep. Finally, with the achieved coordinate information we calculated *distance* between two consecutive GPS-fixes and time in hours between these two locations.

Explanatory variables

For both data sets (wildlife cameras and GPS-data), we used daily temperature in °C and snow depth in cm (both continuous variables) data from Finnish Meteorological Institute. Only winter months (November-March) were included. The start and end of winter (when average daily temperature is below 0 °C) varies depending on latitude. In southern Finland winter starts on average in mid-November and ends in late March. In northern Finland, winter can start already in October and end in April. Nevertheless, the months between November and March are on average partly or totally winter in the whole country.

For wildlife-camera data, we used the length of growth season (days; data by Statistics Finland) in the analysis, to account for the variation in the location of the sites from northeast to the south-west coastal areas of Finland. In northeast, the climate becomes colder with longer winters, deeper snow cover, and a shorter growing season (see Fig. 1). To account for sampling effort variation among the cameras we included variable ´length of observation period´ (on average 7.5 days) in the models. Month was also included as explanatory variable, because the activity of animals (and thus number of observed photos) was expected to increase in the end of winter, when mating season of the study species approaches. To account for repeated measures for cameras within study area (on average 4 per area), and for repeated measures between months, camera ID and study area ID were used as random variables in the models.

For GPS data, we built 3 different types of models (see below) with varying explanatory variables. For activity (model i below), we modelled data from northern and southern study areas separately. Month was included as categorical variable for the same reason as above for wildlife-camera data. The GPS-data was from several years. In south, year (three study years, 2019–2021) was included as a categorical variable. Instead in north, we could analyze the trend in time (study years 2011–2021, see Supplement Table 1). There the year was included as fixed variable (continuous), but also as random variable to take into account for unexplained variation in time, which is not explained by the rough trend in time or other explanatory variables in the model (see e.g. Grosbois et al. 2008). In addition, individual ID was set as random variable in the models of GPS data to account for repeated measures for each tracked individual. In models (ii) below for inactivity periods (indicating winter sleep) we needed to control for number of inactivity periods per individual or the total tracking time of the individual to account for their effects on the studied explanatory variable. Model (iii) below for moved distances was similar as the model (i), but we had to include time lag between two consecutive fixes (hours), because it obviously affects the observed movement distances.

The GPS data was affected by the hunting of partners of the tracked individuals (see above). We built separate models including data on number of partner removals for each tracked individuals as explanatory categorical variable (Supplement Tables 3 and 4; note that after removal of a partner, an individual may quickly have a new a partner. Thus, partner number varied from zero to three in our data). However, because from north we had this data only from ten individuals, we present the main analysis without partner removal.

Statistics

Wildlife cameras

We modelled wildlife-camera observations during winter months with generalized linear mixed models with negative binomial distribution, which better fitted the data than Poisson distribution. The dependent variables were the number of observations of raccoon dogs or red foxes during the observation period. Length of growth season in the study area (days), length of observation period (days), average daily temperature (°C), snow depth (cm) during the observation period, and month (categorical variable: November-March) were the independent variables. In addition, study area (45 areas), and camera id. (175 cameras) were included as random variables.

Raccoon dog GPS-data

We (i) modelled activity of GPS-tracked raccoon dogs during winter months with binomial events/trial model (event: active fixes producing coordinates, trial: all fix attempts per 24 h). Individuals in south ($n=12$ with 1304 observation days) and north ($n=31$ with 3731 observation days) were analyzed in separate models. Month (categorical variable), year, daily average temperature and snow depth were the explanatory variables. For model in north year was also categorical random variable (see above). Individual id was random variable in analysis of GPS individuals both in south and in north.

We (ii) built two models where the dependent variable was length of inactivity periods (days, Gaussian log-transformed model) or the number of inactivity periods (no. of gaps ≥ 2 days in received GPS signal) per individual (negative binomial model). Study area (north vs. south) and month were explanatory categorical variables. In addition, number of inactivity periods per individual (length of inactivity periods model) or the total tracking time of the individual (number of inactivity periods model) were included as explanatory variables in the models. Individual id was the random variable.

Finally (iii), the distance between two consecutive GPS-fixes was modelled separately for south ($n=12$ with 3327 observations) and north ($n=31$ with 11,094 observations) with Gaussian log-transformed models. Month (categorical variable), year, daily average temperature and snow depth and time lag between two consecutive fixes (hours) were the independent variables. Year was treated similarly as above for activity model (south: categorical variable; north: continuous explanatory variable and random variable). Individual id was the random variable.

The analyses were done using lme4-package (Bates et al. 2015; v. 1.1–33) in R (R Core Team 2022; v. 4.2.0) and SAS Glimmix 9.4.

Results

Wildlife-camera data

Altogether, there were 1236 raccoon dog, 1140 red fox, and 109 badger observations in the wildlife-camera data. The badger was observed mainly in November and March and was left out from further analyses (difference in total observation numbers between raccoon dog and badger: $z = 2.6$, $p = 0.01$; Supplement Table 1). The raccoon dog and the red fox were observed during the whole winter (Supplement Table 1).

The raccoon dog observations declined during midwinter (January-February; Table 1), but did not drop to zero (Supplement Table 1; Fig. 2). They remained at low level when the temperature was below – 10°C (Fig. 2), but the effect of temperature was not strong, albeit statistically significant (after controlling for month; Table 1). In addition, snow depth, surprisingly, had a slight positive effect on the raccoon dog observations (Table 1).

Temperature did not affect the red fox observations, but snow depth had negative effect (Fig. 2; Table 1). Observations of red fox did not decline similarly as in raccoon dogs during midwinter (January-February). As expected, both the red fox and the raccoon dog observations declined in regions with short growth season (north and northeast; Fig. 2; Table 1).

Table 1 Effects on observations of raccoon dogs and red foxes (negative binomial distribution) in wildlife cameras in winter 2021/2022 in Finland

	Estimate	Z	p
Raccoon dog			
Intercept	1.11 ± 0.63	1.76	0.08
Length of growth season	0.78 ± 0.17	4.71	**< 0.0001**
Camera days	0.19 ± 0.12	1.64	0.10
Month: November	0		
December	-0.85 ± 0.60	-1.42	0.17
January_start	-1.59 ± 0.72	-2.20	*0.03*
January_end	-1.47 ± 0.62	-2.37	*0.02*
February	-1.79 ± 0.73	-2.43	*0.02*
March	-0.76 ± 0.75	-1.02	0.30
Snow depth	0.52 ± 0.23	2.20	*0.03*
Temperature	0.32 ± 0.16	2.0	*0.045*
Red fox			
Intercept	-0.69 ± 0.63	-1.10	0.27
Length of growth season	0.45 ± 0.19	2.32	*0.02*
Camera days	0.068 ± 0.10	0.67	0.50
Month: November	0		
December	-0.44 ± 0.50	-0.88	0.38
January_start	-0.40 ± 0.61	-0.61	0.51
January_end	0.30 ± 0.56	0.54	0.59
February	1.04 ± 0.72	1.43	0.15
March	1.87 ± 0.78	2.40	*0.01*
Snow depth	-0.82 ± 0.28	-2.97	**0.003**
Temperature	-0.04 ± 0.15	-0.28	0.78

Model random effects, red fox: camera 0.47 ± 0.68, area 0.78 ± 0.88; raccoon dog: camera 1.07 ± 1.03, area 0.28 ± 0.53; $n = 442$, camera $n = 175$; area $n = 45$. Bold $p < 0.01$, italics $0.05 < p > 0.01$

Raccoon dog GPS-data

The raccoon dog activity declined in midwinter and in cold temperature, as expected (Fig. 3a; Table 2). However, they returned active GPS fixes the whole winter and occasionally even during the coldest nights (-35 °C). Snow depth had a negative effect on raccoon dog activity in south, but not in the north (Table 2). However, in the model accounting for partner removal more snow decreased activity also in north (Supplement Table 3).

Inactivity periods (gaps ≥ 2 days in received GPS signal indicating winter sleep) were observed as regularly in south as in north (the model predicted mean number per individual was 2.5 ± 0.6 (s.e.) in south and 2.6 ± 0.4 in north; $F_{1,43} = 0.04$, $p = 0.8$). The length of these periods was also similar in south and north, 4.1 ± 1.1 and 3.0 ± 1.2 days ($F_{1,27.25} = 2.76$, $p = 0.11$), respectively. That is, the typical inactivity period indicating winter sleep was only few days long (Supplement Fig. 1), the longest observed being 21 days and 80 days in south and north, respectively.

Moved distances shortened when temperature decreased and snow cover increased (Table 3; Fig. 3b). That is, raccoon dogs stayed by the nest sites if temperature was below – 10 – -20 °C and snow depth above 40–80 cm. Moved distances increased in March when the mating season approaches. In south, this increase may have started already in February (Fig. 3).

There was no trend (increase or decrease) in time in activity or moved distances in north (where we could analyze the trend in time; variable year in Tables 2 and 3). Instead, removal of partner (by hunting) increased moved distances in south and activity in north (Supplement Tables 3 and 4). Partner removal had no effect on length of activity breaks (breaks ≥ 2 days in GPS signal; $F_{1,15} = 0.64$ $p = 0.43$) and the response to weather variables (in Supplement Tables 3 and 4) seemed similar to that in the models without partner removal (in Tables 2 and 3).

Discussion

We here used wildlife cameras and GPS tracking to infer winter activity of an invasive mesopredator, the raccoon dog, at its northern range. Wildlife-camera data showed that the raccoon dog was clearly more active during winter than the native badger that sleeps during cold months in Finland and was absent from our data during midwinter. Instead, in comparison to other native mesopredator the red fox, the raccoon more clearly responded to cold weather. However, it still was observed in wildlife cameras through the winter, unless there had been < -10°C for a week (the length of observation period). Based on GPS-tracked raccoon dogs,

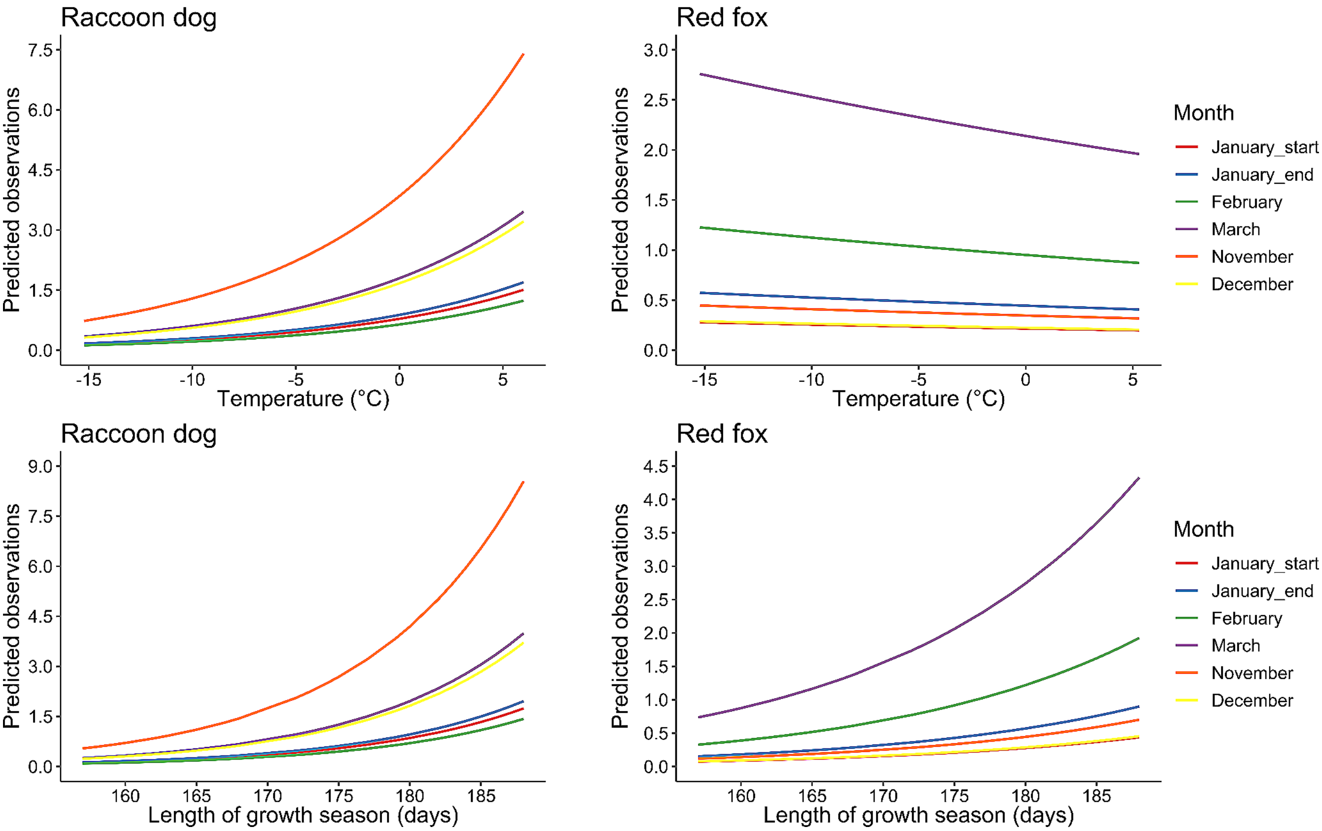

Fig. 2 Number of model predicted wildlife-camera observations during winter in relation to temperature and length of growth season in a study site (after controlling for month) for raccoon dogs and red foxes. Values given for each winter month

the periods during which raccoon dogs may have been in winter sleep remained relatively short and, surprisingly, were similar in length in the south with mild winters and in the north with harsh winters. Nevertheless, raccoon dogs clearly decreased activity and moved distances in cold and snowy weather.

Warming climate will milder the winters and increase primary productivity in northern ecosystems. Especially the latter is expected to allow more species to invade northern regions possibly threatening the species adapted to cold (Callaghan et al. 2004; Post et al. 2009). In the case of the raccoon dog, the climate is expected to be the main factor controlling its expansion (Melis et al. 2007; Fløjgaard et al. 2009). However, our results indicate that the species was active in very cold weather. It clearly decreased activity during cold nights and in midwinter, but was not observed to have longer winter sleep near the Arctic Circle than in hemiboreal and southern boreal areas of southern Finland. In Lithuania it is recently also observed that raccoon dogs can be active occasionally even at temperatures of -13 °C and – 15 °C (Jasiulionis et al. 2023; see also Kauhala et al. 2007; Mustonen et al. 2012). It is clear that the activity of raccoon dogs declines when temperature drops, and, in comparison, the red fox was not affected by cold temperature in our study. However, the effect of temperature on raccoon dog presence in our wildlife-camera data was not very strong (after controlling for month; Table 1), because there was a lot of variation in the data. That is, raccoon dogs occasionally visited camera sites even when the whole observation week had temperature between – 5 and – 10°C. Our wildlife cameras were at feeding stations or had carcasses that provided food resources even at the middle of winter. Thus, it is possible that when food resources are available (like in our case), raccoon dogs may remain active in cold weather. This interpretation fits the view that increase in primary productivity may be the major driver of invasions of northern ecosystems due to climate change (Callaghan et al. 2004; Post et al. 2009; Stoessel et al. 2019).

Anthropization is one factor that may benefit invasive species, and evidently both raccoon dogs and red foxes utilize frequently human provided resources (e.g. in our wildlife-camera data). It is known that red fox expansion to north is related to human subsidies (Hersteinsson and Macdonald 1992) and also raccoon dogs frequently utilize human provided food (Kauhala and Kowalczyk 2011; Tuomikoski et al. 2024) and spend time near human settlements (Toivonen 2023). Thus, human subsidies, especially in winter when resources are scarce, likely have important role behind the

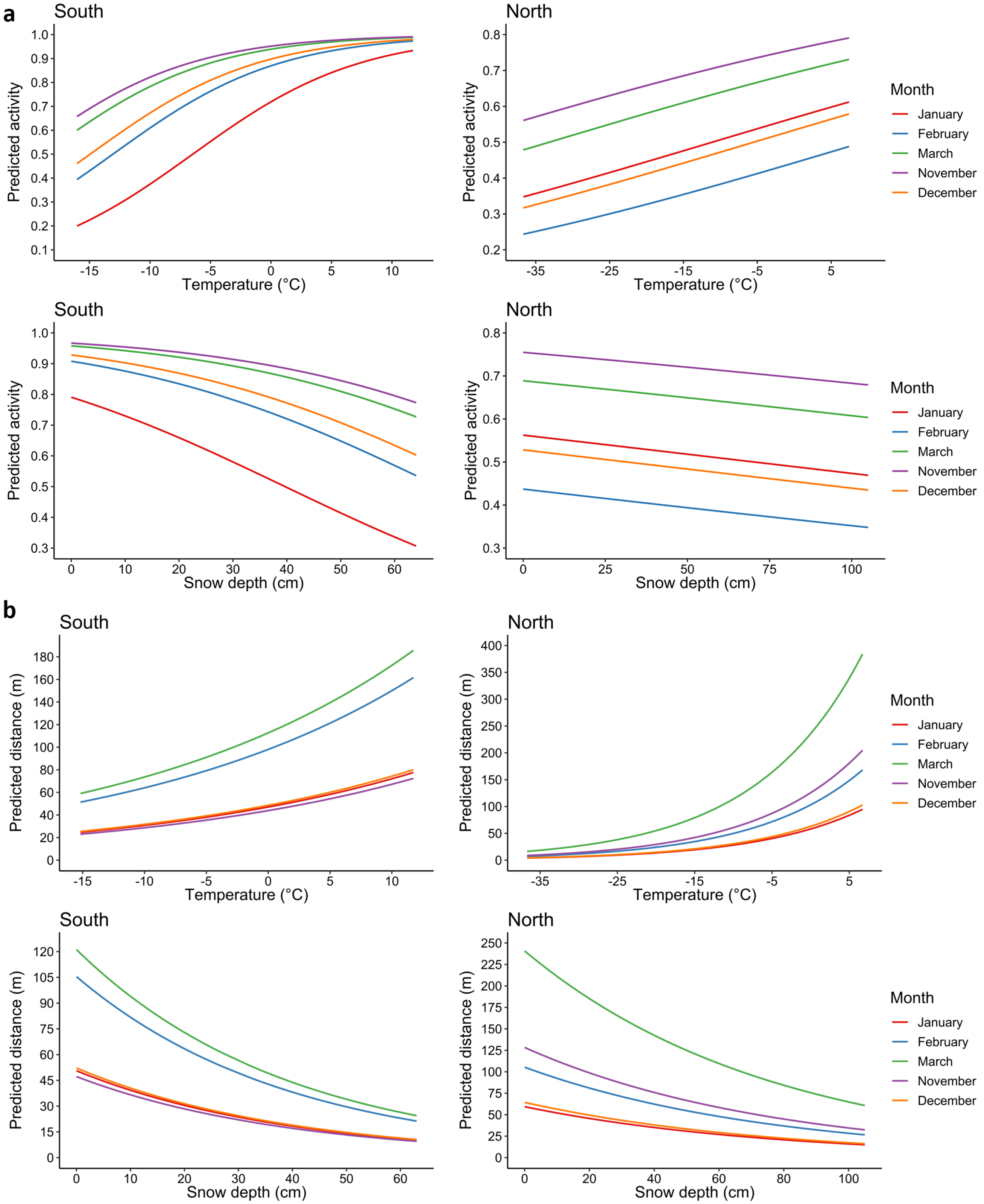

Fig. 3 Model predicted (**A**) activity and (**B**) moved distances of GPS-tracked raccoon dogs in relation to temperature and snow depth (after controlling for month) during winter in southern and northern Finland. Values given for each winter month

Table 2 Effects on activity index (“fixes with coordinates” / ”all fix attempts per 24 h”) of GPS-tracked raccoon dogs during winter in northern ($n = 35$) and southern Finland ($n = 12$). GPS-fix without coordinates means that it did not find satellites, indicating that the individual was underground in the winter nest

	Estimate	Z	*p*
North			
Intercept	-1.43 ± 1.82	-0.79	0.82
Year (continuous)	0.094 ± 0.11	0.83	0.41
Month: November	0		
December	-1.01 ± 0.15	-6.81	**< 0.0001**
January	-0.87 ± 0.20	-4.32	**0.0001**
February	-1.37 ± 0.26	-5.27	**< 0.0001**
March	-0.32 ± 0.28	-1.18	0.24
Temperature	0.18 ± 0.05	3.95	**< 0.0001**
Snow depth	-0.09 ± 0.11	-0.80	0.43
South			
Intercept	3.06 ± 0.72	4.24	0.002
Year: 2019	0		
2020	-1.04 ± 0.69	-1.51	0.13
2021	-1.56 ± 0.75	-2.08	*0.04*
Month: November	0		
December	-0.81 ± 0.31	-2.58	*0.01*
January	-2.04 ± 0.34	-5.90	**< 0.0001**
February	-1.08 ± 0.40	-2.70	**0.007**
March	-0.24 ± 0.35	-0.69	0.49
Temperature	0.74 ± 0.10	7.06	**< 0.0001**
Snow depth	-0.51 ± 0.15	-3.43	**0.0001**

Model random effects, north: id 1.93 ± 1.39, year 0.50 ± 0.70, $n = 3728$, id $n = 35$; year $n = 11$; south: id 0.57 ± 0.76, $n = 1304$, id $n = 12$. Bold $p < 0.01$, italics $0.05 < p > 0.01$

Table 3 Effects on movement step length of GPS-tracked raccoon dogs during winter in northern ($n = 35$) and southern Finland ($n = 12$)

	Estimate	t_{df}	*p*
North			
Intercept	-58.0 ± 122	$-0.48_{14.2}$	0.64
Year (continuous)	0.03 ± 0.06	$0.52_{14.2}$	0.61
Month: November	0		
December	-0.69 ± 0.08	-9.0_{10170}	**< 0.0001**
January	-0.77 ± 0.10	-7.36_{8581}	**< 0.0001**
February	-0.19 ± 0.14	-1.48_{7320}	0.15
March	0.63 ± 0.14	4.64_{6578}	**< 0.0001**
Time lag	0.009 ± 0.001	7.81_{11050}	**< 0.0001**
Snow depth	-0.013 ± 0.002	-5.70_{5897}	**< 0.0001**
Temperature	0.073 ± 0.003	21.4_{11050}	**< 0.0001**
South			
Intercept	3.75 ± 0.41	$9.20_{8.9}$	**< 0.0001**
Year: 2019	0		
2020	1.49 ± 0.45	$3.31_{8.1}$	*0.01*
2021	0.41 ± 0.61	$0.68_{11.3}$	0.52
Month: November	0		
December	0.10 ± 0.09	1.96_{3000}	0.26
January	0.07 ± 0.10	0.68_{2998}	0.49
February	0.80 ± 0.12	6.59_{3001}	**< 0.0001**
March	0.94 ± 0.10	9.30_{2992}	**< 0.0001**
Time lag	0.003 ± 0.0014	2.35_{3000}	*0.02*
Snow depth	-0.025 ± 0.005	-4.73_{2997}	**< 0.0001**
Temperature	0.043 ± 0.008	5.10_{3001}	**< 0.0001**

Model random effects north: id 1.06 ± 1.03, year 0.31 ± 0.56, $n = 11{,}063$, id $n = 35$; year $n = 11$; south: id 0.31 ± 0.55, $n = 3011$, id $n = 12$. Bold $p < 0.01$, italics $0.05 < p > 0.01$

invasion potential of the species. Similarly as observed for the red foxes in arctic (e.g. Elmhagen et al. 2017).

The raccoon dog prefers wetlands (Toivonen 2023), and one consequence of warming climate in northern regions will be the longer ice-free period. This likely is important for raccoon dogs especially in early spring when resources are scarce. Thus, climate change will increase resources for raccoon dogs, such as it does for many other invasive species (e.g. Callaghan et al. 2004). The prey species groups likely most impacted by the raccoon dog are wetland-associated ground nesting birds (Dahl and Åhlén 2018; Holopainen et al. 2021; Selonen et al. 2022a) and amphibians (Tuomikoski et al. 2024). These prey species may be especially vulnerable in north, because the adaptions to harsh and cold environment may make the native northern species sensitive to interactions with invading species (Hersteinsson and Macdonald 1992; Callaghan et al. 2013). Even a small decrease, for example in ground nesting bird reproductive success due to nest losses for raccoon dogs, might be crucial if the prey species already have low densities to begin with. It is also notable that the high reproductive potential of the raccoon dog (Kauhala and Kowalczyk 2011) has led to a situation where it is currently clearly more abundant in southern Finland than native mesopredators (Selonen et al. 2024). Thus, the additive predation by raccoon dog on prey of native mesopredators can be substantial.

Previously, Kauhala et al. (2007) concluded that snow depth is major factor limiting raccoon dog activity. They observed in southern Finland that radio-collared raccoon dogs stayed in nests in winter when the temperature dropped below − 10°C and snow depth was > 35 cm, but similarly as in our study might also move occasionally in colder weather during midwinter (Kauhala et al. 2007). In our study, the effect of snow depth was partly contradictory: GPS-data indicated decreased activity and movement with more snow, but the visits to feeding sites (wildlife-camera data) surprisingly slightly increased with more snow. Perhaps deeper snow cover forced raccoon dogs that were not in winter sleep to use feeding sites, because no other food resources could be found. In comparison, for example the distribution of polecat (*Mustela putorius*) in Sweden (Osinga et al. 2023) is very clearly limited by the presence of snow. Instead, raccoon dogs are able to survive even at regions close to the Arctic Circle in very snowy conditions. In the species native range, it is also known that the species does survive in very snowy conditions in southern Siberia, using winter sleep in cold weather (Novikov 1962; Kauhala and Kowalczyk 2011).

Finally, we point out that our index of activity for GPS-tracked individuals could overestimate winter activity of raccoon dogs, if there were cases that the GPS-signal could be reached from the nest (which should be underground out of reach of GPS signal). For almost all study individuals, there were periods of few days without GPS-signal indicating that the individuals used nest sites without satellite contact (and they did not come out from the nest at all and likely were in sleep). In our northern study area, however, three individuals received satellite contact almost all the time during the coldest months (January and February). Deleting those from the data dropped average activity estimate from 0.57 to 0.50 in north (average activity in south was 0.52 in January). In north, we expect that raccoon dogs require especially good nest sites to survive from the cold, but there is also thick snow cover, which may ease nesting even in shallow underground cavities. It should also be noted that our study individuals in north were from the invasion front and in general moved longer distances than individuals in south move. The individuals responsible for invasion may be selected to be the bold and active individuals (Sih et al. 2004), which could increase activity levels. However, the individuals in the invasion front may also be those that avoid risk taking (Eccard et al. 2023). In any case, we observed that periods of possible winter sleep were typically only few days and an individual had few such periods during winter. Similarly, Mustonen et al. (2012) observed in eastern Finland that periods of winter sleep in GPS-tracked raccoon dogs were relatively short, on average six days, and individuals remained periodically active thorough winter.

We conclude that invasive mesopredator, the raccoon dog, is able to maintain winter activity in very cold environment and utilize human provided subsidies in winter. The species is occasionally active during winter even near the Arctic Circle and surprisingly little was forced to use winter sleep to survive. Thus, it is highly likely that raccoon dogs are to expand their range further north as the climate changes. Indeed, climate change is projected to become the primary driver of biodiversity change in the Arctic and boreal ecosystems (Sala et al. 2000). Especially by strengthening top-down species interactions, that is, predation pressure and interference between predators (Post et al. 2009; Legagneux et al. 2014; Stoessel et al. 2019). The previous of these is the threat that the raccoon dog, the most successful invasive mesopredator in Europe, poses for ground-nesting birds and amphibians (Holopainen et al. 2021; Jaatinen et al. 2022; Tuomikoski et al. 2024).

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10344-024-01824-0.

Acknowledgements This work could not be possible without the raccoon dog projects by Finnish wildlife agency and Metsähallitus. From wildlife agency we thank Kari Karhula and Mikko Alhainen, and Mikko Toivola from Metsähallitus for collaboration. We thank Juha Mäkimartti for the GPS data from the northern Finland; Heikki Kortelainen, Tommy Arfman and the whole of SLHSY ry for GPS data from the southern Finland. Wildlife cameras were set up in the field by hunting groups led by Harri Forsten, Ilkka Järvinen, Jussi Ruskeala, Jyri Mononen, Teppo Kakkonen, Thomas Hagström, Tomi Nevalainen and Veijo Kröger, who and all voluntary hunters participating the project are thanked for their valuable work. Finally, Mitja Denac, Santeri Selonen, Ivar Silfvenius, and Tuija Koivisto helped in the data management.

Author contributions VS conceived the idea. PT, ET and VS analyzed the data and produced figures. VS led the writing of the manuscript, and all the authors gave final approval for the publication.

Funding Open Access funding provided by University of Turku (including Turku University Central Hospital). The study was funded by Finnish Ministry of Agriculture and Forestry (Sotka-project) and Research Council of Finland (project no. 357199 to VS).
Open Access funding provided by University of Turku (including Turku University Central Hospital).

Data availability No datasets were generated or analysed during the current study.

Declarations

Ethical approval Ethics approval was not required for this study.

Competing interests The authors declare no competing interests.

References

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67:1–48

Bellard C, Thuiller W, Leroy B, Genovesi P, Bakkenes M, Courchamp F (2013) Will climate change promote future invasions? Glob Change Biol 19:3740–3748

Callaghan TV, Björn LO, Chernov Y, Chapin T, Christensen TR, Huntley B, Ims RA, Johansson M et al (2004) Biodiversity, distributions and adaptations of arctic species in the context of environmental change. Ambio 33:404–417

Callaghan TV, Jonasson C, Thierfelder T, Yang Z, Hedenås H, Johansson M, Molau U, Van Bogaert R et al (2013) Ecosystem change and stability over multiple decades in the Swedish subarctic: complex processes and multiple drivers. Phil Trans R Soc B 368:20120488

R Core Team (2022) R: A language and environment for statistical computing. R foundation for statistical computing, Vienna, Austria. https://www.R-project.org/

Cunze S, Klimpel S (2022) From the Balkan towards Western Europe: range expansion of the golden jackal (*Canis aureus*)—A climatic niche modeling approach. Ecol Evol 12:e9141

Dahl F, Åhlen P-A (2018) Nest predation by raccoon dog *Nyctereutes procyonoides* in the archipelago of northern Sweden. Biol Invasions 21:743–755

Eccard JA, Mazza V, Holland C, Stuart P (2023) The timid invasion: behavioural adjustments and range expansion in a non-native rodent. Proc R Soc B 2902023082320230823

Elmhagen B, Berteaux D, Burgess RM, Ehrich D, Gallant D, Henttonen H, Ims RA, Killengreen ST, Niemimaa J, Norén K, Ollila T, Rodnikova A, Sokolov AA, Sokolova NA, Stickney AA, Angerbjörn A (2017) Homage to Hersteinsson and Macdonald: climate warming and resource subsidies cause red fox range expansion and Arctic fox decline. Polar Res 36:supl1

Fløjgaard C, Morueta-Holme N, Skov F, Madsen AB, Svenning JC (2009) Potential 21st century changes to the mammal fauna of Denmark – implications of climate change, land-use, and invasive species. IOP Conf Ser: Earth Environ Sci 8:012016

Grosbois V, Gimenez O, Gaillard JM, Pradel R, Barbraud C, Clobert J, Møller AP, Weimerskirch H (2008) Assessing the impact of climate variation on survival in vertebrate populations. Biol Rev 83:357–399

Hersteinsson P, Macdonald DW (1992) Interspecific competition and the geographical distribution of red and arctic foxes *Vulpes vulpes* and *Alopex lagopus*. Oikos 64:505–515

Hof AR, Jansson R, Nilsson C (2012) Future climate change will favour non-specialist mammals in the (sub)arctics. PLoS ONE 7:e52574

Holopainen S, Väänänen V-M, Vehkaoja M, Fox A (2021) Do alien predators pose a particular risk to duck nests in Northern Europe? Results from an artificial nest experiment. Biol Invasions 23:3795–3807

Hong Y, Kim KS, Kimura J, Kauhala K, Voloshina I, Goncharuk MS, Yu L, Zhang Y, Sashika M, Lee H (2018) Genetic diversity and population structure of east Asian raccoon dog (*Nyctereutes procyonoides*): genetic features in central and marginal populations. Zool Sci 35:249–259

Jaatinen K, Hermansson I, Mohring B, Steele BB, Öst M (2022) Mitigating impacts of invasive alien predators on an endangered sea duck amidst high native predation pressure. Oecologia 198:543–552

Jasiulionis M, Stirkė V, Balčiauskas L (2023) The distribution and activity of the invasive raccoon dog in Lithuania as found with country-wide camera trapping. Forests 14:1328

Kauhala K (1993) Growth, size, and fat reserves of the raccoon dog in Finland. Acta Theriol 38:139–150

Kauhala K, Kowalczyk R (2011) Invasion of the raccoon dog *Nyctereutes procyonoides* in Europe: history of colonization, features behind its success, and threats to native fauna. Curr Zool 57:584–598

Kauhala K, Saeki M (2004) Raccoon dogs: Finnish and Japanese raccoon dogs—on the road to speciation? In: Sillero-Zubiri C (ed) The biology and conservation of wild canids. Macdonald DW, Oxford University Press, Oxford, United Kingdom, pp 216–226

Kauhala K, Holmala K, Schregel J (2007) Seasonal activity patterns and movements of the raccoon dog, a vector of diseases and parasites, in southern Finland. Mamm Biol 72:342–353

Killengreen ST, Ims RA, Yoccoz NG, Bråthen KA, Henden J-A, Schott T (2007) Structural characteristics of a low Arctic tundra ecosystem and the retreat of the Arctic Fox. Biol Cons 135:459–472

Kochmann J, Cunze S, Klimpel S (2021) Climatic niche comparison of raccoons *Procyon lotor* and raccoon dogs *Nyctereutes procyonoides* in their native and non-native ranges. Mammal Rev 51:585–595

Kowalczyk R, Zalewski A (2011) Adaptation to cold and predation—shelter use by invasive raccoon dogs *Nyctereutes procyonoides* in Białowieża primeval forest (Poland). Eur J Wildl Res 57:133–142

Kowalczyk R, Jędrzejewska B, Zalewski A, Jędrzejewski W (2008) Facilitative interactions between the eurasian badger (*Meles meles*), the red fox (*Vulpes vulpes*), and the invasive raccoon dog (*Nyctereutes procyonoides*) in Białowieża primeval forest, Poland. Can J Zool 86:1389–1396

Legagneux P, Gauthier G, Lecomte N et al (2014) Arctic ecosystem structure and functioning shaped by climate and herbivore body size. Nat Clim Change 4:379–383

Lindström E (1989) Food limitation and social regulation in a red fox population. Ecography 12:70–79

Macdonald D, Barrett P (1993) Mammals of Britain & Europe. Collins Field Guide. Harper Collins, London, UK

Melis C, Nordgård H, Herfindal I, Kauhala K, Åhlen P-A, Strann KB, Andersen R (2007) Raccoon dogs in Norway - potential expansion rate, distribution area and management implications. NTNU-Vitenskapsmuseet Rapp Zool Ser 3:1–49

Mustonen AM, Nieminen P (2018) A review of the physiology of a survival expert of big freeze, deep snow, and an empty stomach: the boreal raccoon dog (*Nyctereutes procyonoides*). J Comp Physiol B 188:15–25

Mustonen AM, Lempiäinen T, Aspelund M, Hellstedt P, Ikonen K, Itämies J, Vähä V, Erkinaro J, Asikainen J, Kunnasranta M, Niemelä P, Aho J, Nieminen P (2012) Application of change-point analysis to determine winter sleep patterns of the raccoon dog (*Nyctereutes procyonoides*) from body temperature recordings and a multi-faceted dietary and behavioral study of wintering. BMC Ecol 12:27

Novikov GA (1962) Carnivorous mammals of the fauna of the U.S.S.R. (in Russian). Jerusalem:Isr Progr Sci 62

Osinga T, Thurfjell H, Hofmeester TR (2023) Snow limits polecat *Mustela putorius* distribution in Sweden. Wildl Biol 2023:e01051

Parmesan C (2006) Ecological and evolutionary responses to recent climate change. Ann Rev Ecol Evol Syst 37:637–669

Post E, Forchhammer MC, Bret-Harte MS, Callaghan TV, Christensen TR, Elberling B, Fox AD, Gilg O et al (2009) Ecological dynamics across the Arctic associated with recent climate change. Science 325:1355–1358

Sala OE, Chapin FS III, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E, Huenneke LF et al (2000) Global biodiversity scenarios for the year 2100. Science 287:1770–1774

Selonen V, Banks PB, Tobajas J, Laaksonen T (2022a) Protecting prey by deceiving predators: a field experiment testing chemical camouflage and conditioned food aversion. Biol Cons 275:109749

Selonen V, Brommer JE, Holopainen S, Kauhala K, Krüger H, Poutanen J, Väänänen V-M, Laaksonen T (2022b) Invasive species control with apex predators: increasing presence of wolves is associated with reduced occurrence of the alien raccoon dog. Biol Invasions 24:3461–3474

Selonen V, Brommer JE, Klangwald C, Laaksonen T (2024) Successful invasion: camera trap distance sampling reveals higher density for invasive raccoon dog compared to native mesopredators. Biol Invasions. https://doi.org/10.1007/s10530-024-03323-4

Sih A, Bell A, Johnson JC (2004) Behavioral syndromes: an ecological and evolutionary overview. Trends Ecol Evol 19:372–378

Stoessel M, Elmhagen B, Vinka M, Hellström P, Angerbjörn A (2019) The fluctuating world of a tundra predator guild: bottom-up constraints overrule top-down species interactions in winter. Ecography 42:488–499

Toivonen P (2023) Habitat selection of the raccoon dog (*Nyctereutes procyonoides*) during the breeding season of ground-nesting birds. Master's thesis, University of Turku, Finland

Tuomikoski E, Selonen V, Merimaa K, Laaksonen T (2024) Diet of the raccoon dog, an invasive mesopredator, during the breeding season of declining waterbird populations. Glob Ecol Cons 51:e02917

Van Pham T, Trinh MT, Gray RJ et al (2023) Southern extension of raccoon dog *Nyctereutes procyonoides* (Mammalia: Carnivora: Canidae) range in Vietnam with comments on its conservation status in the country. Eur J Wildl Res 69:22

Walther G-R, Post E, Convey P et al (2002) Ecological responses to recent climate change. Nature 416:389–395

Walther G-R, Roques A, Hulme PE et al (2009) Alien species in a warmer world: risks and opportunities. Trends Ecol Evol 24:686–693

Zoller H, Drygala F (2013) Activity patterns of the invasive raccoon dog (*Nyctereutes procyonoides*) in North East Germany. Folia Zool 62:290