Zoologisk rapport 2007-3

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Trondheim, april 2007

Utgiver: Norges teknisk-naturvitenskapelige universitet
Vitenskapsmuseet
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7491 Trondheim
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Tidligere utgivelser i samme serie, se:
http://www.ntnu.no/vmuseet/nathist/nathist_publ.htm

Forsidebilde/Cover photo: www.biopix.dk

ISBN 978-82-7126-763-6
ISSN 0802-0833

ABSTRACT

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

The raccoon dog *Nyctereutes procyonoides* is an alien carnivore species in Scandinavia. Native to eastern Asia, it was introduced in 1929 in the former Soviet Union and since then has spread and established itself in several European countries. In Norway, there have been few reliable observations of this species, all in the northernmost part of country. However, the species is well established in Finland and reproduction has been recorded in Sweden. The proposed climate change is likely to make Norway more suitable to raccoon dogs invasion, for this reason Norway should develop a management strategy for this species that is adequate to accomplish the three-steps system of the European Strategy on Invasive Alien Species: prevent-control-eradicate, in cooperation with Swedish and Finnish management authorities.

Factors affecting body condition of juveniles have a great potential to influence recruitment and are thus vital in predicting the future distribution of this alien species. Therefore, we examined how climatic and plant phenology variables perform in explaining body condition of raccoon dogs by using Finnish data on fat deposition of juveniles. Climatic variables describing spring and late summer conditions explained a large amount of the variation in fat deposition. Conversely, plant phenology variables were not good predictors of body condition in juveniles. These variables, effective in explaining life-history traits in herbivores, might not reflect variation in food abundance and quality for omnivore species. We therefore propose that in Europe raccoon dogs will benefit from climate warming, because of a longer growing season. However, increased spring precipitation in form of snow at higher latitudes might compensate for the effect of greater primary productivity and set the border of their expansion towards harsher environments.

By means of GIS modelling it is possible to produce a suitability map for raccoon dogs in Norway according to published data on habitat preference of the species in its introduced range. We modelled the spatial distribution of suitable habitat for raccoon dogs on the Scandinavian Peninsula based on the following ecological characteristics of the environment: habitat type, elevation and length of the growing season. This helped us identifying potential dispersal corridors for this species from Sweden to Norway. We also illustrate how expansion rate and distribution area might be affected by the proposed climate change according to two possible scenarios (10 and 35 day longer growing season). The different scenarios predicted that the population front will reach Norway in a time period ranging between 10 and 40 years. The invasion is expected to cover all potential areas in a range of 35 to 145 years. Our analyses indicate that a possible control program of the invasion should focus on the valleys connecting central Norway and Sweden in order to prevent both primary and secondary invasions effectively with the lowest management cost.

We point out that it is crucial for both Norway and Sweden to develop a management strategy that focuses on these most likely dispersal corridors. Finland should concentrate their effort on the areas most likely to be source populations for dispersing animals. In these areas populations should be kept as low as possible in order to reduce number of dispersers.

Key words: raccoon dog, invasive species, biology, expansion rate, management strategies

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SAMMENDRAG

Melis, C., Nordgård, H., Herfindal, I., Kauhala, K., Åhlen, P-A., Strann, K.B. & Andersen, R. 2007. Mårhund i Norge - Potensiell spredningshastighet, utbredelsesområde og implikasjoner for norsk forvaltning. NTNU Vitenskapsmuseet Rapp. Zool. Ser. 2007, 3: 1-49

Mårhunden *Nyctereutes procyonoides* er en fremmed art i Skandinavia. Den hører opprinnelig hjemme i Øst-Asia, men ble introdusert til tidligere Sovjet Unionen i 1929. Siden da har mårhunden spredd seg og etablert populasjoner i flere europeiske land. I Norge har det vært få pålitelige observasjoner, hvor alle har vært i de nordligste områdene. Imidlertid er mårhunden godt etablert i Finland og reproduksjon har blitt rapportert fra Sverige. Med de forventede klimaendringene vil Norge mest trolig bli mer egnet for invasjon av mårhund og av den grunn bør Norge utvikle en forvaltningsstrategi som er tilstrekkelig for å oppnå trestegs-systemet fra European Strategy on Invasive Alien Species: hindre – kontrollere- utrydde. Dette bør skje i samarbeid med svenske og finske forvaltningsmyndigheter.

Faktorer som påvirker kroppskondisjonen hos ungdyr, påvirker indirekte rekrutteringen, og er derfor viktige å ha kjennskap til om man skal kunne forutsi fremtidig utbredelse av mårhund. Gjennom undersøkelser av finske data på fettdeponering hos ungdyr, ble det sett på hvordan klima og plantefenologi variabler fungerer som forklaring på variasjon i kroppskondisjon hos ungdyr. Klimavariabler som beskriver vår- og sensommer forhold, forklarte en god del av variasjonen i fettdeponeringen. Derimot var ikke plantefenologiske-variabler gode predikatorer for kroppskondisjonen hos ungdyr. Det er mulig at variablene som effektivt forklarer livshistoriske trekk hos herbivorer, ikke reflekter variasjoner i mattilgang og kvalitet hos omnivore arter. Undersøkelsen viser at mårhunden generelt vil ha fordel av et varmere klima på grunn av en forlenget vekstsesong. Imidlertid vil økt nedbør om våren i form av snø ved nordligere breddegrader kompensere for effekten av økt primærproduksjon, og dermed sette grensen for mårhundens spredning i disse områder.

Ved bruk av GIS og tidligere publisert data over mårhundens habitatpreferanser i områder hvor den er introdusert, er det mulig å produsere kart over områder i Norge egnet for mårhund. Vi modellerte utbredelsen av habitat egnet for mårhund i Skandinavia basert på følgende økologiske beskrivelser av miljøet: habitattype, høyde over havet og lengden på vekstsesongen. Dette gjorde det mulig å identifisere potensielle spredningskorridorer fra Sverige til Norge. Samtidlig illustrerte vi gjennom to mulige scenarier, hvordan spredningshastigheten og utbredelsesområdet kunne bli påvirket av den forventede klimaendringen (10 og 35 dagers lengre vekstsesong). De ulike scenariene viste at invasjonsfronten vil kunne nå Norge i en tidsperiode på mellom 10 – 40 år. Invasjonen er forventet å dekke alle potensielle områder i løpet av 35 -145 år. Vår analyse indikerer at et eventuelt kontrollprogram mot invasjon bør fokusere på dalene mellom Midt-Norge og Sverige for å forhindre både primære og sekundære invasjoner effektivt med lavest mulig forvaltningskostnader.
Vi anser det svært viktig for både Norge og Sverige å utvikle en forvaltningsstrategi som fokuserer på de mest opplagte spredningskorridorene. Finland bør konsentrere sine tiltak mot områder som mest trolig vil være kildepopulasjoner for utvandrende dyr. I disse områdene bør populasjonene holdes på et så lavt nivå som mulig for å redusere antall utvandrende individer.

Nøkkelord: Mårhund, fremmed art, biologi, spredningshastighet, forvaltningsstrategier

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CONTENT

FOREWORD

Invasion by non-indigenous species has been recognized as one of the main threats to global biodiversity, second only to habitat loss and fragmentation, and the impact of such species is a major concern throughout the world.

Raccoon dogs are a non-indigenous species to Europe, and have the potential to seriously affect the ecosystem. Raccoon dogs were originally distributed in eastern-Asia, but after introduction to the wild in the European parts of the former Soviet Union during the first half of the 20th century, they became widespread both in central and northern Europe. In Fennoscandia, only Finland has a large population, while they are documented only in the two northernmost counties in Sweden. In Norway, we have so far only documentation of 4 individuals. There is, however, a growing concern among both regional and national management authorities that raccoon dogs will get a stronger foothold in Norway.

Article 8 in the Convention on Biological Diversity (The Rio Convention) states ‘Prevent the introduction of, control or eradicate those alien species which threaten ecosystems, habitats or species.’ That is, each country needs to have a diverse set of management strategies.

This report summarise relevant existing knowledge of raccoon dogs in Fennoscandia, estimate potential dispersal corridors and distribution area in Norway and produce some guidelines for future management strategies. We thank the Finnish Game and Fisheries Research Institute and Swedish Agricultural University for allowing us to use their data.

The report is financed by the Directorate for Nature Management.

INTRODUCTION

Invasion by non-indigenous species has been recognized as one of the main threats to global biodiversity, second only to habitat loss and fragmentation (Walker & Steffen 1997, Weidema 2000). Today, the impact of non-indigenous species is a major concern throughout the world and their management and control is likely to become a main challenge for conservation biologists and managers in the next decades (Allendorf & Lundquist 2003).

The raccoon dog *Nyctereutes procyonoides* is an opportunistic generalist carnivore, originally distributed only in eastern-Asia, but after introduction to the wild by Russians in European parts of the former Soviet Union during the first half of the 20^{th} century, it became widespread both in central and northern Europe (Helle & Kauhala 1991). According to the Convention on Biological Diversity, Article 8, each country should prevent the introduction of, control or eradicate such alien species. This requires knowledge about the biology of invasive species, including factors affecting population growth rate, their habitat requirements, dispersal behaviour, and potential distribution area, in order to produce adequate management guidelines.

This report is divided in 4 separate sections, where we:

1 Summarise relevant knowledge about the biology of raccoon dogs, and present its population status in Fennoscandia.

2 Investigate how available environmental variables describing spring and summer climate and plant phenology, perform in explaining body condition in the raccoon dog.

3 Model the spatial distribution of preferred habitat in Norway and Sweden and the potential dispersal corridors from Sweden to Norway, and illustrate how dispersal corridors and the distribution of preferred habitat will be affected by the predicted climatic changes.

4 In cooperation with Swedish wildlife researchers, and based on information from 1 – 3, we develop management strategies in order to prevent the introduction of, to control or to eradicate raccoon dogs.

1 POPULATION STATUS AND BIOLOGY OF RACCOON DOGS

1.1 Population status of raccoon dogs

1.1.1 Europe

The raccoon dog is native to East-Asia and was introduced to the former Soviet Union in 1929 because of its valuable fur (Kauhala 1994). Since then it has dispersed and established large populations in Poland, Romania, Bulgaria, Hungary, Germany, Czech Republic, Baltic countries and Finland (Weidema 2000). Its presence was documented for the first time in France in 1979 (Artois & Dunchêne 1982). The first confirmed observation of raccoon dog in Switzerland was made in 1997 in Leuggern, were an individual was killed by a car (Weber *et al.* 2004). In 2005, two individuals were observed in northern Italy (Carnia, Udine, Lapini 2006), but the presence of the species was reported for the first time as early as in 1980 in Slovenia just 10 km far from the Italian border (Rebeć 1981).

1.1.2 Finland

Raccoon dogs established viable populations in Finland shortly after their introduction in the former Soviet Union and have now become the most common carnivore in the country (Kowalczyk 2006). The population reached the first peak at the end of the 1980s. At the beginning of 1990s, the population declined, to rise again at the end of 1990s and at the beginning of 2000s. During the high peak period at the end of the 1980s, the size of the spring population before the start of reproduction was of about 40 000 individuals. These produced ca 130 000 juveniles during summer and, therefore, the population reached the size of 170 000 individuals. The summer mortality of juveniles consisted of about 50 000 individuals. Of the ca 120 000 individuals of the remaining autumn population many died during autumn and winter, since in spring the population was again estimated to about 40 000 individuals. About 50% of the mortality was due to hunting while the rest of the animals died of starvation or was killed by cars (Helle & Kauhala 1991). There are no new population estimates for raccoon dog in Finland, but the annual hunting bag consisted in 2005 of about 130 000 individuals, which can be compared to the 40 000 individuals that were hunted in 1980-1990 (Väänänen 2006). This increase in hunting bag suggests a significantly higher population size in the first decade of 2000 compared to 20 years ago.

The density is highest in the southern and south-eastern part and lowest in the northern parts of the distribution area (Helle & Kauhala 1991). In south-eastern Finland the estimated maximum / minimum density of adult raccoon dogs was 7.7 / 3.8 individuals per 10 km^2. Autumn density (including juveniles) was 21 / 10 individuals per 10 km^2. Home range size varies considerably between areas (0.4–20 km^2), whereas in southern Finland seems to be of average size (9.5 km^2, Kauhala *et al.* 1993a).

The northern limit of distribution lies in areas where the mean temperature is 0˚ C, the snow depth is lower than 80 cm, the duration of the snow cover reaches 175 days and the length of the growing season is 135 days. The growing season is by itself the most important factor for the variation in abundance (Helle & Kauhala 1991).

1.1.3 Sweden

Observation quality for uncommon species varies greatly in precision and reliability (Weber *et al.* 2004). This is clearly documented both in Sweden and Norway. In fact, several sources (*e.g.* Nowak 1984, Bevanger & Ree 1994, Nordic Network on Introduced Species 1997, Mitchell-Jones *et al.* 1999) report that raccoon dogs are distributed both in northern and southern Sweden, however, documented observations of raccoon dogs have only been done in the two northernmost counties – Norrbotten and Västerbotten (Fig. 1). The first observation was reported in 1972, and up to 2005 only three raccoon dogs have been sent to the Swedish Museum of Natural History, all from Norrbotten county. According to the Swedish Association for Hunting and Wildlife Management, beyond these findings a number of individuals have been shot in Norr- and Västerbotten counties (Swedish Association for Hunting and Wildlife Management 2007). However, the first validated evidence of raccoon dog reproduction in Sweden was in 2006 when 13 individuals, one male and 12 juveniles, were shot in Haparanda-Sandskär in Norrbotten county (Åhlén 2007).

1.1.4. Norway

In Norway there have been four documented observations of raccoon dogs, all in the northernmost part of the country (Fig. 1). The first record was in 1983 east of Kirkenes, the second in 1988 in Pasvik (Wikan & Henriksen 1991). A third animal was shot in 1997 in Pasvik and in February 2007 a raccoon dog was hit and killed by a car in Skibotn in Troms county (Directorate for Nature Management 2007).

1.2 Habitat preferences and diet

Two features are typical of the habitat use of raccoon dogs in the areas where it has been introduced: (1) they are often found near water, and (2) they are more or less dependent on fruits and berries during autumn. Both these characteristics affect their habitat use. Raccoon dogs live in many different habitats ranging from subtropical rainforests to boreal coniferous forests (Kauhala1996a), and their habitat use varies between the introduced and natal ranges. In the introduced range raccoon dogs prefer moist deciduous forests with abundant undergrowth (bushes, ferns, etc.). According to Drygala *et al.* (2000) undergrowth is much more important than the tree species community present, because it is used for shelter. Raccoon dogs also prefer the shoreline along of rivers and lakes, especially in early summer (Kauhala 1996a). In late summer and autumn raccoon dogs choose moist heaths with abundant berries (Kauhala 1996a). Furthermore, in the Finnish archipelago they use barren pine forest where they feed on crowberries (Kauhala & Auniola 2001). A telemetry study in Brandenburg (Germany) showed that the use of agricultural areas, especially cornfields, was more intense in summer (Sutor 2004), but in Finland raccoon dogs more or less avoided fields and open areas. They may also occupy a mosaic of woodland and agricultural areas (Drygala *et al.* 2000). Raccoon dogs occur more often at low altitudes, mainly below 300 meters, but can occasionally live at up to 800 m. Only exceptionally they can be found over 1000 m a.s.l. (Nowak 1993).

Raccoon dogs are true generalist omnivores and their seasonal diet shift as food availability changes (Kauhala & Saeki 2004). The diet in Finland consists mainly of small mammals, birds, reptiles, amphibians, fish, invertebrates, carcasses and plants (Viro & Mikkola 1981). The composition of the diet varies between inland and insular habitats (Kauhala & Auniola 2001) and for different parts of their range of distribution (Jensen 2004).

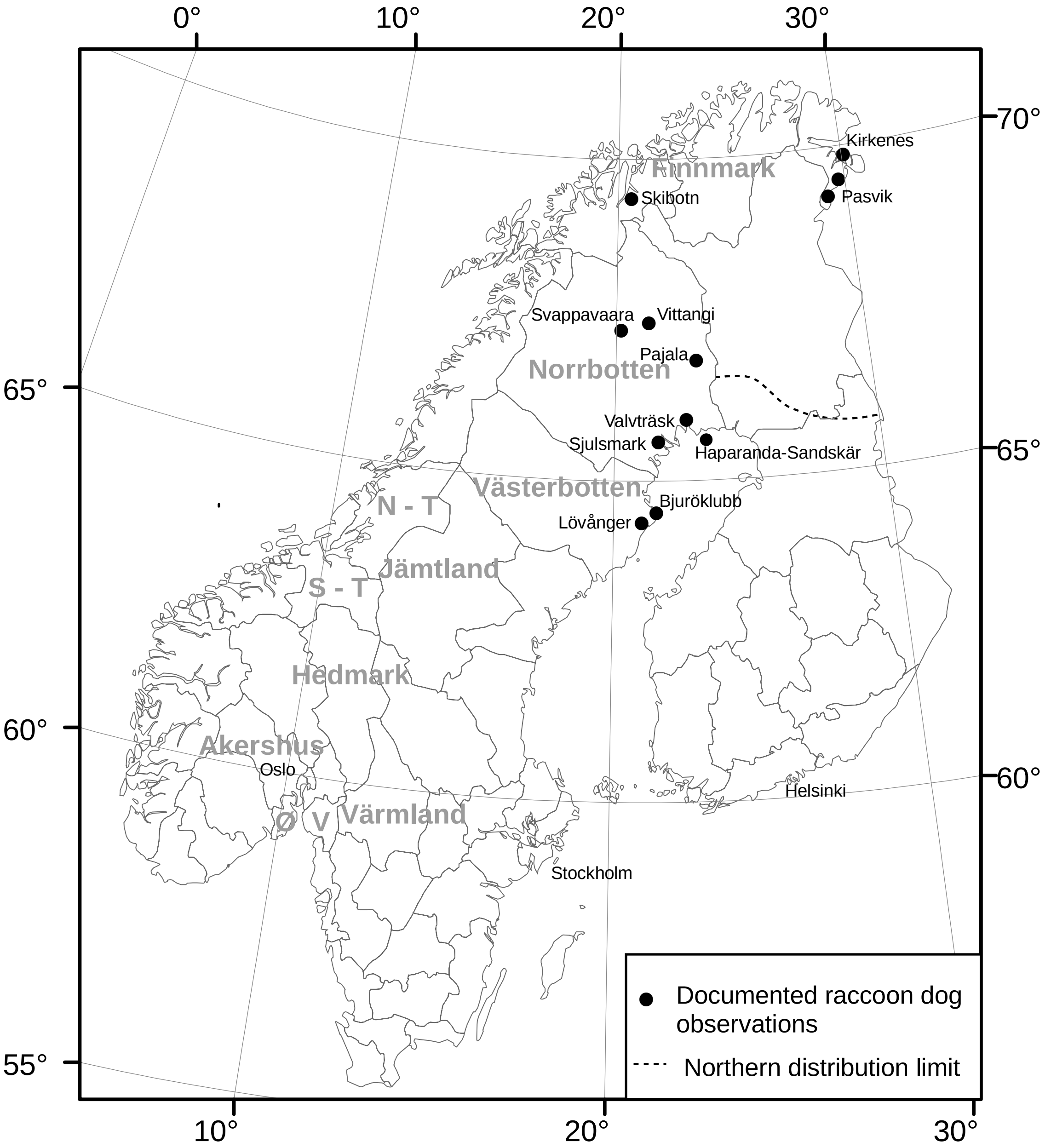

Figure 1. Map of Fennoscandia showing the areas where reliable observations of raccoon dogs have been made (black dots) and the counties of Sweden and Norway mentioned in the text (in grey). The dotted line represents the northern limit of distribution of raccoon dogs, after Kauhala & Helle (1995). The finding in Lövånger was made on floating ice about 10 km far from mainland.

1.3 Social behaviour and reproduction

Raccoon dogs are strictly monogamous. They form permanent pairs (Kauhala et al. 1993a) and this may take place long before the breeding season (e.g. in September). The paired indi-viduals share the same home range, forage together, usually travel together and both defend their territory against conspecifics of the same sex (Kauhala & Saeki 2004). Sexual maturity is reached at 9-11 months, mating occurs from February to April and the cubs are born from April to June. The mean litter size is 6-7 pups, the largest litter recorded is of 12 cubs (Nowak 1993).

1.4 Wintering strategy of raccoon dogs

Many mammals adopt hibernation or winter sleep as wintering strategies, and these strategies have generally been considered a response to a high seasonality in the productivity of the environment, such as food resources, and to very harsh climatic conditions (Swan 1974, Boyce 1979). Hibernation is defined as a prolonged state of regulated hypothermia (*i.e.* lowering of body temperature), during which the animals decrease their metabolism to a very low level, and they gradually use up their body fat reserves to survive. Among canids, winter sleep (lethargy) is a unique feature of raccoon dogs, and in areas where winter is harsh raccoon dog spend the winter asleep (Kauhala & Saeki 2004, but see Sutor 2004 with a description of a population with no indications of winter sleep). Raccoon dogs normally decreases their metabolism by about 25% (Asikainen *et al.* 2002) and their body temperature is lowered a few degrees (Mustonen *et al.* 2004), therefore they are not truly hibernating, but it would be more correct to talk about winter sleeping. For mammals in boreal and arctic regions, seasonal energetic bottlenecks typically occur during winter, when thermoregulatory requirements increase and food resources are scarce (Humphries *et al.* 2004). Survival of hibernating mammals throughout the winter depends primarily on their energy reserves (mainly in form of fat) at the onset of winter sleep, the rate at which the energy stored is depleted during winter, and the length of the winter (Humphries *et al.* 2002). Therefore, both climatic and energetic constraints operate as limiting mechanisms to the geographical distribution of hibernating mammals. However, temporal variation in the environment can also influence population dynamics, *e.g.* through survival and recruitment. Particularly, factors influencing body condition (measured as fat reserves) at the onset of the hibernating period, and the duration of this are expected to be crucial.

1.4.1 Fat reserves

Winter lethargy in raccoon dogs lasts usually from November to March in Finland. The layer of fat that is deposed during the favourable season has both the function to isolate the animal from the temperature of the environment making thermoregulation less costly and to provide energy to sustain its lowered metabolism during winter. An animal that is starting the hibernation period with an inadequate amount of fat reserves will have lowered chance to survive over the winter and to reproduce successfully the next season. In raccoon dogs this is especially true for females, who will benefit of their energy reserves during gestation and lactation throughout the favourable season. Adult raccoon dogs can almost double their weight during this period and in late autumn the mean fat content of an individual is 3.5 kg (43% of the total weight, Kauhala 1993). Fat reserves are localized in a subcutaneous layer and in the body cavity.

1.5 Dispersal behaviour

When raccoon dog juveniles reach 4-5 months of age they disperse, usually between August and October. The juveniles have a strong inclination to stray and can cover long distances. According to a radiotelemetry study conducted in Finland, the greatest reported juvenile dispersal was about 150 km, but most animals (79%) were found within 20 km from the marking location (Kauhala & Helle 1994). A study on dispersal among juveniles in Germany showed a mean dispersal distance of 94 km from the marking place (Sutor 2005). Drygala *et al.* (2000) reported that in eastern Germany during dispersal, two juveniles (one male and one female) travelled together for one month. The longest one night dispersal distance recorded was 5 km.

In the former Soviet Union the species expanded its distribution area with a rate of 40 km per year (Lavrov 1971), while in southern and central Finland the annual rate of expansion was 20 km (Helle & Kauhala 1991). In Brandenburg, Germany, the spread of the raccoon dog population has followed streams and wetlands. As the population increased, suboptimal habitats were colonised. These poorer habitats included dry pinewoods, and outskirts of cities and villages (Drygala *et al.* 2000).

1.6 Potential ecosystem effects

It is important to bear in mind that to predict the impact of an introduced species is challenging. There are several reasons for this, but among them is the possibility that animals change their ecology when they are introduced to new areas (Tømmerås *et al.* 2003). Moreover, because the raccoon dog is a generalist who eats what is available its diet varies between areas causing spatially different pressure on its prey and competitors.

1.6.1 Predation

The raccoon dog is an omnivorous carnivore with a generalist and opportunist feeding behaviour, *i.e.* it has a very wide trophic niche breadth and the ability to exploit food resources according to their availability in the environment. Its predation impact has especially been studied on ground nesting and aquatic birds, with apparently controversial results. One problem with estimating the effect of predation is that most studies are based on the analysis of scats or stomach content, where it is difficult to distinguish whether the remains originate from actual predation or from scavenging. In fact, raccoon dogs have been reported to be very efficient scavengers (Drygala *et al.* 2000, Selva *et al.* 2003). Another problem in evaluating how serious threat raccoon dogs might represent for prey populations is that most concern has been raised about game species (especially birds) and the predation impact on more neglected taxa, like for example amphibians, has not been studied.

For example, a study from Estonia reported damage to waterfowl colonies (Naaber 1971), due to nest robbing, but the same author concluded that raccoon dogs are not likely to be harmful to grouse and hare populations in Estonia. Raccoon dogs are also described as too clumsy to predate effectively on adult birds and hare (Kauhala 1996b). However, a diet analysis conducted in Finland revealed that in summer 2-67% of raccoon dog faeces contained waterfowl remains, but raccoon dogs were estimated to kill only 1.2-3.5% of reproducing female eiders, while the bulk of the bones originated from scavenged carcasses (Kauhala & Auniola 2001). Similarly, many egg shells where found in the scats (11-40%), but the largest amount was found in July, when the eider chicks had already hatched. The authors concluded that it is unlikely that raccoon dogs affected significantly the waterfowl population size. However, the impact on prey populations might be totally different whether predation occurs on mainland or on an insular environment (Kauhala & Auniola 2001). In fact, whereas frogs, reptiles, shrews and carrion occurred frequently in the diet of raccoon dogs on the mainland, they were found only occasionally in the outer archipelago. Raccoon dogs might have already overexploited frog populations on small islands, since they are easily predated and occur frequently in their diet on the mainland. Moreover, after raccoon dog arrival in the seventies to some islands off the southwest coast of Finland, frogs disappeared, but they did not decline in the outer islands, which were not at reach of raccoon dog (reported in Kauhala 1996b). Similarly, small rodents are important prey in early summer for raccoon dogs on the mainland and on inhabited islands, but they are less used in the outer archipelago (Kauhala & Auniola 2001). Therefore, predation impact may also vary according to food availability and community species composition. A removal experiment of medium-sized predators in Finland provided no evidence that raccoon dogs had a negative impact on the breeding success of dabbling ducks (Kauhala 2004). According to Kauhala *et al.* (1993b) the diet of raccoon dogs in Finland consists mainly of small mammals, berries and carcasses. In the inland habitats of Finland, birds occur less often in the diet, and most of them are gallinaceous birds (10%, half of which were introduced *Phasianus colchicus*) and passerines (13%, Kauhala *et al.* 1993b). These results suggest that in mainland Finland raccoon dogs do not impact significantly game animal populations, including gallinaceous birds, waterfowl, and hares. Also in eastern Germany the diversity and composition of the diet of raccoon dogs indicate that it is more a scavenger and gatherer than an active predator (Drygala *et al.* 2000).

Case study

Changes in the breeding population of waterfowl in the lakes Øvrevatn and Nedrevatn in Storfjord municipality, Troms County.

Possible damages caused by raccoon dogs[1].

Breeding populations of Horned grebe (*Podiceps auritus*) (Endangered, IUCN) have been systematically censused in Øvrevatn and Nedrevatn since 1998. Since mid-1990 Black-headed gulls (*Larus ridibundus*) (Near threatened, IUCN) have been established in Nedrevatn, and increased in colony size until 2003. In 2003 10 breeding pairs of Little gull (*Larus minitus*) established and reproduced in the area. In 2004 reproduction was good for all waterfowls in both lakes.

In spring 2005 all waterfowls established, and in Nedrevatn the colony of Black-headed gulls counted 124 pairs, in addition to 6 pairs of Little gull. Revisiting the colony 23.June, all birds except one single Black-headed gull, had left the area. Studies of eggshells found in the colony indicated predation. Observations of red fox in these areas in preceding years indicated that foxes where not able to reach nests surrounded by wetland and open water. Hence, egg predation on Black-headed gulls have been minimal and absent in Horned grebe. In spring 2006, the same pattern as the preceding year was recorded. Black-headed gull colony estimated to 80 breeding pairs, however no birds left in the area 24.June, and predated eggs were recorded.

Number of breeding pairs of Horned grebe in Nedrevatn, Øvrevatn and Sagelvvatn (control) in 2004 – 2006

	2004 Nesting pairs	2004 Pairs with chicks	2005 Nesting pairs	2005 Pairs with chicks	2006 Nesting pairs	2006 Pairs with chicks
Øvrevatn	12	9	11	1	8	0
Nedrevatn	7	5	5	0	3	0
Sagelvvatn (control)	9	7	11	10	10	8

Spatial and temporal comparisons of breeding success in Horned grebe in three different localities (Tab. 1) clearly document the effects of predation. Very few predators will be able to predate eggs of Horned grebe as these birds nest in areas surrounded by open water. There are however, several studies describing the raccoon dog as a specialist egg-predator in such habitats.

[1]Indications: Raccoon dog killed in the area in winter 2007. Bit marks on eggshells different from American mink, and tracks in mud different from red fox. Reliable, but not confirmed observations of raccoon dogs in spring 2007.

1.6.2 Intra-guild competition

The feeding behaviour, body size and ecological niche of the raccoon dog suggest that it might be a potential competitor of sympatric red foxes *Vulpes vulpes* and badgers *Meles meles*.

The diet and trophic niche overlap of these three carnivores has been studied in Finland by Kauhala *et al.* (1998) who concluded that, although these generalists share many food resources, they are also specialized to a certain extent, which might help them to avoid competitive exclusion. In fact, the badger diet is mainly represented by earthworms, whereas voles, shrews and berries are especially important for raccoon dogs. On the other hand the fox is a more strictly carnivorous species and feed also on larger prey. Similar differences between the diet of foxes and raccoon dogs were found by Jędrzejewski *et al.* (1989) in Poland, where raccoon dogs fed more on frogs, invertebrates and plants than did foxes. Moreover, all these food items might be abundant during the favourable season in boreal regions, while competition is expected to occur only when the food resources are limited. Winter is the most critical season in harsh environments, where the winter lethargy of the raccoon dog prevents it from competing severely both at the intra- and interspecific levels.

Sidorovich *et al.* (2000) studied the diet overlap among generalist carnivores in northern Belarus and found that, although the overlap existed, there was little evidence for competition in the favourable season. However, the trophic niches became narrower in winter and most carnivores were forced to feed on carrion, whose availability might have decreased after the raccoon dog had reached a high population density, thus causing other generalist carnivores to decline in abundance. However, the rapid increase of raccoon dogs in Finland did not caused a decline in the native badger population (Kauhala 1995), which has extended its northern limit of about 100 km northwards since the midt-1940s as a consequence of the climatic and habitat changes which occurred during this period.

1.6.3 Diseases and parasites

Raccoon dogs are vulnerable to infections by several viruses and parasites that can be transferred to humans, domestic animals and wildlife. Among these diseases are rabies, sarcoptic mange, piroplasmosis, and several species of helminth infestations (Ward & Wuster-Hill 1990).

Juvenile raccoon dogs can disperse long distances and thereby transmit rabies far from their natal territory (Kauhala *et al.* 2006), in fact a study on the rabies outbreak of 1988 in Finland (which had been rabies-free since 1959) revealed that raccoon dogs accounted for 77% of the cases of rabies in wildlife (Westerling 1991) and were the most important vector of this virus (Nyberg *et al.* 1992). However, the same study showed also that raccoon dogs could be immunized against rabies in the field with vaccine baits originally developed for controlling sylvatic rabies in foxes.

Amongst helminth infestations which are potentially very dangerous to humans are *Trichinella* spp. and *Echinococcus* spp. and raccoon dogs have been reported to be very efficient reservoir for both parasites (Näreaho *et al.* 2000, Jarvis *et al.* 2001).

1.7 Climate change and raccoon dog distribution

Climatic change is a key factor in the issue of introduced species, since the process of invasion is expected to be affected by climate (Weidema 2000). Changed conditions in the ecosystem may affect the distribution range of both native and introduced species by changing their chance to establish themselves (Tømmerås *et al.* 2003). A longer growing season will probably positively affect raccoon dogs, providing better survival and reproductive conditions. Thus, if winters become milder and with less snow, raccoon dogs might expand their range northwards (Kauhala & Saeki 2004) and Norway is likely to become more exposed to invasion by this species.

Climate is the most important factor affecting regional variation in growth rate, density and distribution of the raccoon dog population in Finland (Kauhala & Helle 1995). Therefore, the impact of global warming is expected to be different depending on regional climate (Høgda *et al.* 2001). Milder winters with increased precipitation might lead to a thicker and longer lasting snow cover at high latitudes. In the nemoral and boreonemoral zones of Scandinavia the tendency shows that snow cover will disappear either totally or earlier in the spring (Høgda *et al.* 2001).

2 TEMPORAL VARIATION IN RACCOON DOG LIFE HISTORY TRAITS

2.1 Introduction

Spatial variation in climate and food availability has been found to affect reproductive output of raccoon dogs. For example, the abundance of food in spring (especially voles) and late summer (represented mainly by berries) influenced the body condition of young, measured in terms of fat reserves, and therefore their sexual maturation (Kauhala 1993). On the other hand, harsh spring condition, indicated by high snow depth at the end of March, delayed the time of ovulation of females, thus shortening the period of growth and fat deposition of the young (Helle & Kauhala 1991, 1995).

Temperature, snow depth and snow cover duration have been widely used as a proxy for harsh climatic conditions and productivity of the environment in ecological studies of endotherms (*e.g.* Jędrzejewski *et al.* 2002, Anderson & Jetz 2005, Melis *et al.* 2006).

Remote sensed data can be used to produce vegetation indices, such as normalized difference vegetation index (NDVI) and fraction of photosynthetic absorbed radiation (FPAR), which both correlate consistently with vegetation biomass and net primary production (*e.g.* Myneni *et al.* 1995, 2002). These indices have been recently used as a proxy of food availability for herbivores, linking vegetation to animal performance (reviewed in Pettorelli *et al.* 2005). For example, with time series of NDVI it is possible to estimate dynamics in photosynthetic activity, *i.e.* plant phenology. Such variables have successfully been used to explain variation in life history traits in herbivores (Garel *et al.* 2006, Herfindal *et al.* 2006 a, b, Pettorelli *et al.* 2006), and to relate variation in home range size in carnivores to habitat productivity (Herfindal *et al.* 2005, Nilsen *et al.* 2005). If correlation between plant phenology and body condition were observed in carnivores, *e.g.* because vegetation productivity affects them indirectly through prey abundance, this correlation should be even stronger in a true omnivore, like the raccoon dog, whose diet consists in considerable part of vegetal matter (Kauhala *et al.* 1993b, 1998). Moreover, northern temperate and arctic mammals have a relatively short time of high food abundance to accumulate fat reserves, whether they hibernate or not. Therefore, they are expected to depend even more on the productivity of habitat during the favourable season. This can influence the population growth rate through survival and recruitment. In fact, in raccoon dogs more than 40% of the annual reproductive output is due to yearling females (Helle & Kauhala 1995). Accordingly, factors that affect body condition of the youngest age class have the potential to greatly influence recruitment the subsequent year, since recruitment is related also to the body condition of the mother (Helle & Kauhala 1995).

2.2 Methods of relating body conditions to climatic and environmental variables

Data on fat deposition of juvenile raccoon dogs were collected in Finland from 1987 to 1997 and in 1999 in the province of Häme (827 carcasses) and from 1987 to 1990 in the province of Kymi (240 carcasses) (Fig. 2).

The fat reserves were measured by weighing to the nearest 0.1 gram the fat tissue located around the kidneys and dorsally in the abdominal cavity of animals culled between July and December (see Kauhala 1993 for more details). These data were used to estimate a total of 16 annual fat deposition curves, 12 from Häme and 4 from Kymi, with a minimum sample size of 20 individuals. Since there are no sexual differences in body size and in the amount of fat reserves in juvenile raccoon dogs (Kauhala 1993), we pooled data for males and females. A Gompertz model, which represents an asymmetric sinusoidal growth (France *et al.* 1996), was fitted to each subset of data by a non-linear regression procedure (Venables & Ripley 2002). The four following parameters were extracted from each annual curve (Fig 3, Table 1): (1) start of deposition; (2) max deposition day; (3) max deposition rate and (4) predicted autumn fat (on 5th of November). The 5th of November was chosen because it was the last date on which we had data on fat index from all years. We assumed further fat deposition to be minimal and thus the amount of fat deposed at this date to represent the energy reserves stored at the onset of the hibernating period.

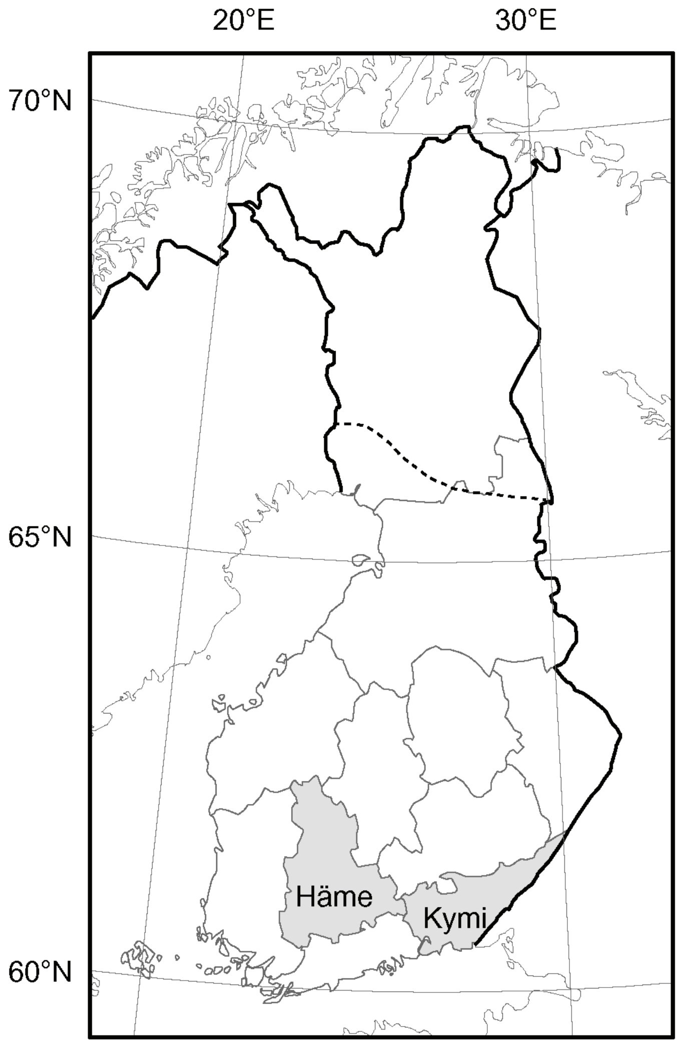

Figure 2. Map of Finland showing the provinces of Häme and Kymi (shaded), where data on fat deposition of juvenile raccoon dogs were collected. The dotted line represents the northern limit of distribution of raccoon dogs, after Kauhala & Helle (1995).

2.2.1 Environmental variables

We used both climatic variables and satellite-derived indices of plant phenology (Global Inventory Monitoring and Modelling System, GIMMS, dataset) to explain the variation in the parameters extracted from the fat deposition curves. Climatic variables were obtained from the Finnish Meteorological Institute (Table 1). These included the duration of snow cover higher than 30 cm, snow depth on the first of April, mean snow depth in March, mean temperature in March, and mean temperature and total precipitation during early summer (May-June), late summer (July-August), autumn (September-October).

The GIMMS dataset consist of the maximum values of NDVI for 15-days periods with a spatial resolution of 8 x 8 km^2, covering the world and available from 1982 until present (Myneni *et al.* 1997). The NDVI is an index of the relationship between reflected red and near-infrared radiation from the ground, and is found to represent the greenness of the vegetation, or the photosynthetic activity (Myneni *et al.* 1995). The GIMMS dataset allows the calculation of annual NDVI-curves and the extraction of variables that describe the annual plant phenology (Reed *et al.* 1994, Pettorelli *et al.* 2005). For each pixel in the GIMMS data we calculated the following plant phenology variables (Table 1): onset of spring, peak time, peak value, annual net primary productivity, onset of autumn and length of the growing season. For a more detailed description of these variables see Reed *et al.* (1994), Garel *et al.* (2006), Herfindal *et al.* (2006a) and Karlsen et al. (2006). The seven plant phenology variables were then averaged annually within each of the two provinces (Fig. 2), excluding pixels representing open water.

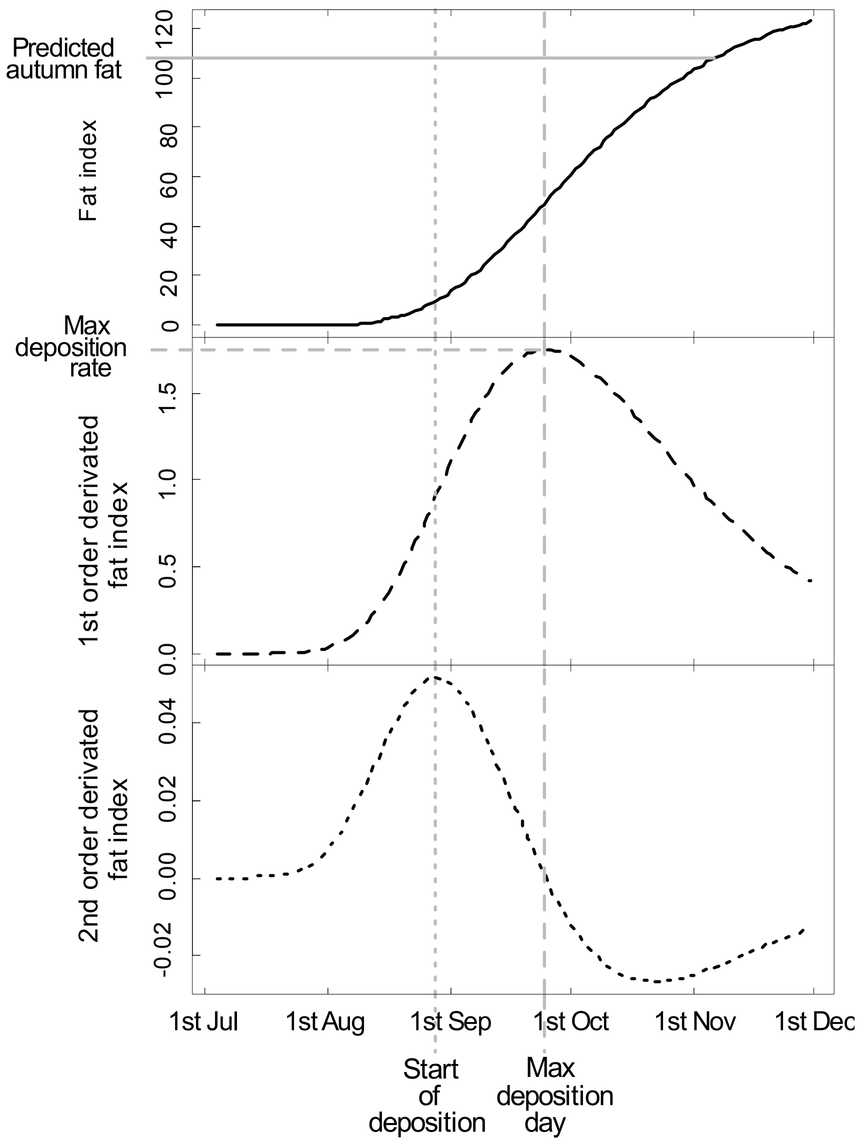

Figure 3. Schematic figure of the four parameters extracted from the annual fat deposition curves of juvenile raccoon dogs in Häme and Kymi.

Table 1. Parameters extracted from the fat deposition curves of juvenile raccoon dogs in Häme and Kymi and environmental (climate and plant phenology) variables used in the regression models.

Parameters extracted from the fat deposition curves	
Start deposition	Maximum value of the second order derivate of the curve, representing the day when the fat deposition starts
Max deposition day	Day when the steepest rate in fat deposition is reached
Max deposition rate	Maximum value of the first order derivate of the curve, representing the maximum rate of fat deposition
Predicted autumn fat	Predicted value of fat on the 5th of November
Climatic variables	
Duration of snow cover	Number of 15 days periods when the snow depth > 30 cm
March temperature	Mean temperature in March (°C)
March snow depth	Mean snow depth in March (cm)
1st April snow depth	Snow depth recorded the 1st of April (cm)
Early summer temperature	Mean monthly temperature from 1st May to 30th June (°C)
Late summer temperature	Mean monthly temperature from 1st July to 31st August (°C)
Autumn temperature	Mean monthly temperature from 1st September to 31st October (°C)
Early summer rainfall	Mean monthly rainfall from 1st May to 30th June (mm)
Late summer rainfall	Mean monthly rainfall from 1st July to 31st August (mm)
Autumn rainfall	Mean monthly rainfall from 1st September to 31st October (mm)
Plant phenology variables	
Onset of spring	Day when NDVI (normalized difference vegetation index) value represents the birch leaf burst
Peak time	Day when NDVI reaches the highest value of the season
Peak value	NDVI value at peak time, maximum productivity of the year
Annual productivity	Time integrated NDVI values for one growing season
Onset of autumn	Day when NDVI falls below the value of the onset of spring
Length growing season	Number of days between onset of spring and onset of autumn

2.2.2 Statistics

Linear regression models were run to find environmental variables that explained the parameters extracted from the curves of fat deposition. Each parameter extracted from the curve of fat deposition was tested against the climatic and plant phenology variables that were expected to have an explanatory significant effect (Table 2). Because of the low sample size ($n = 16$) we used only one explanatory variable in each model. To account for unknown factors that might affect regional variation in growth, province (Häme or Kymi) was always set as covariate. In addition to testing the plant phenology variables separately, we extracted the first principal component from a principal component analysis of the plant phenology variables (phenology principal component) and used this as an explanatory variable in our models (Graham 2003). This was done to see if the plant phenology as a whole influenced the fat deposition parameters, and because correlation between plant phenology variables did not allow us to include several of them in the same model. Squared semi-partial correlations (Tabachnick & Fidell 2001) were run to find the proportion of variance explained by each variable after accounting for the variance explained by province. The analyses were done using R 2.2.1 Software (R Development Core Team 2005).

2.3 Results

Several models were run for each parameter extracted from the fat deposition curves (Table 2), of these only the models where a variable had a significant effect in explaining the dependent one are reported in Table 3.

The first component of the PCA (the phenology principal component) explained 49% of the variance in the phenology variables. It was negatively related to onset of spring ($r_p = - 0.515$), and positively related to peak time ($r_p = 0.304$), peak value ($r_p = 0.166$), annual net primary productivity ($r_p = 0.963$), length of the growing season ($r_p = 0.956$) and onset of autumn ($r_p = 0.842$). The phenology principal component was never significant (all *P*-values > 0.05) in any of the models of fat deposition pattern it was included (Table 2).

The start of fat deposition (start deposition) was positively related to the duration of snow cover higher than 30 cm and to March snow depth (thus delaying it), and was negatively related to March temperature (Table 3, Fig. 4), but was not significantly explained by the onset of spring ($P > 0.05$). The day when the highest value of fat deposition rate was reached (max deposition day) was positively related only to late summer temperature (Table 3, Fig. 4), which means that in warmer summers the highest rate of fat deposition was reached later in the season.

The highest rate of fat deposition (max deposition rate) was not significantly related to any of the climatic or phenology variables we predicted (Table 2), such as duration of snow cover higher than 30 cm, early and late summer temperature and peak value (all *P*-values > 0.05).

The predicted value of fat on the 5th of November (predicted autumn fat) was negatively related to snow depth on the 1st of April (Table 3, Fig. 4). However, it was not significantly explained by any of the other variables that were tested (all *P*-values > 0.05). The snow depth on the 1st of April could either influence the predicted fat at the onset of hibernation through the date when the fat deposition started, or as a more broad effect on the environment through the season. To test for this, we included both snow depth on the 1st of April and start of fat

Table 2. Set of dependent variables extracted from the 16 fat deposition curves of juvenile raccoon dogs in Häme and Kymi, environmental explanatory variables that were tested and predictions. For explanation of these variables, see Table 1 and Fig.2.

Dependent variable	Explanatory variable	Prediction
Start deposition	Duration of snow March temperature March snow depth Onset of spring	Long snow cover, harsh spring and late onset of spring will delay ovulation and birth and therefore the start of fat deposition
Max deposition rate	Early summer temperature Late summer temperature Annual productivity Peak value Early summer rainfall Late summer rainfall	Early summer temperature, summer rainfall, annual productivity and peak value in vegetation productivity will be positive related to the highest rate of fat deposition; high late summer temperature will lead to dry summer and negatively affect the rate of fat deposition
Max deposition rate	Duration of snow	Subadult raccoon dogs will reach a highest rate of fat deposition to compensate for longer snow cover and store enough fat and hence, the fact that they were born late in spring
Max deposition day	Early summer temperature Late summer temperature	Early summer temperature will positively affect abundance of food resources and the day with highest deposition rate will occur earlier in the season, high late summer temperature will lead to dry summer and the day with highest deposition rate will occur later in the season
Max deposition day	Peak time	The peak time in plant phenology will be positively related to the time of highest fat deposition rate
Predicted autumn fat	1st April snow depth Onset of spring Start deposition	Deep snow at the beginning of April, a late onset of spring and a late start of fat deposition will, e.g. by shortening the growing season, negatively affect the total amount of fat deposed at the end of it
Predicted autumn fat	Phenology PCA1 Annual productivity Early summer temperature Late summer temperature Length growing season Early summer rainfall Late summer rainfall Autumn rainfall Peak time Onset of autumn Autumn temperature	All these variables, through their direct and indirect effects on food resources, will positively affect the total amount of fat deposed at the end of the growing period, high summer temperature, by leading to dry summer, will influence the crop of berries and might negatively affect the total amount of fat deposed at the end of the growing period

Table 3. Set of linear regression models explaining four different parameters extracted from the 16 fat deposition curves of juvenile raccoon dogs in Häme and Kymi. Estimate, SE, *P* and Sr^2 (squared semi-partial correlation coefficient) refer to the explanatory variable. Province was always included as co-variate, DF = 13. For explanation of these variables, see Table 1 and Fig.2.

Model	Estimate	SE	t	*P*	R^2	Sr^2
Start deposition ~ Duration of snow	2.920	1.116	2.616	0.021	0.389	0.345
Start deposition ~ March temperature	-3.547	0.767	-4.622	0.001	0.647	0.622
Start deposition ~ March snow depth	0.466	0.154	3.011	0.010	0.450	0.411
Max deposition day ~ Late summer temperature	7.873	3.321	2.370	0.034	0.338	0.302
Predicted autumn fat ~ 1st April snow depth	-0.381	0.174	-2.184	0.048	0.269	0.268

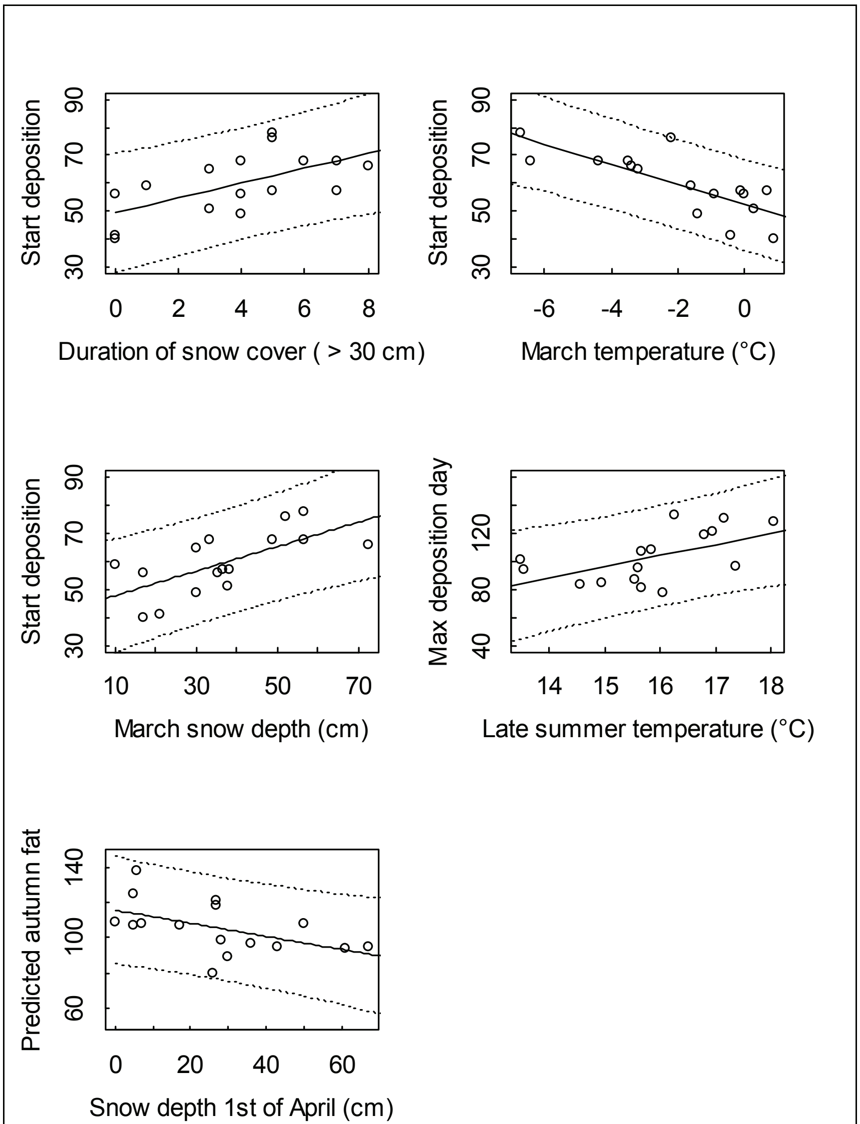

Figure 4. Set of linear regression models where a climatic or plant phenology variable significantly explained one of the parameters extracted from the 16 fat deposition curves of juvenile raccoon dogs in Häme and Kymi. Smooth line = regression line, dotted lines = 95% confidence intervals.

deposition, in addition to province, as explanatory variables to see how much of the variation in the predicted fat value on the 5th of November they explained after accounting for each other. The significance of snow depth then decreased to non-significant (t = -1.570, df = 1, *P* = 0.142), however, the parameter estimate did not change considerably (-0.323 ± 0.206 SE). Moreover, the effect of start of fat deposition was far from significant (t = -0.568, df = 1, *P* = 0.580), showing that the effect of spring not necessarily operates only through the start of fat deposition.

2.4 Discussion

2.4.1 Performance of climatic and plant phenology variables

Contrary to what we expected, plant phenology variables never performed well in explaining the parameters extracted from the fat deposition curves of juvenile raccoon dogs. However, climatic variables describing the conditions at the start and at the end of the hibernating period explained between 27 and 62 % of the variation in fat deposition. This is a rather contradictory result, because climate has often been used in animal ecology studies as a proxy of the productivity of vegetation (reviewed in Stenseth *et al.* 2002).

The start of fat deposition was explained by climatic variables, such as duration of snow cover, temperature and snow depth in spring (Table 3, Fig. 4), which have traditionally been used as indicators of the onset of spring. However, the onset of spring determined by plant phenology did not explain significantly the start of fat deposition. This supports the findings of Helle & Kauhala (1991), that snow depth affects the time of oestrus in females and therefore the day of birth of juveniles, which will in turn affects the start of fat deposition in juveniles. Moreover, food resources exploited by raccoon dog, such as voles, carrion (Kauhala *et al.* 1998, Selva *et al.* 2003) and compost heaps, might be available in spring before the vegetation starts growing again, as long as raccoon dogs can move efficiently around.

The day when the maximum rate of fat deposition was reached was positively related to late summer temperature (the warmer the summer the later the day), but was not explained by the time of peak in vegetation productivity. This might indicate that a food resource that is very important for fat deposition in juvenile raccoon dogs is negatively affected by late summer temperature, such as for example berries. In fact, the mean fat index of raccoon dogs at the end of the growth season has been shown to be related to the availability of berries in late summer-autumn, which is negatively affected by temperature in late summer (Kauhala 1993). High summer temperature leads to a dry summer and this has also been found to negatively affect body mass of herbivores (Herfindal *et al.* 2006a). However, we did not find any relationship between early- and late-summer rainfall and maximum rate of fat deposition. Moreover, we could not take into account a cyclic response of berry crop production and/or vole abundance, which have complex interactions in boreal forest ecosystems (*e.g.* Selås 2002, Oksanen *et al.* 1999).

The predicted value of fat on the 5th of November was only explained by snow depth on the 1st of April, the relationship being negative (see also Kauhala 1993). This suggests that juveniles born later will weigh less at the end of the growth period than juveniles born earlier, no matter how productive the summer was. On the other hand, harsh spring conditions will not only affect food availability, but also how much of their fat reserves females will reabsorb during early spring (Kauhala 1993), which will in turn influence the time of reproduction and the predicted weight of juveniles at the end of the growth period. However, the fact that the fat value on the 5th of November was not related to the start of the deposition suggests that the observed negative effect of snow depth in April on the predicted fat at the onset of winter sleep is not related to a delayed start of fat deposition in juvenile raccoon dogs, but rather some general long-lasting environmental effects of harsh spring. On the other hand, the rather low sample size could also explain the lack of significance of snow depth after accounting for start of fat deposition. Furthermore, there are some constraints in the amount of fat that a hibernating animal can store, which is about 35-50 % of total body mass (Millar & Hickling 1990). At some point, the metabolic cost of maintaining fat reserves, or the risk associated with carrying them, will exceed the benefits (Pond 1981). Therefore, at some stage of the growth period, the juvenile raccoon dog will have to prioritize fat deposition with respect to growth and the body mass reached at that date will constrain the quantity of fat that they can store. So if the juvenile are smaller at birth because of harsh spring conditions, we might expect them to store less fat even if they do not necessarily start later in the season the fat deposition.

Our results indicate that plant phenology parameters are not good measures of food availability for raccoon dog. Such measures have performed well in explaining life history traits in herbivore species (Garel *et al.* 2006, Herfindal *et al.* 2006 a, b, Pettorelli *et al.* 2006), but might not reflect variation in food abundance and quality for omnivore species. Limitations in the use of satellite data such as the presence of a high percentage of coniferous forest in the study area, might have contributed in hiding the relationship between fat deposition in juvenile raccoon dogs and plant phenology, both because the coniferous forest is evergreen and can buffer against extremes of seasonal variation in plant phenology and because the tree canopy might screen the ground vegetation (K.-A. Høgda, personal observation). Furthermore, although we were able to explain a quite high proportion of the temporal variation in fat deposed at the end of the growing season, there is a high amount of variation left, which might be related to other factors we did not account for.

2.4.2 Predictions on the expansion of raccoon dog

The relationship between climatic variables and the pattern of fat deposition in juvenile raccoon dogs (which in turn affects the reproductive output; Helle & Kauhala 1995) allows us to make some predictions on the future distribution of this species in the light of the proposed climate change. Most of the observed climatic changes have been in the direction of reducing climatic constraints to plant growth (Fraedrich *et al.* 2001, Intergovernmental Panel on Climate Change 2007). However, in the climate change scenarios there is a marked contrast between winter and summer change of precipitation pattern, and seasonality is likely to increase. Humphries *et al.* (2004) predicted that seasonally inactive mammal species should experience a substantial increase in abundance and distribution in response to climate change in the Canadian arctic. However, species inactive in winter might experience problems at higher altitudes, because of lack of synchronisation between plant phenology and climatic conditions *i.e.* they emerge earlier in the season, because they use air temperature as a cue, but the snow is still too deep for finding food (Inouye *et al.* 2000). Our results suggest that in Europe raccoon dogs are likely to benefit from climate warming, but more abundant spring precipitation in form of snow at higher latitudes could compensate for the positive effect of increased primary productivity and might become the ultimate constraint to their expansion towards harsher environments.

3 POTENTIAL DISPERSAL CORRIDORS AND TEMPORAL AND SPATIAL DISTRIBUTION OF RACCOON DOGS IN NORWAY

3.1 Introduction

The process of invasions by alien species can be conceived to consist of a two-components process: spatial spread and local population build-up after arrival and settlement (Hengeveld 1994). Recently, it has become highly relevant to understand how climate change might affect the invasion process, *e.g.* by altering the quality of habitats (Weidema 2000) and it must be considered in modelling the invasion of new species.

Dispersal, defined as the one way movement of an individual from its natal territory to a new potential breeding site (Ray *et al.* 2002), plays a major role in population dynamics (Clobert *et al.* 2001). Knowledge about potential dispersal corridors and distribution of preferred habitat is important when planning adequate management programs to prevent invasion by alien species.

Dispersing individuals are exposed to an array of costs and benefits associated with the use of different habitats. These costs and benefits constantly change in space and time through the landscape structure, thus affecting dispersal in a complex way (Wiens 2001). Consequently, distance by itself might not adequately reflect the true cost of dispersal. Alternatively, distance can be weighted by species-specific costs related to the permeability of the habitats that have to be crossed (Ray *et al.* 2002).

Raccoon dog juveniles usually split up and disperse between June and October when they are about 4-5 months (Nowak 1984, Drygala *et al.* 2000) and they can cover long distances. Between 1935 and 1984 raccoon dogs colonised 1.4 million km^2 of Europe (Nowak 1984). The frontier of the raccoon dog population expanded though southern and central Finland (Fig. 5) at an average annual rate of 20 km (Helle & Kauhala 1991). However, in some areas the measured rate of expansion reached 120 km per year (Lavrov 1971, Helle & Kauhala 1991), illustrating the great plasticity of this species in adapting to variable climatic and environmental conditions (Kowalczyk 2006).

Based on the literature on habitat choice of raccoon dogs, it is possible to identify a species-environment relationship showing the distribution of suitable areas (Corsi *et al.* 2000). We defined suitability as the potential of a habitat to meet the needs of the population (Conroy & Moore 2002). Assuming a free distribution (Fretwell & Lucas 1970), high quality habitats are expected to be the most used ones. The relative measure of suitability does not predict the exact estimates of population size, but allows areas to be compared to each other (Dettki *et al.* 2003). In Finland raccoon dog density has been reported to vary depending on the length of the growing season (Helle & Kauhala 1991) where it explained 74 % of the regional variation. Altitude seems also to be an important limiting factor (Nowak 1993). For these reasons, in our model we considered the following ecological characteristics of the environment: habitat type, elevation and length of the growing season.

We therefore: (1) modelled the spatial distribution of habitats suitable for raccoon dogs on the Scandinavian peninsula; (2) identified the potential dispersal corridors of this species from Sweden to Norway and (3) illustrated how these two factors might be affected by the proposed climate change according to two possible scenarios.

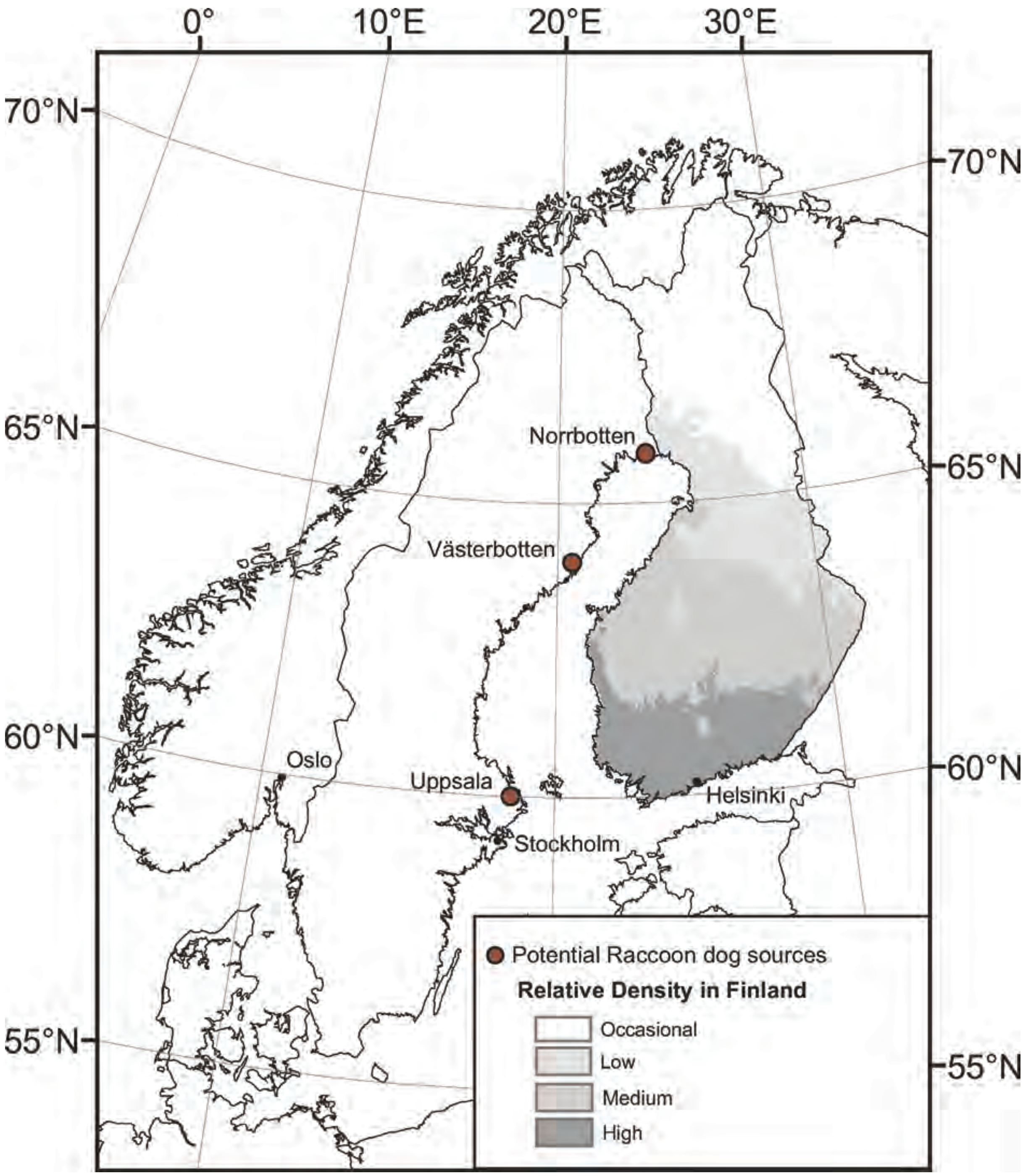

Figure 5. Map of the study area, showing a gradient of relative density of raccoon dog in Finland (shaded areas, after Helle & Kauhala 1991), the potential Swedish sources of expansion (red dots).

3. 2 Methods

All the GIS analyses were done on a raster with 1x1 km^2 resolution. Habitat categories were based on the database Global Land Cover 2000 (Bartholome *et al.* 2002). This database uses the FAO Land Cover Classification System (LCCS), where each land cover category is characterised by vegetation type and cover density. Furthermore, we used a digital elevation model (USGS Earth Resources Observation and Science 2007) and a climatic map covering

the length of the plant growing season (Norwegian Meteorological Institute) to capture differences in the landscape within the habitat types from the Global Land Cover data.
The expansion modelling was done by means of an Arc/Info workstation version 9.1 for Windows (ESRI 2006).

3.2.1 Potential suitability

The criteria for the raccoon dog habitat suitability were based on the literature on habitat use of the species in its introduced range (Table 4). Habitat suitability was defined as a function of the habitat characteristics described through the three following layers: habitat type, elevation, and length of the growing season (Fig. 6). Each of these layers were categorised by four classes (1-4), were four indicates optimal and one indicates unsuitable habitat (see Table 4 for the reclassification schedule). This scale is fine enough to capture differences in the landscape, yet it limits the categories to a number easy to interpret. Finally, the habitat suitability for each 1x1 km^2 pixel was calculated as the sum of the three habitat characteristic layers. Because the three habitat characteristics are not expected to influence raccoon dog equally, they were weighted before summation, according to the following formula: habitat * 0.25 + elevation * 0.25 + growing season * 0.5. The output map was a 1x1 km^2 resolution raster with continuous values ranging from one (low raccoon dog suitability) to four (high raccoon dog suitability).

3.2.2 Potential dispersal corridors and expansion rate

Expansion analysis

The expansion analysis was performed according to the same spatial resolution as the habitat suitability description. The expansion was modelled based on three spatial data layers: a source layer, a cost layer and a survival layer. Together, these layers were used to model the expansion as a stepwise iteration, with the following components: 1) expansion from a source population through dispersion, 2) survival in the new range, 3) further expansion from areas invaded in 1) and were the species survived in 2) (Fig. 7). These three steps were run iteratively until all suitable habitats were invaded.

The cost layer defines the cost, or resistance, of moving through each unit (1x1 km^2 pixel in our case). In population expansion analysis, it is natural to assume that the cost of moving through a unit is higher if the quality of its habitat is poor, *i.e.* that individuals resist moving into poor habitats, whereas the cost of moving through good habitats is low. Thus, the model assumes that population expansion will follow an optimum route by minimizing the exposure to low quality habitat. The cost of moving from a unit (pixel or cell) to one of its four horizontal or vertical neighbour units is then calculated as: (cost of cell 1 + cost of cell 2) / 2. In case of diagonal movement, the cost was calculated as: [(cost of cell 1 + cost of cell 2) / 2] * $\sqrt{2}$. The cost-distance analysis (*e.g.* Walker & Craighead 1997, DeMers 2005) uses these algorithms to calculate the least cumulative cost from the source locations to every unit in the cost layer, constrained by a maximum cost-distance that can be covered. Accordingly, a cost-distance analysis describes the least cost of moving from a source location (defined by the source layer), through a landscape with varying resistance (a cost layer), to a given location. However, instead of calculating the Euclidian distance from one point to another, the cost-distance function uses values of cumulative distance, according to the cost of the cells (DeMers 2005). Therefore, the cost-distance is expressed in cost units rather than geographic units.

Table 4. Set of environmental variables used in the analysis and reclassification ranking of the habitat suitability of raccoon dogs in Scandinavia: 4 = highly suitable habitat, 3 = fairly suitable habitat, 2 = poor habitat and 1 = unsuitable.

Habitat type	**Habitat rating**	**References**
Tree cover, broadleaved, deciduous, closed, open	4	Drygala *et al.* 2000, Kauhala 1996a, Kauhala & Auniola 2001, Sutor 2004
Tree cover, needle-leaved, evergreen	4	
Tree cover, mixed leaf type	4	
Mosaic: tree cover / other natural vegetation	4	
Tree cover, burnt	1	
Herbaceous cover, closed-open	3	Kauhala 1996a
Sparse herbaceous or sparse shrub cover	2	Kauhala 1996a
Wetland: regularly flooded shrub and/or herbaceous cover	4	Drygala *et al.* 2000, Kauhala 1996a
Tree cover, regularly flooded, fresh water	4	
Cultivated and managed areas	3	Kauhala & Saeki 2004
Mosaic: cropland / tree cover / other natural vegetation	3	Drygala *et al.* 2000
Mosaic: cropland / shrub and/or grass cover	2	Kauhala pers. comm. 2007
Bare areas	1	
Water bodies	4	Drygala *et al.* 2000, Kauhala 1996a, Sutor 2004, Ward & Wurster-Hill 1990
Snow and ice	1	
Artificial surfaces and associated areas	3	Kauhala 1994a
Elevation classes (m)		
0 – 300	4	Nowak 1993, Weber *et al.* 2004
300 – 600	3	
600 – 800	2	
800 – 2237	1	
Length of growing season classes (days)		
Less than 135	1	Helle & Kauhala 1991
135 – 150	2	
150 – 165	3	
More than 165	4	

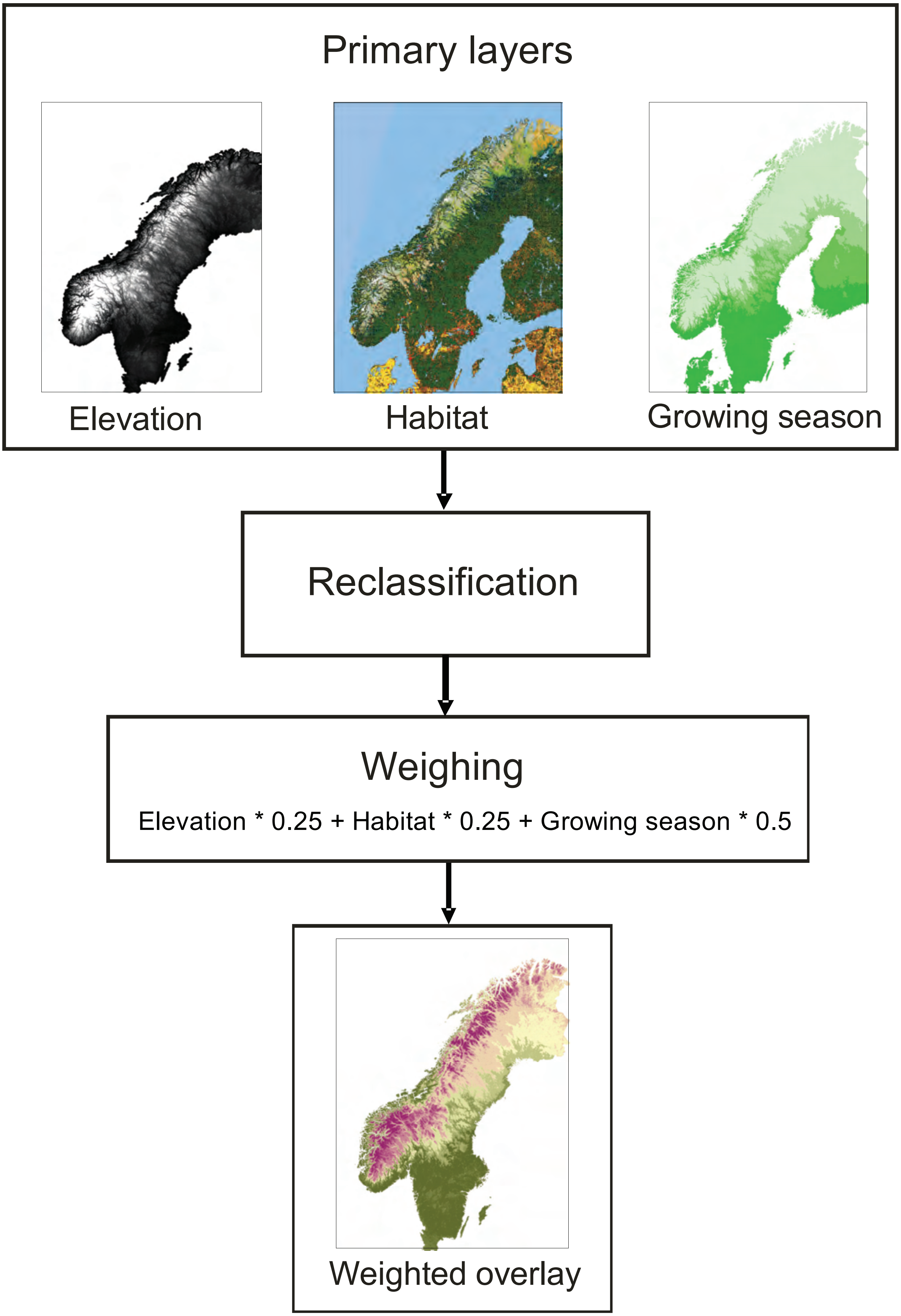

Figure 6. GIS procedure for modelling the distribution of preferred habitat of raccoon dogs in Scandinavia.

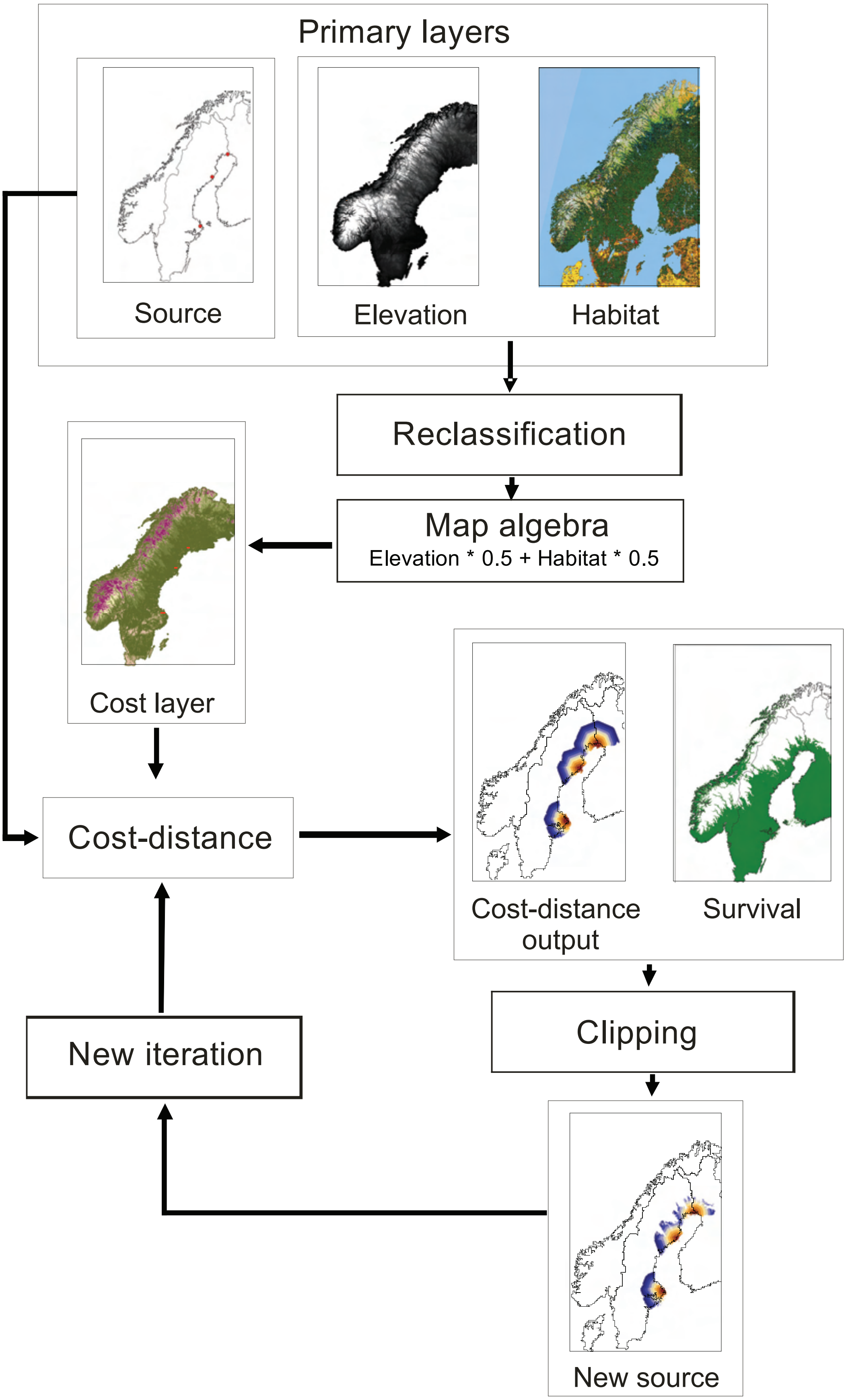

Figure 7. Steps used to perform the cost-distance analysis to evaluate the range and rate of invasion of raccoon dogs in Scandinavia

In an expansion setting, there are constraints on the annual expansion distance, *e.g.* through dispersal distance. Thus, there are limits on the distance which the population can cover each year by expanding, and this distance is influenced by the cost of the area it expands through.

After the dispersal, the individuals have to survive in the newly invaded areas. The dispersal of individuals can cross habitats that are not able to maintain viable populations. However, these areas cannot be considered a source for further expansion the next year. Thus, in the next step of expansion, the source population was defined as all areas that were invaded through the previous step and that were able to maintain viable populations. The number of steps or iterations needed for the expansion to reach an area will represent the minimum number of years needed for the expansion from the source populations to reach the specific area.

Defining the parameters in the expansion analysis

Cost values for different habitat types and elevation categories were chosen according to the literature on raccoon dog habitat preferences (Table 5). We assigned cost value 1 to preferred habitats, assuming a minimum cost of moving through them. Hindering landscape elements like high altitude and not utilized habitats represented relative barriers, restricting but not totally preventing movement. We created two cost layers; one with low range in the cost values, and one where the differences in cost between preferred and un-preferred areas were considerably higher. In the high-cost layer the cost associated to habitat characteristics were squared. Accordingly, the low-cost layer had values ranging from 1 to 4, and the high-cost layer had values ranging from 2–25 (Table 5).

The source layer consisted of three locations in Sweden where raccoon dogs dispersing from Finland had been observed (Fig. 5). These three locations defined the areas where the expansion of raccoon dog into Sweden and Norway was likely to start from.

We used the length of the plant growing season to define viable areas for the survival layer. According to Helle & Kauhala (1991), this parameter is the most important for raccoon dog distribution in Finland, and the limit for areas that can maintain raccoon dog populations was set to minimum 135 days of growing season.

We set the maximum cost-distance value per step, which defined the maximum annual dispersal, to 20 km and 40 km. We assumed that the past expansion rates in Finland and former Soviet Union (Helle & Kauhala 1991) corresponded to the maximum annual dispersal rate into a novel environment. The two dispersal values chosen represent the range of dispersion distance reported (Helle & Kauhula 1991).

3.2.3 Expected effects of climatic change

The predicted climatic change will most likely cause a reduction in the number of days with snow cover in Fennoscandia (Intergovernmental Panel on Climate Change 2007), thus leading to a longer growing season. However, the extent of the change is expected to vary regionally (Vikhamar-Schuler & Førland 2006). In Norway, the length of the snow cover period is expected to be reduced of a minimum of 35-50 days by 2070-2100. Therefore, two scenarios of climatic change were evaluated based on a 10 and a 35 days longer growing season, representing both the uncertainty in the climate change scenarios, and a temporal variation in the start of invasion. This was done by reducing the 135 days critical limit by 10 and 35 days respectively in the growing season dataset that defines the survival range of raccoon dogs in Fennoscandia.

Table 5. Reclassification ranking for cost layer: low values = highly suitable habitat and low cost of movement, high values = unsuitable habitat and high cost of movement.

Vegetation cover	**Habitat rating**		**Rational e for rating**	**References**
	Low cost	**High cost**		
Tree cover, broadleaved, deciduous, closed, open	1	1	These four types of land cover are the most desirable for the raccoon dog. The ideal habitat requirements are met in these types of land cover where it can find food, shelter and den sites. They are all given value 1 to ensure that when the cost-distance analysis is run, the program will highlight dispersal through these land covers	Drygala *et al.* 2000, Kauhala 1996a, Kauhala & Auniola 2001, Sutor 2004
Tree cover, needle-leaved, evergreen	1	1		
Tree cover, mixed leaf type	1	1		
Mosaic: tree cover / other natural vegetation	1	1		
Tree cover, burnt	3	9		
Herbaceous cover, closed-open	2	4	Clear-cut and 3 - 9-year old plantations is not much used	Kauhala 1996a
Sparse herbaceous or sparse shrub cover	3	9	Area dominated by lichen and moss and provides little food or shelter	Kauhala 1996a
Wetland: regularly flooded shrub and/or herbaceous cover	1	1	This is areas near water and shores. Raccoon dog favour forested river, here is often dense undergrowth which provides food and shelter. It also has the ability to escaping into water when attacked; thus raccoon dog prefer to forage near water. Spread followed streams and wetland.	Drygala *et al.* 2000, Kauhala 1996a
Tree cover, regularly flooded, fresh water	1	1		
Cultivated and managed areas	2	4	Oat and other agricultural products are often found in raccoon dog stomachs	Kauhala & Saeki 2004
Mosaic: cropland / tree cover / other natural vegetation	2	4	They may occupy a mosaic of woodland and agricultural areas	Drygala *et al.* 2000
Mosaic: cropland / shrub and/or grass cover	3	9	In Finland they avoid fields and open areas	Kauhala pers. comm. 2007
Bare areas	4	16	This is areas with bare rock and sands.	
Water bodies	1	1	Includes oceans, seas, lakes, reservoirs and rivers. Shores are highly favoured summer and autumn, here it find food and could escaping into water when attacked. Is a very good swimmer	Drygala *et al.* 2000, Kauhala 1996a, Sutor 2004, Ward & Wurster-Hill 1990
Snow and ice	4	16	No habitat requirements a met here	
Artificial surfaces and associated areas	2	4	It is capable of living near human settlement and utilizing man-made food resources	Kauhala 1994b
Elevation classes for low cost layer				
0 – 350	1	-	Raccoon dogs occur more often at low altitudes, mainly below 300 meters, but occasionally can live at up to 800m. Raccoon dogs are seldom found above 600 meters above sea level and only exceptionally they can be found over 1000 meter	Nowak 1993, Weber *et al.* 2004
350 – 700	2	-		
700 – 2237	4	-		
Elevation classes for high cost layer				
0 – 400	-	1	See above	Nowak 1993, Weber *et al.* 2004
400 – 600	-	2		
600 – 800	-	3		
800 – 1000	-	7		
1000 – 1200	-	8		
1200 – 2237	-	9		

3.3 Results

3.3.1 Potential distribution area

The results of the analysis on potential distribution of raccoon dogs in the Scandinavian peninsula are shown in Fig. 8. The map indicates that large areas with suitable habitat exist both in Sweden and in south-eastern Norway (areas with green colours in Fig. 8). These areas have environmental conditions favouring the raccoon dog, *i.e.* long growing season (above 150 days), and the preferred habitat types. The different shades of green indicate areas of different density potential. The most suitable areas (in dark green) have growing season of 165 days or more. These areas have the right environmental conditions potentially supporting the highest population density. Areas with medium green colour have a growing season between 150 and 165, and areas with the lightest green have growing season ranging from 135 to 150 days. Light yellow indicates where the growing season is just below the 135 days limit and are therefore less suitable for population growth. Furthermore, the coastal areas along both countries provides habitat that can sustain viable populations of raccoon dog. However, moving further north, the length of the growing season limits the suitability although the habitat types may be suitable (colours towards yellow in Fig. 8). Still, large parts of inland, both in Sweden and Norway, have environmental characteristics that are not suitable for raccoon dog, and most likely viable populations will not occur in these areas (pink and red colours in Fig. 8).

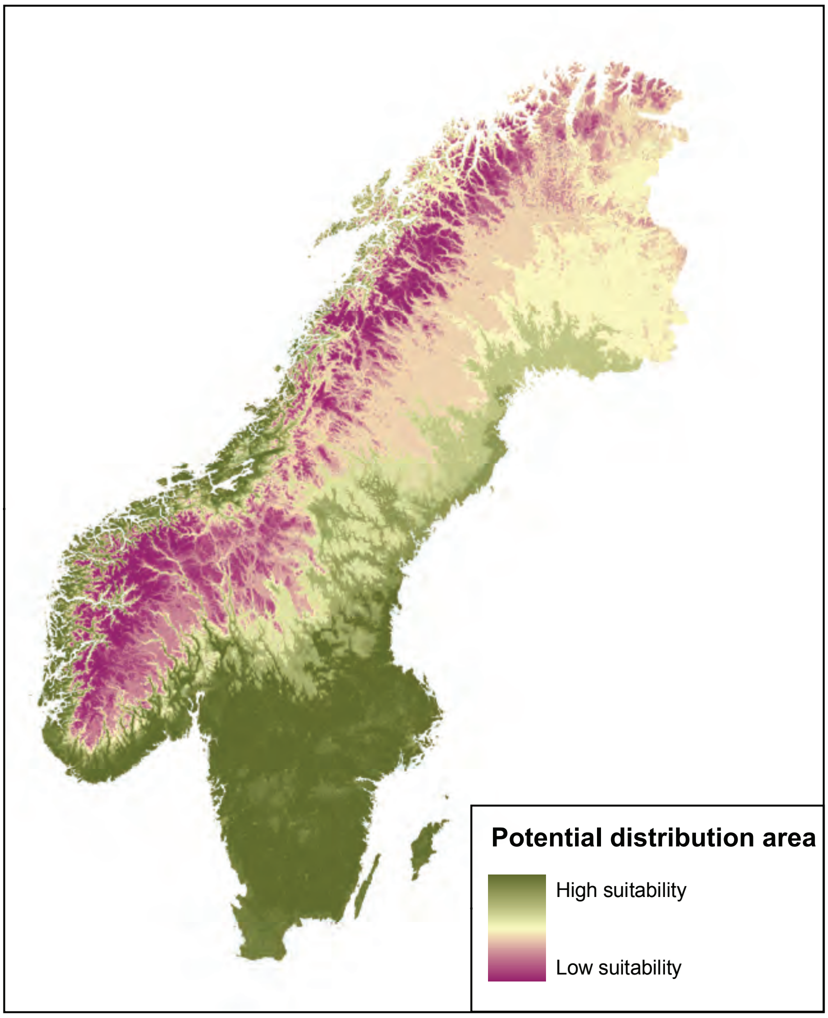

Figure 8. Map of the potential distribution area based on 16 vegetation types, 4 elevation classes, and the length of growing season grouped in 4 categories (see Table 4 for more details).

3. 3.2 Expected expansion rate

Because we combined two different cost layers with two maximum annual cost distances, we obtained four different scenarios of invasion rate of raccoon dog in Fennoscandia (Fig. 9). The population expansion rate differed among the four scenarios, but the area that raccoon dogs are most likely to colonize earliest were relatively stable.

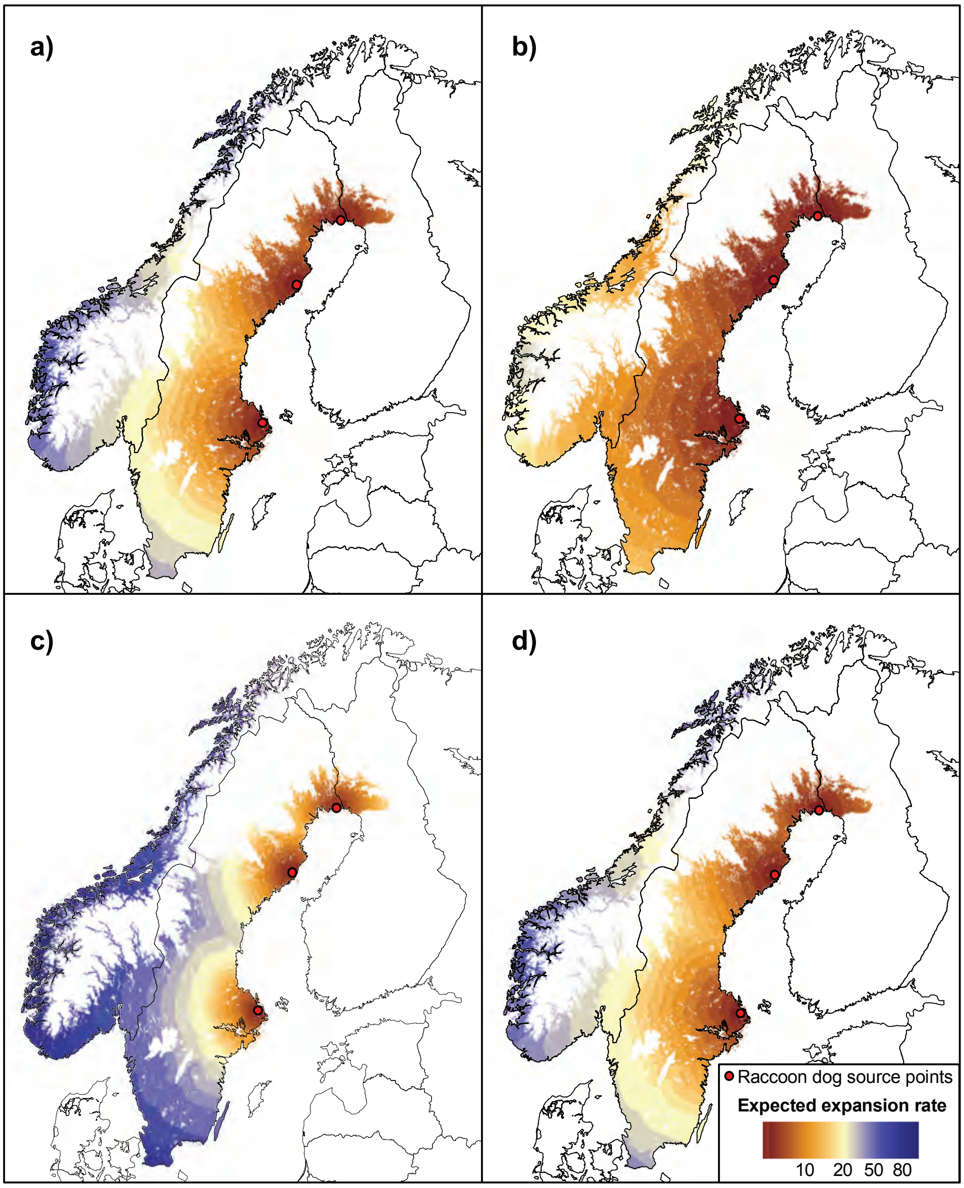

Figure 9. Expected expansion range and rate of raccoon dogs in Scandinavia according to the cost-distance analysis based on habitat type, elevation and length of the growing season. Four different scenarios were evaluated according to the cost layer and the maximum cost-distance used: a) and b) are based on the low-cost layer (cost values = 1 - 4) with a maximum cost-distance of 20 and 40 km respectively. c) and d) are based on the high-cost layer (cost values = 2 - 25) with a maximum cost-distance of 20 and 40 km respectively.

The first analysis (Fig. 9a, b) was based on the low-cost layer (cost values = 1-4). According to the first scenario, were maximum cost-distance (maximum dispersal in the most preferred habitats) was set to 20 km, the front of invasion will reach the Norwegian border from its source areas in Sweden within 20 years, at southern part of Hedmark and Akershus, and in Nord-Trøndelag (Fig. 9a). After 70 years raccoon dogs will have reached all suitable areas in Fennoscandia. When the maximum cost-distance is set to 40 km, thus increasing the annual expansion, the front of the invasion will reach the Norwegian border in 10 years and cover all suitable areas in 35 years.

The second analysis was based on the high-cost layer (cost values = 2-25). The resulting maps (Fig. 9c, d) show a lower expansion rate compared to the low-cost layer (Fig. 9a, b). According to a maximum cost-distance of 20 km, it will take 35-40 years for front of the raccoon dog invasion to reach the Norwegian border. When the maximum cost-dispersal is set to 40 km, it will take approximately 20 years for the invasion front to reach Norway. As for the low-cost analysis, the southern part of Hedmark, Akershus, and Nord-Trøndelag (Fig. 1) will most likely be the first areas to be colonized by raccoon dogs in Norway (Fig. 9c, d).

3.3.3 Potential dispersal corridors

The expansion model revealed two main dispersal corridors from Sweden to Norway. The largest is in south-eastern Norway, in southern Hedmark and Akershus. This corridor is very wide (> 300 km), in contrast with the second corridor. The second potential corridor-area is represented by several valleys cutting through the alpine areas along the border between Trøndelag and Sweden. Although several corridors can be detected in this area (Fig. 9), they are very narrow and some of them even not continuous. Several large alpine areas, *e.g.* in southern Norway, and along the Swedish border from Hedmark and northwards, operates as effective barriers for the invasion.

3.3.4 Effects of climatic changes on expansion rate and dispersal corridors

The expansion pattern changed considerably when we simulated climatic change by increasing the growing season by ten (Fig. 10a) or 35 (Fig. 10b) days. First, we find a large increase in available habitat to sustain viable populations, particularly in the 35-days increase scenario. Second, with the 10-days increase, several new corridors occur along the border between Sweden and Norway up till Trøndelag (Fig. 10a). With the 35-days increase, potential corridors are present even at the northernmost county, Finnmark, where invasion from Finland now become probable. Only the most alpine areas at the Fennoscandian peninsula now operate as real barriers, slowing down the invasion rate (Fig. 10).

3.4 Discussion

Because of the threat which nonindigenous species pose to biodiversity, the availability of potential habitat for raccoon dogs in Scandinavia was a central question in our analysis. We identified large areas of potential raccoon dog habitat in the south-eastern part of Norway and also along the coast. The eastern part of southern Norway (Østfold, Vestfold, Oslo and Akershus counties) might be particularly at risk of invasion, firstly because this region has the right environmental conditions, but also the potential to be reached first by the expansion front. Moreover, this study clearly shows that the southern part of Sweden has large areas of habitat were raccoon dogs can settle at high population densities.

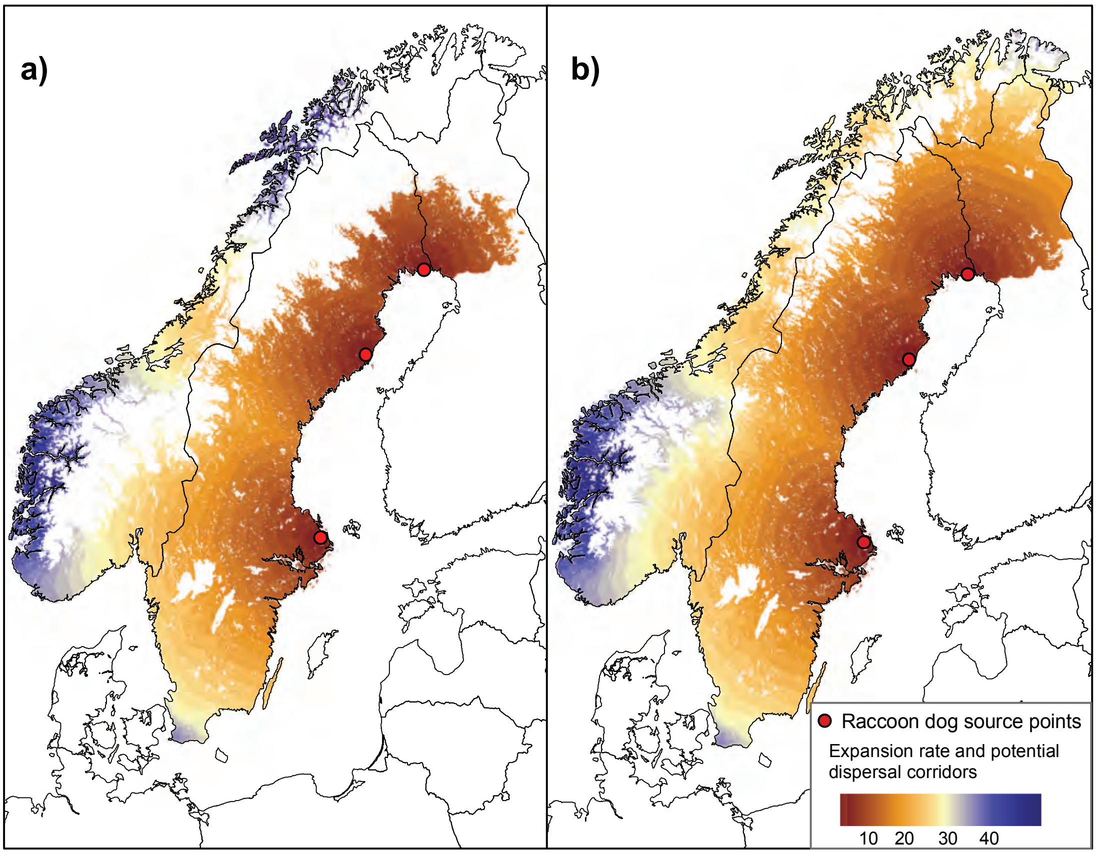

Figure 10. Effect of climate changes on the raccoon dog invasion in Scandinavia, two scenarios were evaluated by cost-distance analysis based on habitat type, elevation and length of the growing season. a) ten days longer growing season, b) 35 days longer growing season.

Although GIS techniques provide the means to effectively model habitat suitability, a model is only as good as the data which it is based upon (Turner *et al.* 1995). Our ability to detect patterns in habitat use is strongly affected by the spatial scale we choose (Wiens 2001). In our model we assumed that raccoon dogs select areas based on a quite broad scale of habitats, however animals might select habitat according to an even finer scale, *i.e.* through resources within habitats (Heglund 2002). For example, the literature reports raccoon dogs to prefer moist deciduous forest and shores of rivers and lakes with abundant undergrowth (Drygala *et al.* 2000). However, we were not able to incorporate undergrowth at this scale in our analyses and the map we used did not include all the rivers, streams and wetlands available. It is also important to underline that our analysis contain little information on the availability of shelter and denning sites. However, although our analysis of the distribution area is based on a quite coarse scale, it is reasonable to assume that it gives a fair picture of which areas will be preferred if raccoon dogs become established in Scandinavia. Thus, it also shows which areas should be prioritized if a control strategy of the species is to be adopted.

It is also important to underline that we based our invasion scenarios on three sources of raccoon dogs in Sweden, Norrbotten, Västerbotten and Uppsala counties (Fig. 1, 5). However, reliable observations have been made only in the first two areas. If Uppsala county does not contain any population source, the scenarios might become substantially different. For example, in that case the areas that will first face the invasion front will most likely be in central Norway (Trøndelag counties) instead than in the southern part of the country.

The length of the growing season appears to play an important role in determining the distribution and density of raccoon dog populations (Helle & Kauhala 1991). The growing season also determines the northern limit of the distribution in Finland which is between 65° N and the Artic Circle (Helle & Kauhala 1991). This limit has been more or less permanent since 1990 so this is probably a good measure of how far north raccoon dogs will spread in the Scandinavian Peninsula. We incorporated the length of the growing season in our model through four length classes. A short growing season restricted the raccoon dog potential distribution in the Scandinavian Peninsula. Still the GIS analysis indicated that there is potential habitat available for raccoon dogs, particularly in Sweden. However, considering that coastal areas have a milder climate than inland ones, the front of invasion could be further north.

Species distribution, however, is not only affected by climatic and topographic variables. Among others, both dispersal and expansion rates contribute in determining it (Garzón *et al.* 2006). Although processes responsible for invasion rate and pattern could not be inferred from our models, we obtained, through different settings of the cost-distance analyses, four possible scenarios for the raccoon dog expansion rate and range. Thus providing a picture of what might be the situation in the future. The four scenarios differed by invasion rate, but the range of expansion of raccoon dogs was the same in all, since it is determined by the areas with environmental conditions suitable for the establishment and growth of a population. The rate of invasion may be driven by factors like dispersal ability and demographic parameters in the source population (Adams 1999). The different scenarios predicted that the population front will reach Norway in a time period ranging between 10 and 35-40 years. The invasion is expected to cover all potential areas in a range of 35 to 145 years.

The actual invasion process varies depending on several factors, among them the behavioural characteristics of the invading individuals and the environmental conditions of the area of invasion (Shigesada & Kawasaki 1997). Biotic and abiotic characteristics of both source and receiving areas can all exert control over dispersal and invasion processes (Adams 1999). In Sweden, the observations of raccoon dogs occurred mainly in Norrbotten county (Åhlén 2007) and this area has quite harsh climate and is almost at the northern border of the raccoon dog distribution compared to Finland. As shown by the potential habitat analysis this area is barely suitable, thus probably not giving ground for high raccoon dog densities. Habitat quality and biotic factors in the matrix surrounding the source population can also influence the tendency of individuals to disperse, the covered distance and the success of dispersal (Hansson 1991). Animals expanding from Norrbotten county may have to cross areas with harsh environmental conditions and consequently are not likely to occur at high population density and expand at a high rate. The results from research in Sweden indicate that individuals have used 'Kvarken' as a dispersal corridor from Finland (Åhlén 2007). Further dispersal and population expansion from this source in Västerbotten county do not have to overcome the same hard environmental conditions as in Norrbotten county. Thus these areas are likely to be at a higher risk of invasion.

The invading process may also depend on the interaction with indigenous species (Shigesada & Kawasaki 1997), especially predators. In fact, predation might affect the survival of dispersing individuals, thus slowing down the dispersal rate. Therefore, habitat selection by dispersing individuals is often based also on the predation risk associated with a habitat (Weisser 2001). Wolves *Canis lupus*, lynxes *Lynx lynx*, wolverines *Gulo gulo*, martens *Martes* spp., golden eagles *Aquila chrysaetos*, sea eagles *Haliaeetus albicilla*, eagle owls *Bubo bubo*, and domestic dogs *Canis familiaris* are all potential predators of raccoon dogs (Ward & Wurster-Hill 1990, Sheldon 1992). However, apart from man, the most important natural predator of raccoon dogs is the wolf (Weber *et al.* 2004). Wolves are still uncommon in western Europe (Salvatori & Linnell 2005) and in Finland the wolf population is scattered especially in the south-eastern part of the country. The low density at which wolf populations occur in Fennoscandia may ease the raccoon dog invasion. In Norway and Sweden stable wolf packs are confined to the counties of Hedmark in south-eastern Norway and Värmlands in southern Sweden (Fig. 1). Therefore, wolf predation might slow down or even stop the species invasion in these areas, despite their high habitat suitability. However, raccoon dogs can live in complex communities including large carnivores such as the wolf and the lynx (*e.g.* Jędrzejewska & Jędrzejewski 1998). Therefore, it is difficult to predict the role of predation in controlling or limiting raccoon dogs populations without taking in account the availability of alternative prey in addition to climate and environmental productivity.

The cost-distance analysis was run according to four different combinations of cost-layers and rate of expansion. However, the potential dispersal corridors between Jämtland and Nord-Trøndelag counties identified by the analysis almost did not change between the different scenarios. This might depend on the fact that we chose a length of growing season of 135 days as survival limit of the raccoon dog invasion, which constrained our simulation more strictly than did altitude and habitat type. However, all these factors are correlated with each other and it is not likely that the results would have changed much if we had used altitude or habitat type as constraining factors.

Our analyses indicate that the valleys going through the mountains between central Norway and Sweden are the areas were a possible control program of the invasion should focus on. This result is very important, since control and eradication of alien species is generally very difficult and expensive (*e.g.* Pimentel *et al.* 2000) and identification of potential dispersal corridors is a key issue to prevent both primary and secondary invasions effectively with the lowest management cost (Byers *et al*. 2002).

GIS-modelling has been widely used to predict dispersal and expansion rate of animal populations. In the last years, some models have tried to incorporate climate change (*e.g.* Schwartz *et al.* 2001), since global warming is expected to cause shifts in species distributions (Parmesan & Yohe 2003, Root *et al.* 2003). The two scenarios presented, based on a 10 and 35 days longer growing season, both provide good examples of how climatic change might interact with the invasion by raccoon dogs. In fact, not only the speed of the invasion process changed dramatically with respect to present climatic conditions, but also the suitability range of the species resulted accordingly enlarged. This affected also the availability of potential dispersal corridors and, therefore, a possible control or eradication program of this species should take climatic changes into account. Again, the evaluation of the effort that should be put in controlling the species can vary considerably between present time and the two different climatic changes scenarios. In the worst case we present (growing season 35 days longer) it might seem a difficult task to prevent or stop the invasion process. However, the scenario allows to focus the management effort to the most affected areas.

It remains open the question about how raccoon dogs could be recovered in the northernmost part of Norway (Kirknes, Pasvik and Skibotn, Fig. 1). Three hypotheses can be done: 1) the animals were long distance dispersing individuals coming from Finland or from Russia; 2) there are other source populations further north than we believe and/or we have underestimated the plasticity of raccoon dogs in adapting to harsh environments; 3) the individuals were transported by humans and released far from their original population. The DNA analyses of the animal recovered in Skibotn might clarify if it originated from the Finnish or from the Russian population and help reconstruct its route northwards.

4 MANAGEMENT STRATEGIES

Management of nonindigenous species is a crucial aspect for maintaining native biodiversity and normal ecosystem functions (Byers *et al.* 2002). The results presented in the previous chapters, emphasize the potential risk of invasion by this species in the Scandinavian Peninsula. This is especially true in the light of the predicted climatic change.

The conventions that Sweden and Norway have ratified demand the adoption of active methods to prevent, control and eradicate alien species. The first step of a policy of control would be to identify the potential corridors through which the species will spread from Finland to Sweden and further to Norway. This can be done based on documented observations and through a cost-distance analysis like the one we presented. The second step could be to adopt efficient methods to capture animals in the areas were they are likely to occur first and at higher density.

It is also important to evaluate the areas which should be prioritized by management actions on the base of the potential effects the invasive species might have on a more fine spatial scale. In fact, an invader might have large effects in some areas and negligible ones in others (Byers *et al.* 2002). This has been proved for raccoon dogs in Finland, where the species had a much heavier impact on the avian and amphibian fauna in insular with respect to mainland environments (Kauhala & Auniola 2001). Another important aspect that should be considered is the level at which raccoon dogs should be maintained to minimize their impact on the native community.

When planning a control action against an invasive species it should be taken into account not only the threat that the species might represent to the ecosystem, but also the consequences of the management policy itself (Byers *et al.* 2002). In some cases, the measures adopted to protect an invaded ecosystem may be worse than the problem (Arnold *et al.* 1998). If little information is available about the effects of invasive species, the impact of control efforts on the ecosystem is even less known. These disturbance effects should be evaluated not only for specific environments and communities, but also over different time scales, since immediate and delayed effects of control actions may not coincide (Byers *et al.* 2002).

It is likely that the management strategies adopted in Norway will have been previously tested in Sweden, which will presumably experience the raccoon dog invasion earlier. Therefore, we report below an example of control strategy that has been proposed for raccoon dogs in Sweden.

4.1 A plan to control raccoon dogs in Sweden

We like to pinpoint that the Swedish authorities have not endorsed a final management plan. We are just presenting a short summary of a plan proposed by Åhlén (2007) commissioned by the Swedish Environmental Protection Agency.

A grid of traps arranged along the coasts of Norr- and Västerbotten should work as an efficient system to detect the possible presence and ongoing reproduction of raccoon dog in the country. A grid of Nyborg traps (the most effective carnivore traps that are at present available to capture foxes and badgers in Sweden) should be arranged with two possible alternatives:

1) in cooperation with non-governmental organisations like the Swedish Association for Hunting and Wildlife Management and the Swedish Society for Nature Conservation and with the help voluntary hunters with a sincere interest in nature conservation.

2) by means of seasonal employed people who maintain and check the traps.

In the initial phase, a grid of ca 100 Nyborg traps should be established on the coast of Norr- and Västerbotten (Fig. 1) along several lines with a density of about 1 trap / 1000 ha. In addition, more traps should be put strategically were the species has been previously captured or shot and in areas were it has been reliably observed. Since the Nyborg traps use live bait (tame doves), their use is constrained to the period from April to October, because of animal welfare issues. This period corresponds to the season when raccoon dogs are active. This type of trap is however illegal in Norway.

The capture of raccoon dogs in this area should be performed according to the following procedure: all the raccoon dogs that are captured should be marked with radio transmitters and tracked for one or two weeks to see if they interact with other individuals. The areas used by the animals and their dens should be identified with the help of the radio transmitters and searched with hunting dogs of terrier type. In this way, during spring and early summer it will be possible to effectively find and control potential reproductive events. Moreover, in late summer and autumn, it will be possible to find the individuals generated by the previously captured animals. A radiocollared individual which during the monitoring period did not have any contact with other animals should be removed and the radio transmitter should be put on the next captured animal. Since the species is monogamous and forms a stable couple, it would also be possible to sterilize and release the males to see if they find a new partner for the next season. These animals should be marked with an ear-tag and a bright collar so that they are not removed by mistake.

A captured raccoon dog which, after being followed with the radio transmitter, did not get in touch with several conspecifics, should be removed instead than sterilized, since it is not likely that would form a couple. In case it is observed that there are several new arrivals, the trapping effort should be increased together with the use of hunting dogs at night in the relevant habitats.

An autopsy should be performed on all the animals that are culled and they should also be checked for presence of parasites such as *Echinococcus* spp. and *Trichinella* spp. and tested for rabies. In addition to these analyses, several parameters of body condition should be collected from the carcasses. All animals should be aged to obtain a picture of the structure of the Swedish population, which might help us understand whether the population is mainly consisting of dispersing individuals or if there is a substantial ongoing reproduction.

4.2 Development of a Norwegian strategy

How raccoon dogs could be recovered in the northernmost part of Norway (Kirkenes, Pasvik and Skibotn, Fig. 1) remain an open question. Four hypotheses can be put forward: 1) the animals were long distance dispersing individuals coming from Finland or from Russia; 2) we have underestimated the plasticity of raccoon dogs in adapting to harsh environments; 3) there are other source populations further north that we are unaware of; 4) the individuals were transported by humans and released far from their original population.

Although 20 km is the average dispersal distance for juvenile raccoon dogs, some animals have been reported to disperse 150 km in a year (Kauhala & Helle 1994). Still, this is considerably shorter than the distances from known source populations to confirmed observations in northern Norway. However, there is still a possibility that a low number of animals may have survived the winter along their dispersal route, and reach northern Norway the next year. At present there is no reliable information regarding fur production using raccoon dogs in Russian areas close to the Norwegian border. Thus, there is also a possibility that raccoon dogs observed in the eastern part of Finnmark county, may have escaped from fur farms in Russia. That raccoon dogs should be transported by humans and released in northern Norway seems to be the least possible explanation.

Based on the present situation with strong populations of raccoon dogs in Finland, an increasing number of verified observations in Sweden and sporadic observations in Norway, we will shortly point out some general recommendations for a management strategy.

- Norway should develop a management strategy for raccoon dogs that is adequate to accomplish the three-steps system of the European Strategy on Invasive Alien Species: prevent-control-eradicate.

- Thus, the development of a management strategy should be a cooperation between Swedish, Norwegian and Finnish management authorities.

- There should be in the interest of both Sweden and Norway to urge Finland to focus their effort on the areas most likely to be source populations for dispersing animals. In these areas populations should be kept as low as possible in order to reduce number of dispersers.

- Likewise, it should be of vital importance for Norway to support any actions in Sweden which aims to prevent, control and eradicate raccoon dogs.

- In order to locate possible source populations for dispersing individuals in Sweden and Norway, a DNA screening of Finnish populations and animals from north-western parts of Russia, should be performed.

- Norway should establish and formalise a permanent data base which includes DNA material from individual raccoon dogs killed in Norway. This data base should involve other terrestrial mammalian invasive species as well. The Museum of Natural History and Archaeology, Norwegian University of Science and Technology, have the expertise, equipment and will to host such a data base.

- In case present national legislation prevents the use of effective means to eradicate raccoon dogs, or other invasive species, legislation has to be changed.

Acknowledgements

We would like to thank C.J. Tucker at Goddard Space Flight Center (USA) for providing the GIMMS data set, K.-A. Høgda, NORUT IT and K. Isaksen, DNMI. This project was funded by the Norwegian Directorate for Nature Management. We are also grateful to all the Finnish hunters, who collected the carcass material and all the technical assistants who examined the carcasses. Finnish Academy of Sciences financed the raccoon dog project.

References

Adams, S.B. 1999. Mechanisms limiting a vertebrate invasion: Brook trout in mountain streams of the Northwestern USA. - Doctoral Thesis in Philosophy. The University of Montana.

Åhlén, P.-A. 2007. Mårdhund - Förebyggande Naturvård. - Vilt Fisk och Miljö, SLU, Umeå.

Allendorf, F.W. & Lundquist, L.L. 2003. Introduction: population biology, evolution, and control of invasive species. - Conservation Biology 17: 24-30.

Anderson, K.J. & Jetz, W. 2005. The broad-scale ecology of energy expenditure of endotherms. - Ecology Letters 8: 310-318.

Arnold, G.W., Weeldenberg, J.W. & Leone, J. 1998. Herbicide control of exotic annual plant species in *Acacia acuminata*-*Eucalyptus loxephleba* woodland in south-western Australia and effects on native ground flora. - Plant Protection Quarterly 13: 39–43.

Artois, M. & Dunchêne, M.-J. 1982. Première identificacion du chien viverrin (*Nyctereutes procyonoides* Gray, 1834) en France. Mammalia 46: 265-267.

Asikainen, J., Mustonen, A.M., Nieminen, P., Pasanen, S., Araja-Matilainen, H. & Hyvarinen, H. 2002. Reproduction of the raccoon dog (*Nyctereutes procyonoides*) after feeding or food deprivation in winter. - Journal of Animal Physiology and Animal Nutrition 86: 367-375.

Bartholome, E., Belward, A. S., Achard, F., Bartalev, S., Carmona-Moreno, C., Eva, H., Fritz, S., Gregoire, J.-M. & Mayaux, P. 2002. GLC 2000, Global Land Cover mapping for the year 2000. Project status November 2002. - European Commission, Joint Research Centre, Institute for Environment and Sustainability.

Bevanger, K. & Ree, V. 1994. Fugler og pattedyr. Pp 107 in Tømmerås, B.Å. (ed.). Introduksjoner av fremmede organismer til Norge. - Norsk Institutt for Naturforskning, Trondheim.

Boyce, M.S. 1979. Seasonality and patterns of natural selection for life histories. - The American Naturalist 114: 569–583.

Byers, J.E., Reichard, S., Randall, J.M., Parker, I.M., Smith, C.S., Lonsdale, W.M., Atkinson, I.A.E., Seastedt, T.R., Williamson, M., Chornesky, E. & Hayes, D. 2002. Directing research to reduce the impacts of nonindigenous species. - Conservation Biology 16: 630-640.

Clobert, J., Wolff, J.O., Nichols, J.D., Danchin, E. & Dhondt, A.A. 2001. Introduction. Pp. 17-21 in Clobert, J., Danchin, E., Dhondt, A.A., Nichols, J.D. (eds.). Dispersal. - Oxford University Press, New York. 452 pp.

Conroy, M.J. & Moore, C.T. 2002. Wildlife habitat modelling in an adaptive framework: the role of alternative models. Pp. 205-218 in Scott, J.M., Heglund, P., Morrison, M.L., Haufler, J.B., Raphael, M.G., Wall, W.A. & Samson, F.B (eds.) Predicting species occurrences - Issues of accuracy and scale. - Island Press, Washington. 868 pp.

Corsi, F., de Leeuw, J. & Skidmore, A. 2000. Modelling species distribution with GIS. Pp 389-434 in Boitani, L. & Fuller, T.K. (eds.). Research techniques in animal ecology:

controversies and consequences. - Columbia University Press, New York. 442 pp.
DeMers, M.N. 2005. Measurement. Pp 195-219 in Fundamentals of Geographic Information Systems, Third edition. - John Wiley & Sons, Inc, Hoboken. 467 pp.
Dettki, H., Löfstrand, R. & Edenius, L. 2003. Modelling habitat suitability for moose in coastal northern Sweden: Empirical vs process-oriented approaches. - Ambio 32: 549-556.
Directorate for Nature Management. 2007. Mårhund påkjørt i Skibotn i Troms. - Available at: http://www.dirnat.no/ (Last access on 24.04.2007)
Drygala F., Mix, H.M., Stier, N. & Roth, M. 2000. Preliminary findings from ecological studies of the raccoon dog (*Nyctereutes procyonoides*) in eastern Germany. - Zeitschrift für Ökologie und Naturschutz 9: 147-152
ESRI 2006. ArcGIS Version 9.2. Environmental Systems Research Institute. Redlands, California.
Fraedrich, K., Gerstengarbe, F.-W. & Werner, P.C. 2001. Climate shifts during the last century. - Climatic Change 50: 405-417.
France, J., Dijkstra, J. & Dhanoa, M.S. 1996. Growth functions and their application in animal science. - Annales de Zootechnie 45: 165–174.
Fretwell, S.D. & Lucas, H.L. jr. 1970. On territorial behavior and other factors influencing habitat distribution in birds. - Acta Biotheoretica 19: 16-36.
Garel, M., Solberg, E.J., Saether, B.-E., Herfindal, I. & Høgda, K.-A. 2006. The length of growing season and adult sex ratio affect sexual size dimorphism in moose. Ecology 87: 745-758.
Garzón, M.B., Balzek, R., Neteler, M., de Dios, R.S., Sainz Ollero, H. & Furlanello, C. 2006. Predicting habitat suitability with machine learning models: the potential area of *Pinus sylvestris* L. in the Iberian Peninsula. - Ecological Modelling 197: 383-393.
Graham, M.H. 2003. Confronting multicollinearity in ecological multiple regression. - Ecology 84: 2809-2815.
Hansson, L. 1991. Dispersal and connectivity in metapopulations. - Biological Journal of the Linnean Society of London 42: 89-103.
Heglund, P.J. 2002. Foundations of species-environment relations. Pp. 35-41 in Scott, J.M., Heglund, P., Morrison, M.L., Haufler, J.B., Raphael, M.G., Wall, W.A. & Samson, F.B. (eds.). Predicting species occurrences - Issues of accuracy and scale. - Island Press, Washington. 868 pp.
Helle, E. & Kauhala, K. 1991. Distribution history and present status of the raccoon dog in Finland. - Holarctic Ecology 14: 278-286.
Helle, E. & Kauhala, K. 1995. Reproduction in the raccoon dog in Finland. - Journal of Mammalogy 76: 1036-1046.
Hengeveld, R. 1994. Small-step invasion research. - Trends in Ecology & Evolution. 9: 339-342.
Herfindal, I., Linnell, J.D.C., Odden, J., Nilsen, E.B. & Andersen, R. 2005. Prey density, environmental productivity and home-range size in the Eurasian lynx (*Lynx lynx*). - Journal of Zoology 265: 63-71.
Herfindal, I., Sæther, B.-E., Solberg, E.J., Andersen, R. & Høgda, K.-A. 2006a. Population characteristics predict responses in moose body mass to temporal variation in the environment. - Journal of Animal Ecology 75: 1100-1118.
Herfindal, I., Solberg, E.J., Sæther, B.-E., Høgda, K.A., & Andersen, R. 2006b. Environmental phenology and geographical gradients in moose body mass. - Oecologia 150: 213-224.
Høgda K.A., Karlsen, S.R & Solheim, I. 2001. Climatic change impact on growing season in Fennoscandia studied by a time series of NOAA AVHRR NDVI data. - International Geosciences and Remote Sensing Symposium 3: 1338-1340.

Humphries, M.M., Thomas, D.W. & Speakman, J.R. 2002. Climate-mediated energetic constraints on the distribution of hibernating mammals. - Nature 418: 313-316.

Humphries, M.M., Umbanhowar, J. & McCann, K.S. 2004. Bioenergetic prediction of climate change impacts on northern mammals. - Integrative and Comparative Biology 44: 152-162

Inouye, D.W., Barr, B., Armitage, K.B., & Inouye, B.D. 2000. Climate change is affecting altitudinal migrants and hibernating species. - Proceedings of the National Academy of Sciences of the United States of America 97: 1630-1633.

Intergovernmental Panel on Climate Change. 2007. Climate Change 2007: The Physical Science Basis. - Switzerland, Geneva. Available at: http://www.ipcc.ch/ (Last access on 24.04.2007)

Jarvis, T., Miller, I. & Pozio, E. 2001. Epidemiological studies on animal and human trichinellosis in Estonia. - Parasite - Journal De La Societe Francaise De Parasitologie 8: 86-87.

Jędrzejewska, B. & Jędrzejewski, W. 1998. Predation in vertebrate communities. The Białowieża Primeval Forest as a case study. Springer Verlag, Berlin.

Jędrzejewski, W., Jędrzejewska, B. & Szymura, A. 1989. Food niche overlaps in a winter community of predators in the Białowieża Primeval Forest, Poland. - Acta Theriologica 34: 487-496.

Jędrzejewski, W., Schmidt, K., Theuerkauf, J., Jędrzejewska, B., Selva, N., Zub, K. & Szymura, L. 2002. Kill rates and predation by wolves on ungulate populations in Białowieża Primeval Forest (Poland). - Ecology 83: 1341-1356.

Jensen, B. 2004. Mårdhund. Pp. 194-199 in Nordens däggdjur. - Bokförlaget Prisma, Stockholm. 324 pp.

Karlsen, S.R., Elvebakk, A., Høgda, K.A. & Johansen, B. 2006. Satellite-based mapping of the growing season and bioclimatic zones in Fennoscandia. Global Ecology and Biogeography 15: 416-430.

Kauhala, K. 1993. Growth size and fat reserves of the raccoon dog in Finland. - Acta Theriologica 38: 139-150.

Kauhala, K. 1994. The raccoon dog: a successful canid. - Canid News 2: 37-41.

Kauhala, K. 1995. Changes in distribution of the European badger *Meles meles* in Finland during the rapid colonization of the raccoon dog. - Annales Zoologici Fennici 32: 183-191.

Kauhala, K. 1996a. Habitat use of raccoon dogs, *Nyctereutes procyonoides*, in southern Finland. - Zeitschrift fur Säugetierkunde 61: 269-275.

Kauhala, K. 1996b. Introduced carnivores in Europe with special reference to central and northern Europe. - Wildlife Biology 2: 197-204.

Kauhala, K. 2004. Removal of medium-sized predators and the breeding success of ducks in Finland. - Folia Zoologica 53: 367-378.

Kauhala, K. & Auniola, M. 2001. Diet of raccoon dogs in summer in the Finnish archipelago. - Ecography 24: 151-156.

Kauhala, K. & Helle, E. 1995. Population ecology of the raccoon dog in Finland - a synthesis. - Wildlife Biology 1: 3-9.

Kauhala, K. & Helle, E. 1994. Supikoiran elinpiireistä ja yksiaviosisuudesta Etelä-Soumessa. - Soumen Riista 40: 32- 41.

Kauhala, K. & Saeki, M. 2004. Raccoon dog, *Nyctereutes procyonoides* (Gray 1834). Pp. 136-142 in Sillero-Zubiri, C., Hoffmann, M. & Macdonald, D.W. (eds.). Canids: foxes, wolves, jackals and dogs : status survey and conservation action plan. - IUCN Publication services, UK, Cambridge. - Academic Press, San Diego. 248 pp.

Kauhala, K., Helle, E. & Taskinen, K. 1993a. Home range of the raccoon dog (*Nyctereutes*

procyonoides) in southern Finland. - J. Zool. Lond. 231, 95-106.
Kauhala, K., Kaunisto, M. & Helle, E. 1993b. Diet of the raccoon dog, *Nyctereutes procyonoides*, in Finland. - Zeitschrift Fur Saugetierkunde 58: 129-136.
Kauhala, K., Laukkanen, P. & von Rege, I. 1998. Summer food composition and food niche overlap of the raccoon dog, red fox and badger in Finland. - Ecography 21: 457-463.
Kauhala, K., Holmala, K., Lammers, W. & Schregel, J. 2006. Home ranges and densities of medium-sized carnivores in south-east Finland, with special reference to rabies spread. - Acta Theriologica 51: 1-13
Kowalczyk, R. 2006. NOBANIS – Invasive Alien Species Fact Sheet – *Nyctereutes procyonoides*. – Available at the online database of the North European and Baltic Network on Invasive Alien Species, NOBANIS: www.nobanis.org. (Last access on 24.04.2007)
Lapini, L. 2006. Il cane viverrino *Nyctereutes procyonoides ussuriensis* Matschie, 1908 in Italia: segnalazioni 1980-2005 (Mammalia: Carnivora: Canidae). - Boll. Mus. Civ. St. Nat. Venezia 57: 235-239.
Lavrov, N.P. 1971. The results of introductions of the raccoon dog (*Nyctereutes procyonoides* Grey) in different provinces in the USSR. - Trudy kafedry biologii MGZPI 29.
Melis, C., Szafranska, P.A., Jędrzejewska, B. & Barton, K. 2006. Biogeographical variation in the population density of wild boar (*Sus scrofa*) in western Eurasia. - Journal of Biogeography 33: 803-811.
Millar, J.S. & Hickling, G.J. 1990. Fasting endurance and the evolution of mammalian body size. - Functional Ecology 4: 5-12.
Mitchell-Jones, A.J., Reijnders, P., Ziman, J.M. 1999. *Nyctereutes procyonoides* (Grey, 1834). Pp. 320-321 in The atlas of European mammals. - Poyser, London.
Mustonen, A.M., Nieminen, P., Puukka, M., Asikainen, J., Saarela, S., Karonen, S.L., Kukkonen, J.V.K. & Hyvarinen, H. 2004. Physiological adaptations of the raccoon dog (*Nyctereutes procyonoides*) to seasonal fasting-fat and nitrogen metabolism and influence of continuous melatonin treatment. - Journal of Comparative Physiology B-Biochemical Systemic and Environmental Physiology 174: 1-12.
Myneni, R.B., Hall, F.G., Sellers, P.J. & Marshak, A.L. 1995. The interpretation of spectral vegetation indexes. - IEEE Transactions on Geosciences and Remote Sensing 33: 481-486.
Myneni, R.B., Hoffmann, S., Knyazikhin, Y., Privette, J.L., Glassy, J., Tian, Y., Wang, Y., Song, X., Zhang, Y., Smith, G.R., Lotsch, A., Friedl, M., Morisette, J.T., Votava, P., Nemani, R.R. & Running, S.W. 2002. Global products of vegetation leaf area and fraction absorbed PAR from year one of MODIS data. - Remote Sensing of Environment 83: 214-231.
Myneni, R.B., Keeling, C.D., Tucker, C.J., Asrar, G. & Nemani, R.R. 1997. Increased plant growth in the northern high latitudes from 1981 to 1991. - Nature 386: 698-702.
Naaber, J. 1971. Kahrikkoer. - Eesti Lodus 14: 449-455.
Näreaho, A., Sankari, S., Mikkonen, T., Oivanen, L. & Sukura, A. 2000. Clinical features of experimental trichinellosis in the raccoon dog (*Nyctereutes procyonoides*). - Veterinary Parasitology 91: 79-91.
Nilsen, E.B., Herfindal, I. & Linnell, J.D.C. 2005. Can intra-specific variation in carnivore home-range size be explained using remote-sensing estimates of environmental productivity? - Ecoscience 12: 68-75.
Nordic Network of Introduced Species. Naturvårdsverket. 1997. Introduksjon av främmande arter i svensk landmiljö. - Nordic Network of Introduced Species. Available at: http://www.sns.dk/ (Last access on 24.04.2007)

Vikhamar-Schuler, D. & Førland, E.J. 2006. Comparison of snow water equivalent estimated by the HIRHAM and the HBV (GWB) models: current conditions (1961-1990) and scenarios for the future (2071-2100). Report of Norwegian Meteorological Institute 6: 1-36.

Nowak, v.E. 1984. Verbeitungs- und Bestandsentwickung des Marderhundes, *Nyctereutes procyonoides* (Gray, 1834) in Europa. - Zeitschrift fur Jagdwissenschaft 30: 137-154.

Nowak, v.E. 1993. *Nyctereutes procyonoides* Gray 1834, Marderhund. Pp 215-248 in Stubbe, M., Krapp, F. & Demeter, A. (eds.). Handbuch der Säugetiere Europas. AULA Verlag, Wiesbaden. 528 pp.

Nyberg, M., Kulonen, K., Neuvonen, E., Ekkommonen, C., Nuorgam, M. & Westerling, B. 1992. An epidemic of sylvatic rabies in Finland - descriptive epidemiology and results of oral vaccination. - Acta Veterinaria Scandinavica 33: 43-57.

Oksanen, T., Schneider, M., Rammul, Ü., Hambäck, P. & Aunapuu, M. 1999. Population fluctuations of voles in North Fennoscandian tundra: contrasting dynamics in adjacent areas with different habitat composition. - Oikos 86: 463–478

Owen, M.R. & Lewis, M.A. 2001. How predation can slow, stop or reverse a prey invasion. - Bulletin of Mathematical Biology 63: 655-684.

Parmesan, C. & Yohe, G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. - Nature 421: 37-42.

Pettorelli, N., Vik, J.O., Mysterud, A., Gaillard, J.M., Tucker, C.J. & Stenseth, N.C. 2005. Using the satellite-derived NDVI to assess ecological responses to environmental change. - Trends in Ecology & Evolution 20: 503-510.

Pettorelli, N., Gaillard, J.-M., Mysterud, A., Duncan, P., Stenseth, N.C., Delorme, D., Van Laere, G., Toïgo, C. & Klein, F. 2006. Using a proxy of plant productivity (NDVI) to find key periods for animal performance: the case of roe deer. - Oikos 112: 565-572.

Pimentel, D., Lach, L., Zuniga, R. & Morrison, D. 2000. Environmental and economic cost of nonindigenous species in the United States. - BioScience 50: 53-65.

Pond, C.M. 1981. Storage. Pp 190–221 in Townsend, C.R. & Calow, P. (eds.). Physiological ecology: an evolutionary approach to resource use. Blackwell Scientific Publications, Oxford, UK. 393 pp.

R Development Core Team. 2005. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ray, N., Lehmann, A. & Joly, P. 2002. Modelling spatial distribution of amphibian populations: a GIS approach based on habitat matrix permeability. - Biodiversity and Conservation 11: 2143-2165.

Rebeć, M. 1981. Prvi enok ali kunji pes uplenjen v SR Sloveiji. - Lovec 64: 50-52.

Reed, B.C., Brown, J.F., Vanderzee, D., Loveland, T.R., Merchant, J.W. & Ohlen, D.O. 1994. Measuring phenological variability from satellite imagery. - Journal of Vegetation Science 5: 703-714.

Root, T. L., Price, J.F., Hall, K.R., Schneider, S.H., Rosenzweig, C. & Pounds, J.A. 2003. Fingerprints of global warming on wild animals and plants. - Nature 421: 57-60.

Salvatori, V. & Linnell, J. 2005. Report on the conservation status and threats for wolf *Canis lupus* in Europe. Convention on the conservation of European wildlife and natural habitats. Strasbourg. Available at: http://www.lcie.org/ (Last access on 24.04.2007)

Schwartz, M.W., Iverson, L.R. & Prasad, A.M. 2001. Predicting the potential future distribution of four tree species in Ohio using current habitat availability and climatic forcing. - Ecosystems 4: 568-581.

Selås, V. 2000. Seed production of a masting dwarf shrub, *Vaccinium myrtillus*, in relation to previous reproduction and weather. - Canadian Journal of Botany 78: 423–429

Selva, N., Jędrzejewska, B., Jędrzejewski, W. & Wajrak, A. 2003. Scavenging on European bison carcasses in Białowieża Primeval Forest (eastern Poland). - Ecoscience 10: 303-311.

seNorge.no. 2007. Snø, vær, vann og klima i Norge. Endring i antall dager i året med snødekke fra 1961-1990 til 2071-2100. - Available at: http://www.senorge.no/ (Last access on 24.04.2007)

Sheldon, J.W. 1992. Genus *Nyctereutes*. Pp. 109-116 in Wild dogs: the natural history of nondomestic Canidae.

Shigesada, N. & Kawasaki, K. 1997. Biological invasions: theory and practice. - Oxford University Press Inc., New York. 205 pp.

Sidorovich, V.E., Polozov, A.G., Lauzhel, G.O. & Krasko, D.A. 2000. Dietary overlap among generalist carnivores in relation to the impact of the introduced raccoon dog *Nyctereutes procyonoides* on native predators in northern Belarus. - Zeitschrift Fur Saugetierkunde-International Journal of Mammalian Biology 65: 271-285.

Stenseth, N.C., Mysterud, A., Ottersen, G., Hurrell, J.W., Chan, K.S. & Lima, M. 2002. Ecological effects of climate fluctuations. - Science 297: 1292-1296.

Sutor, A. 2004. Raccoon dog *Nyctereutes procyonoides:* habitat use, activity pattern, diet compositions - a telemetry study in Brandenburg. In Alien species in changing landscapes. Nachrichten der Gestellshaft fur ökologie. Gfö. Annual Conference, June 2004.

Sutor, A. 2005. Der Marderhund *Nyctereutes procyonoides* als potenzieller Prädator bodenbrütender Vögel? - Auswahl brandenburgicher Ergebnisse. - Vogelwelt 126: 376-378.

Swan, H. 1974. Thermoregulation and bioenergetics: patterns for vertebrate survival. Elsevier, New York.

Swedish Association for Hunting and Wildlife Management 2007. Första säkra mårdhundsföryngringen i Sverige. Available at: http://www.jagareforbundet.se/ (Last access on 24.04.2007)

Tabachnick, B.G. & Fidell, L.S. 2001. Using multivariate statistics, 4th edition. Allyn & Bacon, Boston, MA.

Turner, M.G., Arthaud, G.J., Engstrom, R.T., Hejl, S.J., Liu, J., Loeb, S. & McKelvey, K. 1995. Usefulness of spatially explicit population models in land management. - Ecological Applications 5: 12-16.

Tømmerås, B.Å., Hofsvang, T., Jelmert, A., Sandlund, O.T., Sjursen, H. & Sundheim, L. 2003. Introduserte arter. Med fokus på problemarter for Norge. - NINA oppdragsmelding 772: 1- 58.

USGS Earth Resources Observation and Science 2007. Anon, GTOPO30 Documentation. Available at: http://edc.usgs.gov/ (Last access on 24.04.2007)

Väänänen, V-M., 2006. Mårdhundsworkshop, SLU, Umeå , Sweden, 31.01.06.

Venables, W.N. & Ripley, B.D. 2002. Modern applied statistics with S. 4th edition. Springer, New York.

Viro, P. & Mikkola, H. 1981. Food composition of the raccoon dog *Nyctereutes procyonoides* Grey, 1834 in Finland. - Sonderdruck aus Zeitshrift für Säugetierkunde 46: 20-26.

Walker, B. & W. Steffen. 1997. An overview of the implications of global change for natural and managed terrestrial ecosystems. - Conservation Ecology [online], 1: 2. Available at: http://www.consecol.org/ (Last access on 24.04.2007)

Walker, R. & Craighead, L. 1997. Least-cost-path corridor analysis: Analyzing wildlife, movement corridors in Montana using GIS. Proceedings of the 1997 ESRI User's conference. Available at: http://gis2.esri.com/ (Last access on 24.04.2007)

Ward, O.G. & Wurster-Hill, D.H. 1990. *Nyctereutes procyonoides*. - Mammalian Species 358: 1-5.

Weber, J.-M., Fresard, D., Capt, S. & Noel-Kora, C. 2004. First records of raccoon dog, *Nyctereutes procyonoides* (Gray, 1834), in Switzerland. - Revue Suisse de Zoologie 111:

935-940.
Weidema, I.R. 2000. Introduced species in the Nordic countries. - Nord 13: 1-242.
Weisser, W.W. 2001. The effects of predation on dispersal. Pp. 180-188 in Clobert, J., Danchin, E., Dhondt, A.A. & Nichols, J.D. (eds.). Dispersal. Oxford University Press, New York. 452 pp.
Westerling, B. 1991. Rabies in Finland and its control 1988–90. - Suomen Riista 37: 93–100. [In Finnish with English summary]
Wiens, J.A. 2001. The landscape context of dispersal. Pp. 96-109 in Clobert, J., Danchin, E., Dhondt, A.A. & Nichols, J.D. (eds.). Dispersal. Oxford University Press, New York. 452 pp.
Wikan, S. & Henriksen, G. 1991. Mårhund - ny art i Norge. - Fauna 44: 211-213.

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«Norges teknisk-naturvitenskapelige universitet, Vitenskapsmuseet Rapport zoologisk serie» er en videreføring av »Vitenskapsmuseet Rapport Zoologisk Serie» og presenterer stoff fra de zoologiske fagområdene ved Vitenskapsmuseet. Serien bringer i hovedsak arbeider fra oppdragsprosjekter og andre undersøkelser og forskning ved Seksjon for Naturhistorie. Serien er ikke periodisk og antall numre varierer pr. år. Serien startet i 1974 og det finnes parallelle botaniske og arkeologiske rapportserier ved Vitenskapsmuseet. Mindre arbeider og utredninger som av ulike grunner trenger en rask publisering og distribusjon presenteres i en egen notatserie: »Norges teknisk-naturvitenskapelige universitet, Vitenskapsmuseet Zoologisk notat».

Til forfatterne

Manuskripter
Manuskripter bør leveres som papirutskrift og som tekstfil i Word. Vitenskapelige slekts- og artsnavn kursiveres. Manuskripter til rapportserien skal skrives på norsk, unntatt abstract (se nedenfor). Unntaksvis, og etter avtale med redaktøren, kan manuskripter på engelsk bli tatt inn i serien. Tekstfilen(e) skal inneholde en ren «brødtekst», dvs. med færrest mulig formateringskoder. Hovedoverskrifter skal skrives med store bokstaver, de øvrige overskrifter med små bokstaver. Manuskriptet skal omfatte:

1. Eget ark med manuskriptets tittel og forfatterens/forfatternes navn. Tittelen bør være kort og inneholde viktige henvisningsord.
2. Et referat på norsk på maksimum 200 ord. Referatet innledes med bibliografisk referanse og avsluttes med forfatterens/forfatternes navn og adresse(r).
3. Et abstract på engelsk som er en oversettelse av det norske referatet.

Manuskriptet bør for øvrig inneholde:

4. Et forord som ikke overstiger en trykkside. Forordet kan gi bakgrunnen for arbeidet det rapporteres fra, opplysninger om eventuell oppdragsgiver og prosjekt- og programtilknytning, økonomisk og annen støtte, institusjoner og enkeltpersoner som bør takkes osv.
5. En innledning som gjør rede for den faglige problemstillingen og arbeidsgangen i undersøkelsen.
6. En innholdsfortegnelse som viser stoffets inndeling i kapitler og underkapitler.
7. Et sammendrag av innholdet. Sammendraget bør ikke overstige 3 % av det øvrige manuskriptet. I spesielle tilfeller kan det i tillegg også tas med et «summary» på engelsk.
8. Tabeller og figurer leveres på separate ark og skrives i egne filer. I teksten henvises de til som «Tabell 1», «Figur 1» osv.

Litteraturhenvisninger
En oversikt over litteratur som det er henvist til i manuskriptteksten samles bakerst i manuskriptet under overskriften «Litteratur». Henvisninger i teksten gis som Haftorn (1971), Arnekleiv & Haug (1996) eller, dersom det er flere enn to forfattere, som Sæther *et al.* (1981). Om det blir vist til flere arbeider, angis det som «som flere forfattere rapporterer (Haftorn 1971, Thingstad *et al.* 1995, Arnekleiv & Haug 1996,)», dvs. forfatterne nevnes i kronologisk orden, uten komma mellom navn og årstall. Litteraturlisten ordnes i alfabetisk rekkefølge: det norske alfabetet følges: aa = å (utenom for nederlandske, finske og etniske navn), ö = ø osv. Flere arbeid av samme forfatter i samme år angis ved a, b, osv. (Elven 1978a, b). Ved lik alfabetisk prioritet går to forfattere foran tre eller flere («*et al.*»).

Eksempler:

Tidsskrift/serie
Slagsvold, T. 1977. Bird song activity in relation to breeding cycle, spring weather, and environmental phenology. – Ornis Scand. 8: 197-222.

Arnekleiv, J.V. & Haug, A. 1996. Fiskebiologiske undersøkelser i Holmvatnet og Rundtuvvatnet, Rana kommune, Nordland, 1995. – Vitenskapsmuseet Rapp. Zool. Ser. 1996, 3: 1-22.

Kapittel
Nilsson, S.G. & Ericson, L. 1992. Conservation of plants and animal populations in theory and practice. s. 71-112 i Hansson, L. (red.). Ecological principles of nature conservation. – Elsevier Appl. Sci., London.

Monografi/bok
Urke, H. A. 2001. Utvikling av sjøtoleranse og vandringsåtferd hos Atlantisk laks (*Salmo salar* L.) med og utan oppdrettsbakgrunn. – Cand.scient. oppgave i akvakultur. Norges teknisk-naturvitenskapelige universitet, Zoologisk institutt. 79 s. Upubl.

Haftorn, S. 1971. Norges Fugler. – Universitetsforlaget, Oslo. 862 s.

Illustrasjoner
Figurer (i form av fotografier, tegninger osv.) leveres separat, på egne ark, dvs. de skal ikke inkluderes eller monteres i brødteksten. På papirutskriften av manuskriptet skal det i venstre marg angis hvor i teksten figurene ønskes plassert. Strekfigurer, kartutsnitt o.l. figurer skal være trykkeferdige fra forfatterens hånd. Skal rapporten inneholde fargebilder, bør også disse leveres som jpg-filer.

Opplag
Rapporten trykkes vanligvis i et opplag på 150-300 eksemplarer.

ISBN 978-82-7126-763-6
ISSN 0802-0833

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Det skapende universitet