

## The distribution of mountain hares *Lepus timidus* in Europe: a challenge from brown hares *L. europaeus*?

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### ABSTRACT

1. Throughout the most recent glacial period (Weichsel), the mountain hare *Lepus timidus* had a continuous distribution in the tundra habitat south of the ice-rim. When the ice retreated, mountain hares colonized deglaciated land, and spread over northern Europe.

2. Since the Weichsel, the mountain hare's distribution in Europe has been gradually reduced and at present comprises Ireland and the Scottish Highlands, high altitudes in the Alps, isolated forests in eastern Poland, most of Fennoscandia and from the Baltic countries eastwards through Russia. Declines during the last century have been observed in Sweden and Russia.

3. This review defines and evaluates causes for this gradual reduction and fragmentation of the mountain hare's distribution, with special focus on interactions with brown hares *Lepus europaeus*. The relative importance of diseases, predation, cultivation and interactions with other herbivores than brown hares are discussed.

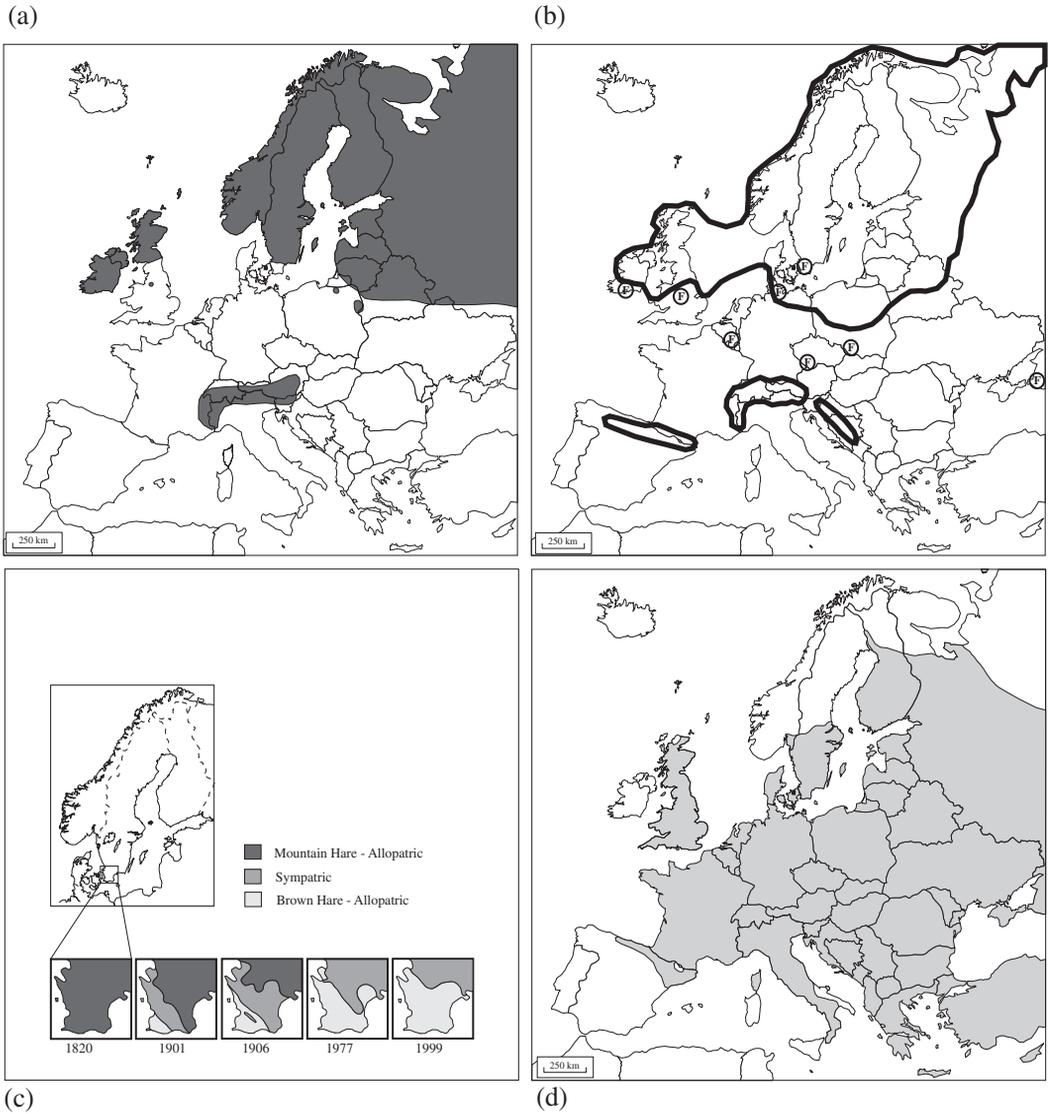
4. A plausible cause of the possible permanent disappearance of mountain hares in Europe appears to be exclusion by interspecific competition and hybridization with, and/or epidemic diseases mediated by, the congeneric brown hare.

*Keywords:* competition, hybridization, lagomorph, leporid, population decline

### THE MOUNTAIN HARE IN EUROPE

The mountain hare (*Lepus timidus*, L. 1758) is an arctic/subarctic species that has a fragmented distribution in Europe (Fig. 1a). It occurs in Ireland and in the Scottish Highlands in the west (also reintroduced to parts of England and the Isle of Man), at high altitudes in the Alps in Central Europe, in the isolated Augustow and Rominty forests in eastern Poland and in most of Fennoscandia in northern Europe (Angerbjörn & Flux, 1995). The distribution is continuous eastwards, from the Baltic countries and throughout the Russian tundra and taiga belt. It belongs to a circumpolar species complex, and is replaced by the arctic hares *L. othus* in Beringia and *L. arcticus* in North America and northern Greenland (Flux & Angerman, 1990; Angerbjörn & Flux, 1995). The mountain hare is opportunistic and survives under poor environmental conditions and with limited food sources (Hewson, 1991; Angerbjörn & Flux, 1995). The distribution extends beyond 77°N on the Taimyr peninsula in the Russian arctic (Flux & Angerman, 1990). Thus, the mountain hare inhabits a wide range of biotas, from extreme tundra with permafrost in northern Russia to rich agricultural areas in Ireland (Dingerkus & Montgomery, 2002).

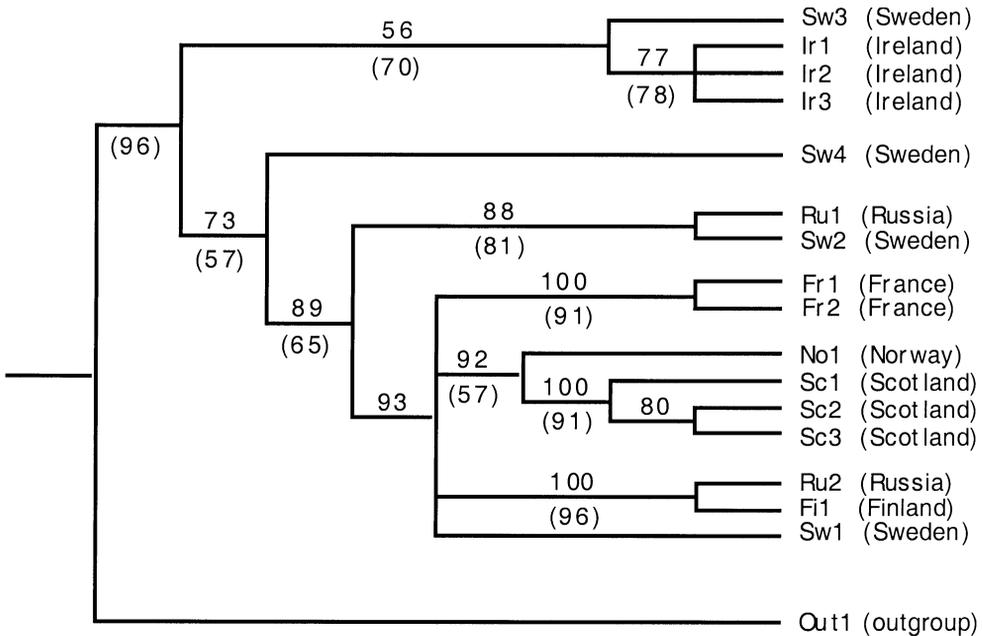
At the height of the most recent glacial period (Weichsel), 18 000 years ago, northern Europe and parts of central Europe were covered with ice (Fig. 1b) (Soffer & Gamble, 1990). Throughout the glacial period, mountain hares were continuously distributed south of the ice-rim (Stuart, 1974; Corbet, 1986; Yalden, 1999). Ice-age remains of mountain hares have



**Fig. 1.** (a) The current distribution of mountain hares in Europe, according to Angerbjörn & Flux (1995) and Mitchell-Jones *et al.* (1999). (b) The maximal ice-extension in Europe at the height of the most recent glacial period (Weichsel) approximately 18 000 years ago, depicted from Soffer & Gamble (1990). Mountain hare fossil findings (F) from, and after, the last glacial period are indicated in Ireland (Woodman *et al.*, 1997), England (Turk, 1964), Belgium (Gautier, 1973), northern Germany (Lüttchwager, 1956), southern Sweden (Lepiksaar, 1986), Czech Republic (Mostecky, 1969), southern Poland (Kowalski, 1959) and northern Caucasus (position not correct) (Knyazev & Savinetsky, 1994). (c) Distribution of brown hares and mountain hares in southern Sweden before and after the introduction of brown hares, depicted from Nilsson (1820), Lönnberg (1908) and Gerell (1977). The present distribution (i.e. 1999) is based on a survey with local hunters (Thulin, 2000). (d) The distribution of brown hares in Europe, after Hewson (1991) and Mitchell-Jones *et al.* (1999).

been found in, for example, Belgium (Gautier, 1973), Germany (Lüttchwager, 1956) and Ireland (Woodman, McCarthy & Monaghan, 1997) (see Fig. 1b). When the ice-sheet over Europe gradually disappeared, mountain hares followed the deglaciated land to the north, spread over the British Isles and colonized Scandinavia. As the sea rose, the mountain hares in England were separated from the Irish ones by the Irish sea. The oldest remains of mountain hares in Sweden are more than 10 000 year old and are found in the far south (Lepiksaar, 1986; Liljegren & Lagerås, 1993). As most other parts of Scandinavia were covered with ice at this time, these remains likely originate from mountain hares that colonized Scandinavia along the land bridge that temporarily connected Sweden with Denmark (Björk, 1995). A recent origin of the European mountain hares from a panmictic population during Weichsel is supported by genetic investigations: Suchentrunk *et al.* (1999) find low levels of allozyme differentiation between the five European subspecies. Similarly, Thulin, Isaksson & Tegelström (1997a) detect highly diverged mitochondrial DNA (mtDNA) haplotypes with a paraphyletic distribution among mountain hares from Scandinavia and the British Isles (Fig. 2). The results from these investigations also seem to find support in nuclear microsatellite DNA data (R. Hamill, personal communication).

Something has happened with the mountain hare populations in Europe during the years that have passed since the glacial period. The formerly continuous distribution in central Europe has become restricted to remnant populations above 1300 m in the Alps and in remote forests in Poland. Mountain hares still occur all over Ireland and in the Scottish Highlands, but have been absent from England and Wales during historical times, except for one (out of three) reintroduced populations that survives in the English Peak District (Yalden, 1984,



**Fig. 2.** Parsimonious phylogeny of a 410 base-pair mitochondrial DNA (mtDNA) control region fragment from European mountain hares (depicted from Thulin *et al.*, 1997a). The numbers above branches indicate percentage of the trees (out of 200) that support that branch, when using the 'branch and bound' function in the program PAUP 3.1 (Swofford, 1993). Bootstrap values are given in parentheses. The outgroup (Out 1) consists of mtDNA from a brown hare from southern Sweden.

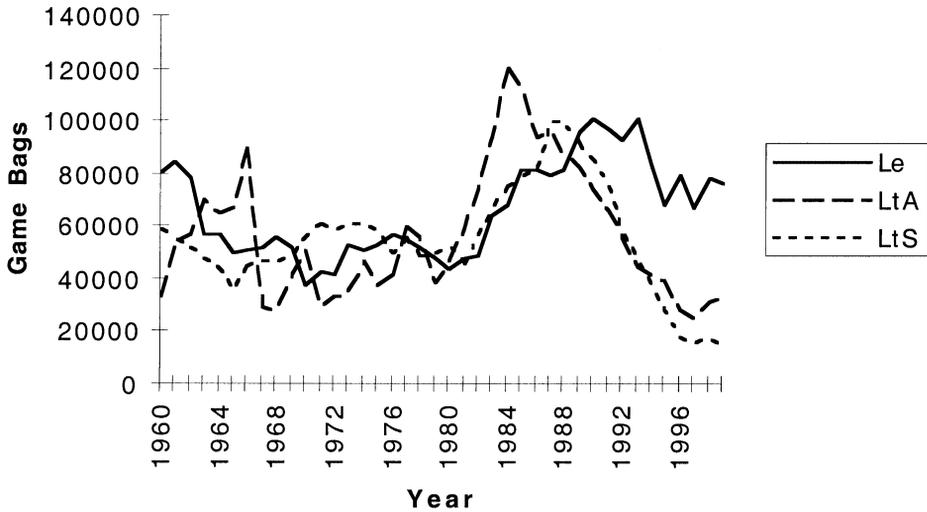


Fig. 3. Game bags of mountain hares and brown hares in Sweden from the hunting seasons 1960/61–1999/2000, provided by the Swedish Association for Hunting and Wildlife Management (Wildlife Monitoring). The respective curves represent the game bags of brown hares (Le), mountain hares sympatric with brown hares (LtS) and allopatric mountain hares (LtA).

1999). In Scandinavia, and eastwards, the distribution is still continuous, but there are historical and recent signs of a restriction in range and population density in southern and central Sweden. At the turn of the last century, the mountain hare inhabited all of Sweden, but then disappeared gradually from the far south (Fig. 1c). Lönnberg (1908) describes a restriction in the distribution over 5 years, from 1901 to 1906. Approximately 70 years later, a survey made by Gerell (1977) indicates that there were few mountain hares still present, while a recent survey by the author shows that the mountain hares have vanished in the far south (Thulin, 2000). Furthermore, hunters claim that there has been a decline in mountain hare populations in Central Sweden over the last decades, which is also documented in the game bags from the hunting seasons 1960/61–1999/2000 (Fig. 3). Finally, in Russia, the finding of an approximately 2000-year-old mountain hare skeleton in northern Caucasus indicates that the former distribution of mountain hares in this area extended much further south (Knyazev & Savinetsky, 1994). The current distribution of mountain hares in European Russia has recently been greatly reduced, and the southern margin today reaches about 52°N with some isolated populations further south in the Ukraine and along the Don River (A. Averianov, personal communication).

Here, I wish to review possible causes for these gradual and continuous reductions of the mountain hare range throughout Europe, and also suggest research areas that may explain this phenomenon.

## INTERACTIONS WITH THE BROWN HARE

### The brown hare

The brown hare *L. europaeus*, Pall. 1778 is the second of the two hare species that occur in northern and central Europe. The current distribution (Fig. 1d) includes most of the European lowlands, except Ireland, northern Scandinavia and the Iberian peninsula, and extends eastwards through Russia and adjacent countries to Lake Baikal (Corbet, 1986; Hewson,

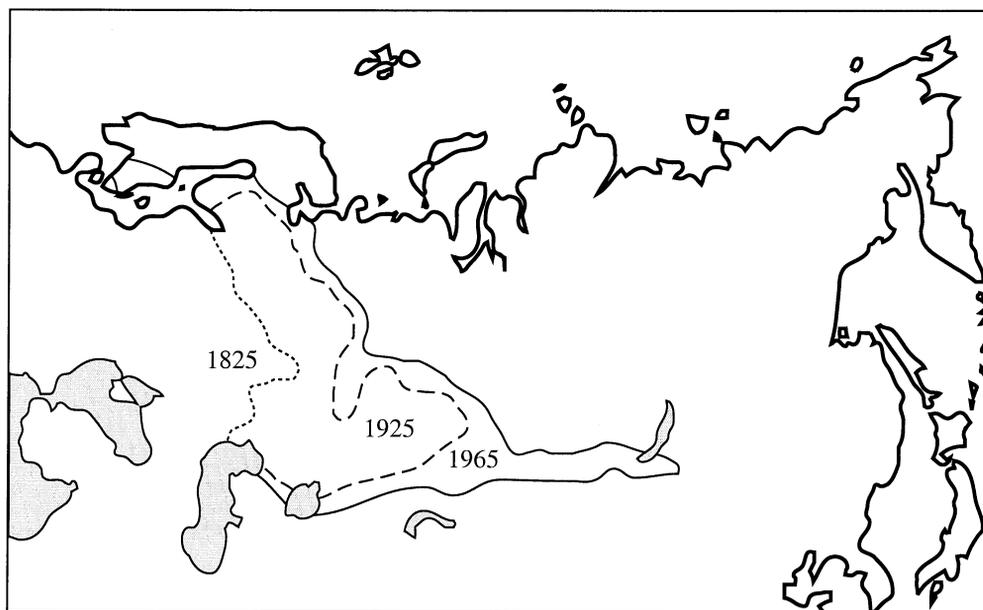


Fig. 4. The brown hare's expansion eastwards in Russia, according to Thenius (1980).

1991). The brown hare is an open landscape specialist that is presumably evolved in the Middle-Asian steppes, and has been favoured by the forest clearings and the subsequent spread of agriculture (Tapper, 1987). It is possible that the brown hare's colonization of Europe has been associated with western civilizations and the development of the agricultural landscape, which started about 10 000 years ago (Roberts, 1998). Expansions to the north and the north-east have taken place during the last 200 years (Fig. 4) (Folitarek, 1940; Thenius, 1980).

The origin of the British brown hares is unclear; Corbet (1986) and Tapper (1987) assume that they were introduced by the Romans, that is, 100–400 AD. Recently, Yalden (1999) suggests that they might have been present during the Bronze Ages (i.e. 1700–700 BC), as there are pre-Roman fossils dated 1900 BC (Turk, 1964). The different authors agree that brown hares were introduced to Britain by humans. This is plausible, as the confirmed fossil findings are much more recent than the post-glacial landbridges that connected the British Isles with the continent until 8000–8500 years ago and, thus, enabled natural colonization (Andersen & Borns, 1997). Brown hares were extensively introduced to Ireland during the late 19th and early 20th century, but recent records suggest that they only remain in Co. Tyrone, Northern Ireland (S.K. Dingerkus, personal communication). In Sweden, the Brown Hare was introduced during the late 19th century (Lönnberg, 1905), and has subsequently spread throughout south and central Sweden and into eastern Norway (cf. Mitchell-Jones *et al.*, 1999). Even though attempts to introduce Brown Hares north of the *limes norlandicus* in central Sweden failed (G. Zetterberg, personal communication), there are indications that the extension northwards in Sweden continues. A few 'brown hares' (i.e. without white winter pelage) have been reported north of the current Swedish range during the last 3 years (Swedish Association for Hunting and Wildlife Management, Wildlife Monitoring), but their specific status as brown hares has not yet been confirmed. As the northward expansion of brown hares during the last century has been documented in Russia and Finland (Folitarek,

1940; Thenius, 1980), east of Scandinavia (Fig. 4), it is likely that Brown Hares will colonize the Scandinavian peninsula naturally from the north-east, especially as the distribution in Finland reaches the border with Sweden (Mitchell-Jones *et al.*, 1999).

### Competitive exclusion

A comparison of the distributions of the mountain hare and the brown hare in Europe (see Fig. 1) shows that in most places where the latter occurs, the former seems restricted to high altitudes and deep forests. Separation of each species into different habitats seems to be a general characteristic of hares (Flux, 1981). There are three major boundaries between different hare species that shift north-south: *L. arcticus* give way to *L. americanus* in Canada; *L. townsendii* to *L. californicus* in central USA; and, finally, mountain hares give way to brown hares in Europe and Russia (Flux, 1981). Competition is inferred because each species of the pair will occupy the preferred habitat of the other in its absence, and Flux (1981) therefore argues that sympatric occurrence of hares is rare and likely to be a transient phenomenon. Although the mechanism of competitive exclusion between lagomorphs is generally unknown, there is evidence that it is a remarkably powerful force: Flux (1993) shows that rabbits *Oryctolagus cuniculus* in New Zealand can be removed from islands more efficiently by competition with brown hares than by conventional shooting and trapping, predation by cats, or even myxomatosis. Thus, brown hares and mountain hares, which may be even closer ecological equivalents than rabbits and hares, should be in stronger competition.

Although mountain hares are less sensitive than brown hares to toxic phenolic substances in their food (cf. Iason & Palo, 1991), it does not prevent them from feeding on similar plant species to brown hares. Recent investigations of food preferences of Irish mountain hares (Wolfe, Whelan & Hayden, 1996; Dingerkus & Montgomery, 2001) show that the mountain hares in Ireland utilize much more grass and herbs than mountain hares that occur in sympatry with brown hares (e.g. Hewson, 1962; Angerbjörn & Pehrson, 1987; Hulbert, Iason & Racey, 1996). Subsequently, Wolfe *et al.* (1996) argue that competitive exclusion by brown hares, rather than habitat preferences related to species-specific food utilization, may underlie much of the restriction in the mountain hare's distribution. Lind (1963) studied where the mountain hares have their forms in sympatry and allopatry with brown hares in Finland and found that in sympatry the mountain hares tend to have their forms in denser forests and further away from open fields than if they are allopatric. Furthermore, Hewson (1976) notes that brown hares in Scotland extend their distribution and habitat use when mountain hare population densities are low. Similar observations have been made in the English Peak District by Yalden (1971) and on Isle of Man by Fargher (1977). Furthermore, the reductions in the mountain hare range in southern Sweden (Fig. 1c) coincide with the establishment and expansion of brown hares in these areas (Lönnerberg, 1908; Thulin, 2000). Finally, Yalden (1999) points out that the last remains of naturally distributed mountain hares in England coincide with the first findings of brown hares, as remains of both species are found in layers at the Bronze Age site of Hartledale in England (Turk, 1964), after which only brown hare remains are detected. These investigations all indicate that in direct contact with brown hares, the mountain hares disappear from the optimal brown hare habitats, and that there is a potential for brown hares to expand into mountain hare territory.

### Hybridization and introgression

It has long been considered that mountain hares and brown hares may hybridize (Lönnerberg, 1905; Fraguglione, 1959; Gustavsson, 1971; Schröder *et al.*, 1987). Hybrids are easily acquired in captivity, where the mountain hare female spontaneously mates with a brown hare male,

while the reciprocal crossing has to be performed with artificial insemination (Gustavsson & Sundt, 1965). The  $F_1$  hybrids are morphological intermediates between the species and are often considered fertile (Lönnerberg, 1905; Gustavsson, 1971; Schröder *et al.*, 1987). Recently, mtDNA lineages of mountain hare origin were detected among brown hares in Sweden (Thulin, Jaarola & Tegelström, 1997b). These lineages are transferred over the species barrier through interspecific hybridization between brown hares and mountain hares wherever the two species occur in sympatry (Thulin & Tegelström, 2002). Brown hare males mate mountain hare females and, at least, the female hybrids back-cross to brown hare males, so that the mtDNA is transmitted over the species barrier. As no mountain hare was detected with brown hare mtDNA, introgression of mtDNA seems unidirectional, which is supported by the behavioural barrier to reproduction observed in the captive breeding experiments (Gustavsson & Sundt, 1965).

Every time a mountain hare female hybridizes with a brown hare male, the local mountain hare population will lose a species-specific litter. Thus, the observed loss of range, and the decrease in population density of mountain hares, may actually be a direct consequence of unidirectional hybridization. This phenomenon, 'extinction by hybridisation', has been previously described by Rhymer & Simberloff (1996) and is a possible effect of hybridization between native and introduced species (Ebenhard, 1988; Simberloff, 1996). Possibly, the mating behaviour of hares may promote hybridization. During courtship, several males usually follow the females prior to, and up to, oestrus (Flux, 1970; Holley & Greenwood, 1984; Hewson, 1991). Among brown hares, dominant males commonly mate-guard a female that is close to oestrus, and as a consequence they gain more matings than their subordinates (Holley, 1986). Such mate guarding does not seem to occur among mountain hares (cf. Flux, 1970), so when males of both species court a mountain hare female, the brown hare males may simply chase away the mountain hare males [as Hewson (1990) observed for a single brown hare male watched while interacting with mountain hares]. Thus, the mountain hare female will be constrained in her mate-choice to a brown hare male as she approaches oestrus. Even if she has an opportunity to reject him and search for a conspecific male, it may be more costly to do so, and risk the attempted reproduction, than to accept him as a mate. The importance of these priorities, which depend on time for oestrus and male availability, has been shown to affect choosiness among species with single-sex discrimination (Real, 1990). Alternatively, if hare females rely on indirect mate choice (described by Wiley & Poston, 1996), they will automatically choose the dominant mate-guarding male upon oestrus. Thus, in sympatry, and especially if brown hare population density is high and mountain hare density is low, mountain hare females may frequently be confined to dominant, mate-guarding brown hare males throughout the reproductive season, with hybridization as a possible outcome.

In Sweden, there is a difference in the frequency of introgressed mtDNA between brown hares in current and former sympatry with mountain hares, as the percentage brown hares with transmitted mtDNA varies between areas of former species sympatry (0.6%) and areas of current sympatry (15%) (Thulin & Tegelström, 2002). Presumably, the disappearance of transmitted mtDNA is because of a functional incompatibility between the cytoplasmic mtDNA genome of a mountain hare and the nucleic genome of brown hares, whereby brown hare specimens with alien mtDNA experience a fitness reduction compared to brown hares with species-specific mtDNA. This would explain why no tendencies of mtDNA introgression have been detected among Austrian brown hares (cf. Hartl *et al.*, 1993), which occasionally may be, and certainly were, in contact with mountain hares. Thus, it seems that mtDNA from mountain hares is incorporated into brown hares in sympatry, but disappears gradually in

allopatry when there is no continuous interspecific gene flow. This scenario resembles the changes in species composition at estates in south Sweden right after the introduction of brown hares (cf. Lönnberg, 1905). The game bags rapidly switch from mountain hares to brown hares until mountain hares vanish completely. A few of the presumed hybrids (i.e. morphological intermediates) are shot during the following seasons, but they too disappear and only brown hares are seen in the later records. Thus, hybridization, introgression and subsequent disappearance of incorporated mountain hare mtDNA may be considered as a refined form of competitive exclusion in that the traces of mountain hares are purged away from the brown hares ecologically as well as genetically.

## ALTERNATIVE CAUSES OF DECLINES

### Diseases

Epidemic, infectious diseases and parasites are presumably the most important factors that affect population densities of many species, prey as well as predators, and the mountain hare is no exception. There are numerous infectious diseases and parasites that spread through and affect mountain hare populations (see Angerbjörn & Flux, 1995). Diseases and parasites may also account for population crashes, in combination with food shortage and predation (Angerbjörn, 1983). Pathogens are, however, usually dependent on dense and continuous populations to spread and may therefore have less impact if density is low and/or sub-populations are separated. Also, after an epidemic, the normal population density levels are often regained in a very short time. If pathogens are causing restrictions in the mountain hare range, it is odd that there is uniformity between the areas where mountain hares prevail, that is, dense forests and high altitudes.

Pathogens could, however, have a considerable impact if the original host is less susceptible than sympatric conspecifics. Tularaemia, caused by the bacterium *Francisella tularensis*, is an important pathogen that affects mountain hares, whereas brown hares seem less susceptible (Mörner, 1994; and references therein). Another disease that may have different epidemic impact on the two species is the European Brown Hare Syndrome (EBHS), caused by a calicivirus (Mörner, 1999). Possibly, brown hares may be sub-clinical vectors for the virus, while it may cause instant death of mountain hares. Thus, tularaemia, EBHS or other pathogens could certainly prevent long-term sympatric occurrence of mountain hares and brown hares. The importance of such interactions between the species needs further evaluation.

### Predation

The red fox *Vulpes vulpes* is the most important predator on adult and juvenile mountain hares (Hewson, 1991; Angerbjörn & Flux, 1995), exemplified by the increase in mountain hare game bags in association with the sarcoptic mange outbreak among foxes in Sweden (Lindström *et al.*, 1994) and Norway (Smedshaug *et al.*, 1999) during the 1970s. Thus, a mountain hare population is heavily predated and affected by the local fox populations, which is especially apparent when populations of rodents crash and foxes need to switch prey species (Marcström, Kenward & Engren, 1988). However, it is highly unlikely that predation may constitute a long-term threat to mountain hare populations, and subsequently cause permanent restrictions in the distribution. The capacity of mountain hare populations to survive and increase after heavy fox predation in a cyclic manner must not be underestimated. The mountain hare is not the most important prey species for foxes, rather an alternative when vole populations are low (cf. Lindström *et al.*, 1987; Marcström *et al.*, 1988), and only under particular circumstances, as on smaller islands, may the presence of foxes constantly regulate

mountain hare populations (cf. Angerbjörn, 1989). Rather, as Kauhala, Helle & Korhonen (1999) observed in their study area in northern Finland, mountain hare population density may increase despite high numbers of predators and vole populations in decline. It also appears unlikely that foxes, or other predators, selectively prey on mountain hares in areas of sympatry with brown hares, although I am not aware of any investigations that substantiate this statement.

### **Deforestation and cultivation**

The deforestation and subsequent spread of agriculture through Europe from 10 000 to 5700 years ago have had considerable impact on the development of the European landscape (see Roberts, 1998). What once was tundra turned into dense forests, and then gradually into open farmland in step with cultivation. Possibly, this obvious change of the habitat has caused the continuous restrictions in the mountain hare distribution because the mountain hares are better adapted to the tundra and, presumably, taiga habitats than to the agricultural landscape. However, the Irish mountain hares frequent open agricultural landscapes and also graze more than other mountain hares (cf. Wolfe *et al.*, 1996; Dingerkus & Montgomery, 2002). Similarly, the mountain hares in northern Sweden frequent medium-sized cities (<100 000 citizens) and often forage in open areas, such as infields and moors (F. Dahl, personal communication). Why, then, should a species with such adaptive potential as the mountain hare have difficulty utilizing the open agricultural landscape? Presumably, it is not the agricultural landscape in itself that is the limiting factor, rather the brown hares that it favours.

### **Interactions with other herbivores**

During the recent century, many ungulate populations in Europe have recovered from declines because of heavy hunting pressure throughout the 19th century, and even increased in numbers (Mitchell-Jones *et al.*, 1999). Supposedly, interspecific competition between mountain hares and dense populations of ungulates could have a negative effect on mountain hare distribution and population density. Interspecific competition has been observed between moose and snowshoe hare in North America (Dodds, 1960), and may occasionally have a heavy impact on the hare populations (Belovsky, 1984). However, there is no reason to believe that such competition for resources has long-term impacts on the mountain hare distribution. Ungulates in variable densities must have been present in sympatry with hares throughout the evolution of genus *Lepus*, that is, approximately the last million years (Kurtén, 1968; Averianov, 1995). Also, Hewson (1990) observed mountain hares and red deer *Cervus elaphus* graze on the same pastures in Scotland. The only caution taken by mountain hares was to keep at sufficient distance (i.e. >10 m) to avoid being trampled upon if the deer should flee.

The rabbit has spread naturally and/or by introductions to north-west Europe from the Iberian peninsula and southern France, seemingly favoured by changes in agriculture during the 1800s (Hewson, 1991). Thus, the presence and expansion of rabbits coincides with the disappearance of the mountain hare in southern Sweden, and possibly also in parts of Scotland. Although Flux (1970) argues that rabbits may keep mountain hares in Scotland away from lower altitudes because of interspecific interactions, this observation may also be a habitat effect because the rabbits suppress the vegetation so much that it becomes unattractive to mountain hares. Also, Flux (1970), and later Hewson (1990), made observations of mountain hares chasing away rabbits from feeding areas rather than the opposite. As brown hares simultaneously utilized the study areas of Flux (1970), they could also be responsible

for the absence of mountain hares there. The distribution of rabbits is fragmented and patchy because of the specific demands required by their burrows for colony building (Hewson, 1991; Hulbert *et al.*, 1996), so any form of competitive exclusion between rabbits and mountain hares is likely to be restricted to areas around rabbit colonies and not to extend over wider geographical areas.

### DESIRABLE RESEARCH AREAS

To elucidate the relative role of species interactions between brown hares and mountain hares and other potential factors, considerable research efforts have to be conducted in the following areas:

#### Competitive interactions

There is to my knowledge only one empirical investigation (Lind, 1963) that deals with the means of competition between mountain hares and brown hares. As Lind (1963) detected indications of competitive exclusion of mountain hares, this is a highly relevant area of future research. Examples of interesting aspects are: (i) the forms of physical interference, where the brown hare may have an advantage over the mountain hare (cf. Hewson, 1990); (ii) the niche separation and habitat utilization of the species in areas of allopatry and sympatry, respectively; (iii) potential differences between the species in food preferences, especially as the investigations by Wolfe *et al.* (1996) and Dingerkus & Montgomery (2001) indicate that allopatric mountain hares in Ireland eat a wider range of plant species than sympatric conspecifics. Further, the demographic parameters (i.e. fitness, survival, fecundity, etc.) resulting from species' interactions suggested above needs to be examined. For example, do mountain hares in sympatry with brown hares have lower survival rates because they are suppressed in their home range? Finally, Ireland appears to be an exception to other areas, and may therefore deserve specific attention. In Ireland, brown hares seem to have difficulty in establishing (cf. Tapper, 1987). Thus, are the mountain hares in Ireland more competitive, or are simply the environmental conditions unsuitable for brown hares?

#### Effects of hybridization

Continuous investigation of interspecific geneflow between the species is necessary to determine the importance of hybridization for the species' coexistence. There are, for example, still question marks regarding the extent of paternal geneflow over the species barrier (cf. Thulin, 2000). Although the investigations in Sweden provide valuable information (cf. Lönnberg, 1905, 1908; Thulin *et al.*, 1997b; Thulin, 2000), it is important to extend the efforts to include natural contact zones between the species. Suitable areas are the British Isles, the Alps, Finland and eastwards in the Baltic countries and Russia. The importance of the behavioural ecology and reproductive biology of hares for hybridization requires an evaluation. Further, the possibility that brown hares facilitate their expansion northwards (Fig. 4) by adaptation through hybridization and introgression, a principle first suggested by Anderson & Stebbins (1954), must be considered. Such adaptation is an important evolutionary force among plants (e.g. Arnold, 1997), and has recently been described among the hybridizing flycatcher species *Ficedula hypoleuca* and *F. albicollis* (Veen *et al.*, 2001). Interestingly, brown hares in northern Russia shift to white winter pelage (Gureev, 1964), a characteristic normally assigned to mountain hares. Is this an adaptation sprung out of the general plasticity in hare physiology (cf. Flux & Angerman, 1990) or incorporation of the necessary genes through hybridization with mountain hares?

### Disease susceptibility

The possibility that mountain hares are more susceptible to certain pathogens than brown hares (cf. Mörner, 1994, 1999) is of great importance for the coexistence of the species. Thus, the relative susceptibility of brown hares and mountain hares in natural populations to the numerous diseases that affect the species has to be evaluated. In combination with other factors, such as food shortage and intense predation, infectious diseases can severely depress mountain hare population densities, especially within already isolated populations on islands (cf. Angerbjörn, 1983) and, presumably, in delimited forest patches.

Finally, regular inventories are important to update the accurate distribution of hares in areas of allopatry and sympatry. Special emphasis should be undertaken to detect isolated populations of mountain hares, because isolation induces sensitivity to stochastic events and, thus, increases the risk of local extinction.

### CONCLUSION

The mountain hare is a very popular and well-known species, an important game for hunters and prey for carnivores and raptors. Thus, the declining numbers of mountain hares in Sweden and Russia are of great concern to many hunters and naturalists, and the ecological role of the mountain hare is significant. The causes of mountain hare population crashes are summarized by Angerbjörn (1983) as changes in the interactions between mountain hares and: (i) plants that develop toxins in response to heavy grazing; (ii) epidemic pathogens and parasites that ravage the populations; (iii) predators with intensified search images for hares. However, even though these factors regulate mountain hare populations, they may only locally restrict the distribution. Plausible causes of permanent disappearance of mountain hares in Europe are exclusion by interspecific competition and hybridization with, and/or epidemic diseases mediated by, the congeneric brown hare. The relative role of different factors requires further assessment, and is certainly a future challenge for conservation and evolutionary biologists in Europe.

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### REFERENCES

- Andersen, B.G. & Borns, H.W. Jr (1997) *The Ice Age World*. Scandinavian University Press, Oslo.
- Anderson, E. & Stebbins, G.L. Jr (1954) Hybridization as an evolutionary stimulus. *Evolution*, **8**, 378–388.
- Angerbjörn, A. (1983) Proximate causes of mountain hare population crashes: a review. *Finnish Game Research*, **41**, 29–38.
- Angerbjörn, A. (1989) Mountain hare populations on islands: effects of predation by red fox. *Oecologia*, **81**, 335–340.
- Angerbjörn, A. & Flux, J.E.C. (1995) *Lepus timidus*. *Mammalian Species*, **495**, 1–11.
- Angerbjörn, A. & Pehrson, Å. (1987) Factors influencing winter food choice by mountain hares (*Lepus timidus* L.) on Swedish coastal islands. *Canadian Journal of Zoology*, **65**, 2163–2167.
- Arnold, M.L. (1997) *Natural Hybridization and Evolution*. Oxford University Press, Oxford.

- Averianov, A. (1995) Osteology and adaptations of the early Pliocene rabbit *Trischizolagus dumitrescuae* (Lagomorpha: Leporidae). *Journal of Vertebrate Paleontology*, **15**, 375–386.
- Belovsky, G.E. (1984) Moose and snowshoe hare competition and a mechanistic explanation from the foraging theory. *Oecologia (Berlin)*, **61**, 150–159.
- Björk, S. (1995) A review of the history of the Baltic sea, 13.0–8.0 ka BP. *Quaternary International*, **27**, 19–40.
- Corbet, G.B. (1986) Relationships and origins of the European lagomorphs. *Mammal Review*, **16**, 105–110.
- Dingerkus, S.K. & Montgomery, W.I. (2001) The diet and landclass affinities of the Irish hare *Lepus timidus hibernicus*. *Journal of Zoology, London*, **253**, 233–240.
- Dingerkus, S.K. & Montgomery, W.I. (2002) A review of the status and decline in abundance of the Irish hare (*Lepus timidus hibernicus*) in Northern Ireland. *Mammal Review*, **32**, 1–12.
- Dodds, D.G. (1960) Food competition and range relationships of moose and snowshoe hare in Newfoundland. *Journal of Wildlife Management*, **24**, 52–60.
- Ebenhard, T. (1988) Introduced birds and mammals and their ecological effects. *Swedish Wildlife Research (Viltrevy)*, **4**, 5–107.
- Fargher, S.E. (1977) The distribution of the brown hare (*Lepus capensis*) and the mountain hare (*Lepus timidus*) in the Isle of Man. *Journal of Zoology*, **182**, 164–167.
- Flux, J.E.C. (1970) Life history of the mountain hare (*Lepus timidus scoticus*) in north-east Scotland. *Journal of Zoology, London*, **161**, 75–123.
- Flux, J.E.C. (1981) Field observations of behaviour in the genus *Lepus*. In: *Proceedings of the World Lagomorph Conference* (Ed. by K. Myers & C.D. MacInnes), pp. 377–394. University of Guelph, Guelph, Australia.
- Flux, J.E.C. (1993) Relative effect of cats, myxomatosis, traditional control, or competitors in removing rabbits from islands. *New Zealand Journal of Zoology*, **20**, 13–18.
- Flux, J.E.C. & Angerman, R. (1990) The hares and jackrabbits. In: *Rabbits, Hares and Pikas: Status Survey and Conservation Action Plan* (Ed. by J.A. Chapman & J.E.C. Flux), pp. 61–94. IUCN, Gland, Switzerland.
- Folitarek, S.S. (1940) Geographic distribution of the European hare *Lepus europaeus* Pall. in the USSR. *Proceedings of Severev Institute of Evolutionary Morphology, Academy of Sciences of USSR*, **1**, 79–97. [In Russian.]
- Fraguglione, D. (1959) Les anomalies du pelage chez les lièvres commun et variable. *Diana*, **4**, 57–59.
- Gautier, A. (1973) The fauna of the Palaeolithic site of Maisières-Canal: Fossil Mammalia. *Institut Royal Sciences Naturelles de Belgique, Mémoires*, **172**, 1–20.
- Gerell, R. (1977) Skånes däggdjur – Resultat från en intervjuundersökning. *Skåne Jakt*, **2**, 6–14.
- Gureev, A.A. (1964) *Fauna USSR. III. Lagomorpha*. Izvestii Akademii Nauk SSSR, Moscow, Leningrad.
- Gustavsson, I. (1971) Mitotic and meiotic chromosomes of the variable hare (*Lepus timidus* L.), the common hare (*Lepus europaeus* Pall.) and their hybrids. *Hereditas*, **67**, 27–34.
- Gustavsson, I. & Sundt, C.O. (1965) Anwendung von künstlicher befruchtung bei der hybridisierung von zwei hasenarten. *Zeitschrift für Jagdwissenschaft*, **11**, 155–158.
- Hartl, G.B., Suchentrunk, F., Nadlinger, K. & Willing, R. (1993) An integrative analysis of genetic differentiation in the brown hare *Lepus europaeus* based on morphology, allozymes and mitochondrial DNA. *Acta Theriologica*, **38**, 33–57.
- Hewson, R. (1962) Food and feeding habits of the mountain hare *Lepus timidus scoticus* Hilzheimer. *Proceedings of the Zoological Society of London*, **139**, 515–526.
- Hewson, R. (1976) A population study of mountain hares (*Lepus timidus*) in north-eastern Scotland from 1956–1969. *Journal of Animal Ecology*, **45**, 395–414.
- Hewson, R. (1990) Interactions between mountain hares (*Lepus timidus*) and other mammals. *Journal of Zoology (London)*, **221**, 302–305.
- Hewson, R. (1991) Lagomorphs: Order Lagomorpha. In: *Handbook of British Mammals* (Ed. by G.B. Corbet & S. Harris), pp. 146–175. Blackwell Scientific Publications, Oxford.
- Holley, A.J.F. (1986) A hierarchy of hares: dominance status and access to oestrus does. *Mammal Review*, **16**, 181–186.
- Holley, A.J.F. & Greenwood, P.J. (1984) The myth of the mad March hare. *Nature*, **309**, 549–550.
- Hulbert, I.A.R., Iason, G.R. & Racey, P.A. (1996) Habitat utilization in a stratified upland landscape by two Lagomorphs with different feeding strategies. *Journal of Applied Ecology*, **33**, 315–324.
- Iason, G.R. & Palo, R.T. (1991) Effects of birch phenolics on a grazing and a browsing mammal – a comparison of hares. *Journal of Chemical Ecology*, **17**, 1733–1743.
- Kauhala, K., Helle, E. & Korhonen, J. (1999) Impact of predator removal on predator and mountain hare populations in Finland. *Annales Zoologici Fennici*, **36**, 139–148.
- Knyazev, A.V. & Savinetsky, A.B. (1994) On the history of distribution of mountain hare (*Lepus-timidus*) in the southern part of European Russia. *Zoologicheskyy Zhurnal*, **73**, 143. [In Russian.]

- Kowalski, E. (1959) *A Catalogue of the Pleistocene Mammals of Poland*. Academia Nauk, Warsaw.
- Kurtén, B. (1968) *Pleistocene Mammals of Europe*. Weidenfeld & Nicolson, London.
- Lepiksaar, J. (1986) The Holocene history of theriofauna in Fennoscandia and Baltic countries. *Striae*, **24**, 51–70.
- Liljegren, R. & Lagerås, P. (1993) *Från Mammutstätt Till Kohage: Djurens Historia I Sverige*. Wallin & Dalholm Boktryckeri AB, Lund.
- Lind, E.A. (1963) Observations on the mutual relationship between the snow hare (*Lepus timidus*) and the field hare (*L. europaeus*). *Suomen Riista*, **16**, 128–135.
- Lindström, E.R., Andrén, H., Angelstam, P., Cederlund, G., Hörnfeldt, B., Jäderberg, L., Lemnell, P.-A., Martinsson, B., Sköld, K. & Swenson, J.E. (1994) Disease reveals the predator: Sarcoptic mange, fox predation, and prey populations. *Ecology*, **75**, 1042–1049.
- Lindström, E., Widén, P., Angelstam, P. & Andrén, H. (1987) Do predators synchronize vole and grouse fluctuations? – An experiment. *Oikos*, **48**, 121–124.
- Lönnberg, E. (1905) On hybrids between *Lepus timidus* L. & *Lepus europaeus* Pall. from southern Sweden. *Proceedings of Zoological Society of London*, **1**, 278–287.
- Lönnberg, E. (1908) Några villebrädsarters nutida utbredning i Skåne. *Svenska Jägareförbundets Tidskrift*, **46**, 7–16.
- Lüttschwager, J. (1956) Vorgeschichtliche Säugetierwelt in Schleswig-Holstein. *Säugetierkundliche Mitteilungen*, **4**, 27–30.
- Marcström, V., Kenward, R.E. & Engren, E. (1988) The impact of predation on boreal tetraonids during vole cycles: An experimental study. *Journal of Animal Ecology*, **57**, 859–872.
- Mitchell-Jones, A.J., Amori, G., Bogdanowicz, W., Krystufek, B., Reijnders, P.J.H., Spitzenberger, F., Stubbe, M., Thissen, J.B.M., Vohralik, V. & Zima, J. (1999) *Atlas of European Mammals*. Academic Press, London.
- Mörner, T. (1994) *Tularemia in Hares in Sweden with Special Reference to Identification of Francisella tularensis*. PhD Thesis, p. 131 Swedish University of Agricultural Sciences & National Veterinary Institute, Uppsala.
- Mörner, T. (1999) Monitoring diseases in wildlife – a review of diseases in the orders Lagomorpha and Rodentia in Sweden. *Proceedings Symposium of Zoo Animals, Vienna, Austria*, **39**, 255–262.
- Mostecký, V. (1969) Late Pleistocene mammals from the 'Chlupac Cave' on Kobyla hill near Koneprusy (Bohemian Karst). *Sbornik Národního Muzea Praze*, **25**, 1–55.
- Nilsson, S. (1820) *Skandinavisk Fauna Del 1: Däggande Djuren*. Berlingska boktryckeriet, Lund.
- Real, L. (1990) Search theory and mate choice. I. Models of single-sex discrimination. *American Naturalist*, **136**, 376–404.
- Rhymer, J.M. & Simberloff, D. (1996) Extinction by hybridization and introgression. *Annual Review in Ecology and Systematics*, **27**, 83–109.
- Roberts, N. (1998) *The Holocene. An Environmental History*. Oxford Blackwell Ltd, Oxford.
- Schröder, J., Soveri, T., Soumalainen, H.A., Lindberg, L.-A. & van der Loo, W. (1987) Hybrids between *Lepus timidus* and *Lepus europaeus* are rare although fertile. *Hereditas*, **107**, 185–189.
- Simberloff, D. (1996) Hybridization between native and introduced wildlife species: importance for conservation. *Wildlife Biology*, **2**, 143–150.
- Smedshaug, C.A., Selas, V., Lund, S.E. & Sonerud, G.A. (1999) The effect of a natural reduction of red fox *Vulpes vulpes* on small game hunting bags in Norway. *Wildlife Biology*, **5**, 157–166.
- Soffer, O. & Gamble, C. (1990) *The World at 18 000 BP. 1. High Altitudes*. Unwin-Hyman, London.
- Stuart, A.J. (1974) Pleistocene history of the British vertebrate fauna. *Biological Reviews*, **49**, 225–266.
- Suchentrunk, F., Polster, K., Giacometti, M., Ratti, P., Thulin, C.-G., Ruhle, C., Vasil'ev, A.G. & Slotta-Bachmayr, L. (1999) Spatial partitioning of allozyme variability in European mountain hares (*Lepus timidus*): gene pool divergence across a disjunct distributional range? *Zeitschrift für Säugetierkunde*, **64**, 308–318.
- Swofford, D.L. (1993) *PAUP: Phylogenetic Analysis Using Parsimony, Version 3.1*. Illinois Natural History Survey, Champaign.
- Tapper, S. (1987) *The Brown Hare*. Shire Publications Ltd, Aylesbury.
- Thenius, E. (1980) *Grundzüge der Faunen- und Verbreitungsgeschichte der Säugetiere. Eine Historische Tiergeographie*. Gustav Fisher Verlag, Stuttgart.
- Thulin, C.-G. (2000) *Hybridisation between introduced brown hares and native mountain hares in Sweden*. PhD Thesis, p 110. Uppsala University, Uppsala.
- Thulin, C.-G., Isaksson, M. & Tegelström, H. (1997a) The origin of Scandinavian mountain hares (*Lepus timidus*). *Gibier Faune Sauvage*, **14**, 463–475.
- Thulin, C.-G., Jaarola, M. & Tegelström, H. (1997b) The occurrence of mountain hare mitochondrial DNA in wild brown hares. *Molecular Ecology*, **6**, 463–467.

- Thulin, C.-G. & Tegelström, H. (2002) Biased geographical distribution of mitochondrial DNA that passed the species barrier from mountain hares to brown hares (genus *Lepus*): an effect of genetic incompatibility and mating behaviour? *Journal of Zoology, London*, **258**, 299–306.
- Turk, F.A. (1964) Blue and brown hares associated together in a Bronze Age fissure cave burial. *Proceedings of the Zoological Society of London*, **142**, 185–188.
- Veen, T., Borge, T., Griffith, S.C., Saetre, G.-P., Bures, S., Gustafsson, L. & Sheldon, B.C. (2001) Hybridization and adaptive mate choice in flycatchers. *Nature*, **411**, 45–50.
- Wiley, R.H. & Poston, J. (1996) Indirect mate choice, competition for mates, and coevolution of the sexes. *Evolution*, **50**, 1372–1381.
- Wolfe, A., Whelan, J. & Hayden, T.J. (1996) The diet of the mountain hare (*Lepus timidus hibernicus*) on coastal grassland. *Journal of the Zoological Society of London*, **240**, 804–810.
- Woodman, P., McCarthy, M. & Monaghan, N. (1997) The Irish Quaternary fauna project. *Quaternary Science Reviews*, **16**, 129–159.
- Yalden, D.W. (1971) The mountain hare (*Lepus timidus* L.) in the Peak District. *Naturalist*, **918**, 81–92.
- Yalden, D.W. (1984) The status of the mountain hare, *Lepus timidus*, in the Peak District. *Naturalist*, **109**, 55–59.
- Yalden, D.W. (1999) *The History of British Mammals*. T & A.D. Poyser, London.

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