

An overview of the current status and protection of the Brown Hare (Lepus Europaeus) in the UK

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Executive Summary

1. Brown hare populations have declined across Europe since the 1960s. Hence, the species is included in the UK Biodiversity Action Plan with a target of doubling spring numbers by 2010.
2. The Steering Group responsible for the brown hare Species Action Plan has recently been considering hare numbers, the contribution that agri-environment schemes might play and the question of a close season on culling.
3. The information relevant to these issues that is currently in the public domain has been reviewed here on behalf of Defra's European Wildlife Division.
4. The current winter brown hare population in Britain is estimated to be approximately 750,000 and there is evidence that numbers have been relatively stable in recent years.
5. There are complex interactions between factors such as predation, habitat quality, agronomy and land management practices, including game keeping, influencing hare populations.
6. One approach to resolving this complexity and informing conservation strategy would be the development of a spatially explicit population model. This would reflect current knowledge of the way hare populations operate in the mosaic of isolated oases of high quality habitat within generally inhospitable pastoral landscapes.
7. Enhancing survival and particularly leveret (juvenile hare) survival should be a specific target for conservation action. Unfortunately, comparative data are lacking on this key population parameter across habitats where hare densities vary. Hence, there is currently limited information available on which to base habitat management aimed at enhancing leveret survival.
8. A requirement of the Species Action Plan is to review the use of legislation pertaining to the shooting and selling of hares. Some have argued that this should include the introduction of a close season.
9. There is currently no evidence that the introduction of a close season would significantly enhance hare numbers. Hare numbers have declined throughout Europe despite protection by close seasons, while, contrarily, the available data on population dynamics suggest that intensive culls in February, typical of game shoots, have no long-term impact on hare numbers.
10. It could be argued that the introduction of a close season might be beneficial in terms of animal welfare through a reduction in culling of lactating females with dependent offspring. However, consideration would need to be given to allowing culling, presumably under licence, during any close season in the context of pest control. Furthermore, the current practice of culling

hares, often during the breeding season, to reduce illegal poaching and coursing represents further ambiguity with regard to welfare concerns. It is thus unclear what net benefit the introduction of a close season would represent in terms of animal welfare.

Introduction

The issues surrounding the UK brown hare (*Lepus europaeus*) population are complex. This is partly because the species is a quarry for both sport and meat trade, but is sometimes regarded as a pest, and it is also of conservation concern. It is the latter interest that has stimulated this review, given the challenging target under the national Biodiversity Action Plan of doubling spring numbers by 2010 (Anon. 1995). The Steering Group responsible for the brown hare Species Action Plan has recently been considering research into hare numbers, the contribution that agri-environment schemes might play and the question of a close season on culling. The information relevant to these issues that is currently in the public domain has been reviewed here on behalf of Defra's European Wildlife Division. The review considers the history, legislative status and population biology of the species and then uses this to inform the linked themes of population trends, pest and conservation status. *Key hypotheses, conclusions and recommendations are highlighted in italicised, bold type.*

History in the UK

The archaeological record indicates that the brown hare was not present in postglacial Britain when the English Channel was formed between 7,000 and 9,500 years ago (Yalden 1999). It could thus be argued that the brown hare is not a native species. Understanding the history is complicated by difficulties in distinguishing the bones of the mountain hare (*L. timidus*) from those of the brown hare. However, there are virtually no records of any hare bones from England or Wales between the early Mesolithic (circa 9,000 years ago) and the Neolithic (circa 5,000 years ago) periods. This suggests that the brown hare was absent prior to the formation of the Channel, while the mountain hare declined in England and Wales as the treeless, open habitats present in late glacial periods gave way to woodland. The brown hare originates from the open steppe grasslands of Eurasia (Tapper 1987a) and probably spread through Europe as woodland was cleared for agriculture (Lever 1994). There are numerous records of the presence of hares, almost certainly brown hares, from Iron Age sites (circa 3,000 years ago) in southern England. There are also some from Bronze Age sites. It thus seems probable that the brown hare was introduced into Britain around 4,000 years ago and began to thrive in the habitats created by Neolithic and later agricultural and land management practices. The species is apparently better adapted to these habitats than the truly native mountain hare whose range became limited to upland habitats. However, as Yalden (1999) points out, the presence of brown hares at earlier sites might have gone unrecorded, since their presence would have been regarded as unremarkable before it was realised that the species might be introduced rather than native. Nevertheless, had the brown hare not arrived in Britain, it seems probable that the range of the fully native *L. timidus* would, because the absence of competition from brown hares (e.g. Thulin 2003), now extend to habitats below 500m. This is currently the case for the race of mountain hare in Ireland (e.g. Wolfe & Hayden 1996, Dingerkus &

Montgomery 2001), where the brown hare was introduced relatively recently (Yalden 1999).

Current legislative status of the brown hare in the UK

The brown hare is not listed under either Schedule 5 or 6 of the Wildlife and Countryside Act 1981 and is thus not afforded any special protection under this legislation. The Agriculture Act 1947 enables Defra to serve notice to control pest species, including hares, to protect crops, pasture, foodstuffs, trees, banks, hedges or works on any land. Specific legislation regarding the brown hare begins with the Hare Act 1848, which enabled persons to kill hares without first gaining a game licence. This shift from absolute protection as a game species to sporadic persecution as a pest was strengthened under the Ground Game Act 1880 which gave tenant farmers the right to kill hares on their land at any time of the year to protect crops. However, the Hare Preservation Act 1892 forbade the sale of hares during the notional main breeding season of 1 March to 31 July inclusive. This legislation was intended to protect hare numbers and noted a dramatic decline in brown hares due to their “inconsiderate slaughter”. The intention was to reduce the number of hares killed during the defined period in the absence of refrigeration to preserve any surplus (Stroud *et al.* 1999). With modern refrigeration facilities it may be possible to store hares killed during the relevant period or export them. Tapper & Stoate (1992) estimated that approximately 137,000 hares were exported per year during the late 1980s.

According to the FACE Handbook of hunting in Europe volume 1 1995, quoted by White *et al.* (2000), hares are protected by a close season on hunting throughout much of Europe (Austria, Belgium, Denmark, Finland, France, Germany, Greece, Hungary, Ireland, Italy, Luxembourg, Netherlands, Poland, Portugal, Slovenia, Spain, Sweden, Switzerland), although licences can be given to cull hares outside the hunting season. (e.g. in the Netherlands - Broekhuizen & Maaskamp 1980). Typically the open season lasts from 1 October through to 31 December which, in general, is the period when few (<10%) of adult females are pregnant or lactating. In some countries (Finland, Germany, Ireland, Poland, Spain, and parts of Sweden) the season is extended into January or February. ***Overall the Brown hare is thus subject to less formal protection in the UK than elsewhere in Europe.***

Population biology

Breeding

Breeding can occur throughout the year. However there is a main breeding season when the majority of adult females are pregnant. In the UK this lasts from February through to August (Norfolk - Lincoln 1974, Scotland - Hewson & Taylor 1975) and a similar pattern is reported elsewhere in Europe (e.g.

Netherlands - Broekhuizen & Maaskamp 1981, Poland - Raczynski 1964). Breeding is extended by mild autumn conditions (Hewson & Taylor 1975). Gestation lasts approximately six weeks (Martinet 1977). Mean litter size varies inversely with mean annual temperature but is around 2.7 in the UK and is highest at the peak of the breeding season in late spring (Raczynski 1964, Hewson & Taylor 1975, Broekhuizen. & Maaskamp, 1981). Broekhuizen. & Maaskamp (1981) estimated that number of litters per female per year in the Netherlands as 4.1, which is similar to Pepin's (1989) estimate of 4-5 for agricultural habitats in France. The estimated total number of young produced per female per year in these studies was 9.4-11.3. Similar figures were observed by Kovaks (1983a) in Hungary and Slamecka *et al.* (1997) in Slovakia, while Marboutin *et al.* (2003) estimated average fecundity at 13.4 in lowland agricultural landscapes in France. Frylestam (1980) derived lower estimates for annual production of between 6.8 and 8.9 young per female in southern Sweden, while only 5 per female was reported by Hansen (1992) in Denmark. Even these lower figures represent a high potential intrinsic rate of increase, thus enabling local populations to recover rapidly from perturbation and attain the carrying capacity of the habitat. Leverets are at a relatively precocious growth stage when born with a full coat of fur, eyes open and mobile, in contrast to the relatively altricial developmental stage of newborn rabbit kittens. This reflects the contrasts between leverets being born above ground, rather than with the protection against predation and climate afforded by the underground nest of the rabbit (Cowan & Bell 1986). Nursing care maintains sophisticated defence against predation (Broekhuizen & Maaskamp 1980, Broekhuizen *et al.* 1986). The young are nursed for only a few minutes each day, urine & excreta are removed by the mother and, between nursing episodes, the leverets disperse into cover and remain apart. Martinet *et al.* (1970) found that litters born to captive hares are fed milk typically for 1 month. Broekhuizen & Maaskamp (1980) demonstrated considerable variation in the nursing period, extended nursing, in excess of 67 days, being observed late in the breeding season. This suggests that females continue to feed the current litter if they do not become pregnant *post partum*. However, Broekhuizen & Maaskamp (1981) suggest that leverets are only reliant on milk up to around 17 days of age, after which it is supplementary to green food (see also Pielowski 1971).

Mortality

The high productivity of hares is offset by low survival. Approximate estimates of annual mortality amongst adults range from 48-65% across Europe (e.g. Albildgard *et al.* 1972, Broekhuizen 1979, Kovacs 1983b, Pepin 1987). Annual mortality in pastoral habitats in the UK is at the upper end of this range at 65% (University of Bristol 2003). Some of the variation in the reported figures reflects hunting interests with mortality ranging from 41-49% in the absence of hunting compared to 48-65% in its presence (Marboutin & Peroux 1995). Recent reanalyses of some of these data reveal that adult female mortality (50% per annum) can be higher than that for males (45% per annum) (Marboutin & Hansen 1998). They also showed that overwinter mortality of yearling hares is inversely related to temperature with lighter animals

particularly prone. Mortality rates for leverets (juveniles in the year of their birth) can vary considerably, although accuracy of estimates can be compromised by calculation usually being based on observations of productivity in relation to the age structure of shot population samples. In Poland, mortality of leverets between birth and autumn can be as high as 85-95% (Wasilewski 1991). In southern Sweden, Frylestam (1980) recorded 73-84% losses for mainland populations compared to 35-56% on an island. Hansen (1992) derived a range of 68-91% in Denmark. In France postnatal mortality from birth to shooting ranged, between years within the same area, from 52-75% (Pepin 1989) with a higher range of 71-86 % derived by Marboutin *et al.* (2003). Estimates are sparse for the UK. However, Macdonald *et al.* (2000), when developing a population model, used data on the age structure of animals killed during spring shoots on 22 English game estates in 1971 and 1972, given in Tapper (1991) to estimate mortality of 62.6% from birth to 1 year of age. White *et al.* (2000), in developing their population model, used unpublished data on leveret survivorship figures from East Anglia. These reflected 50-60% mortality by the following year for young born in January and February, 90% for those born between April and July and then 40-50% amongst the small numbers born in October and November. Leveret mortality is thus highest for young born during the period when productivity is also at its peak, in terms of both litter production and litter size. Relatively low mortality for early born young has also been recorded in a particular agricultural landscape in France (Pepin 1989). This may be an important factor in explaining why populations in eastern England have not declined to the same degree as those in pastoral landscapes (see below).

Causes of mortality

i. Predation

The main predator of the brown hare is generally acknowledged, throughout Europe, to be the red fox (*Vulpes vulpes*), 3-46% of whose diet can consist of hares (Pielowski 1976, von Schantz 1980, Erlinge *et al.* 1984, Goszczynski & Wasilewski 1992, Reynolds & Tapper 1995a). Goszczynski & Wasilewski (1992), working in Poland, estimated that fox predation accounted for more than 50% of all hare mortality during the winter compared to 20% of all mortality during the summer. They showed that, between March and October, foxes took 17% of young and 10% of adult hares. In Sweden, Erlinge *et al.* (1984) estimated that foxes removed at least 40% of the annual production of leverets, although they did not infer cause and effect between predation and hare numbers. Nevertheless, high levels of predation could potentially impact directly on population size. As modelled by Reynolds & Tapper (1995b), fox predation accounted for 75-100% of annual production in a southern England hare population, allowing for lost potential production of animals killed by foxes. ***The key issue is the extent to which such mortality is additive to other causes or reflects mortality that would be exacted in any case by some other force in density-dependent processes that harvest a "doomed" surplus.***

There is circumstantial evidence that predation is linked to the size of game bags and perhaps hare population density. Higher density hare populations, with lower mortality rates, have been found on islands where foxes are absent than for nearby mainland populations in both Denmark (Abildgard *et al.* 1972) and Sweden (Frylestam 1980). However, inferences based on such observations are potentially confounded by dispersal being absent for island populations. Natural experiments have occurred where red fox populations have been reduced by disease, such as sarcoptic mange: subsequent increases in hare populations were observed followed by declines as the red fox populations recovered (e.g. Lindstrom *et al.* 1994). A questionnaire survey by Vaughan *et al.* (2003) revealed that, in England and Wales, hares were rarely seen where foxes were seen frequently. Similar inverse relationships between fox and hare populations have been observed in relation to predator control by humans (Tapper *et al.* 1991). Nevertheless, these observations do not demonstrate cause and effect between fox predation and reduced hare population size. If increased fox predation results in compensatory reductions in some other mortality factor that is density-dependent, then hare populations may be buffered. However, it remains plausible that under some circumstances fox predation can influence hare population densities. Indeed Vaughan *et al.* (2003) point out that the association in their study of between hare numbers and large fields, permanent cover and medium to low fox numbers is consistent with the hypothesis that predation by foxes limits numbers of hares. This finding also highlights the potential importance of habitat quality on the impact of predation. ***There are thus likely to be complex interactions between factors such as predation, habitat quality and land management practices, including game keeping, that will determine the impact of predation on hare populations.*** Thus considering predation in isolation within the conservation strategy is unlikely to be a productive way forward.

ii. Disease

Hares are subject to a range of diseases that can lead directly or indirectly to death, particularly amongst high density autumn populations with a high proportion of juveniles (Lamarque *et al.* 1996). European Brown Hare Syndrome (EBHS), caused by a *Lepus* specific calicivirus (rabbits infected with EBHS will produce antibody but will not exhibit clinical symptoms; the same is true of hares with respect to the rabbit calicivirus that causes rabbit haemorrhagic disease RHD), has been recognised since the 1980s and its status in the UK has been documented by Duff *et al.* (1994, 1997). In parts of Europe it can cause substantial mortality (e.g. Sostaric *et al.* 1991). In the UK coccidiosis (the infective agent being a single celled gut parasite, *Eimeria spp.*) causes more deaths than any other disease in the UK, particularly amongst juveniles (Whitwell 1997). Leporine dysautonia, also known as grass sickness, arising from lesions in the central nervous system of unknown origin (Griffiths & Whitwell 1993), toxoplasmosis caused by infection with the single celled parasite *Toxoplasma gondii*, (Sedlak *et al.* 2000) and pseudotuberculosis, caused by infection with the bacterium *Yersinia pseudotuberculosis*, (Whitwell 1997), can all cause mortality.

iii. Agricultural practices

Since the herbicide paraquat was introduced in the early 1960s, at around the time when some hare populations began to decline, there has been concern regarding a link, especially as there were specific reports of hare deaths associated with paraquat use. However, wildlife incident investigation schemes in both the UK and France have confirmed very few hare deaths have been caused directly by paraquat (Edwards *et al.* 2000). These authors also argue that some of the early reports of hare deaths arising from liver damage attributed to paraquat poisoning could actually have been cases of EBHS. Nevertheless, other pesticides have sometimes been suggested as significant causes of juvenile mortality. For instance, in France an insecticide application against a particularly heavy aphid infestation of cereals in a particular month was associated with poor representation of the cohort born at that time in the population hunted during the subsequent autumn (Pepin 1989). Furthermore, herbicide treatments are sometimes reported to cause deaths (Hutchings & Harris 1996). Cause and effect for such associations is, however, so far unproven as is any direct effect of environmental pollution (e.g. Paukert 1988).

Other agricultural activities can have a direct impact on mortality. Preparation of fields for planting of spring crops can be a direct threat to young leverets which cannot escape (Durdik 1981). Leverets using crops for cover are vulnerable when these are harvested. Harvesting of lucerne fields, which happens up to four times during the growing season, leads to approximately 50% mortality amongst the leverets born in such fields (Kaluzinski & Pielowski 1976). Milanaova & Dimov (1990) also report significant losses of leverets when alfalfa fields are harvested. However, harvesting operations do not appear to represent a major threat to adults (Marboutin & Aebischer 1996).

iv. Hunting

The most important human activity that contributes directly to hare mortality is hunting, primarily for sport. This takes three forms namely “beagling” sometimes generically considered as “hunting with hounds”, coursing and shooting.

Beagling involves hunting on foot with beagle hounds or on horseback with slightly larger harrier hounds and takes place between September and March. Stoate & Tapper (1993) estimated that only 7% of hunted populations were killed by beagling, implying that the effects on local hare populations are negligible. Furthermore, it has been estimated that nationally only 1,650 (Macdonald *et al.* 2000) to 6,000 (White *et al.* 2000) hares are killed annually by beagling so that any national impact on hare populations from this activity is trivial.

Formal coursing involves competition between pairs of fast running dogs. Stoate & Tapper (1993) estimate that only 6% of hunted populations are killed. Furthermore, only a small proportion of the country is subject to this activity, leading to perhaps as few as 600 hares being killed annually, although there may be additional effects involving the removal of hares from

high density populations to restock coursing areas (Stoate & Tapper 1993, Hutchings & Harris 1996). Overall, however, formal coursing activity has no major impact on hare populations other than local perturbation. This is not necessarily the case for uncontrolled coursing. This will generally be illegal poaching using lurchers (collie-greyhound crosses). The level of such activity is unclear although White *et al.* (2000) quote a figure of 70,000 dogs being used nationally in coursing which could have a direct effect on hare numbers. In areas where coursing takes place, hares are more likely than elsewhere to remain in their forms than flee when approached (Hutchings & Harris 1995). This variation in antipredator behaviour is strong circumstantial evidence for local effects of coursing, although whether it reflects natural selection or learning is unclear. A potentially important indirect effect is that landowners and farmers may try to reduce hare populations simply in order to reduce trespass and poaching (Stoate & Tapper 1993). Hutchings & Harris (1996) found this to be the case particularly for farms without gamekeepers in arable areas of eastern England. Furthermore, White *et al.* (2003) reported that, of the 27% of land managers who considered the hare to be a pest, 41% did so because of the potential encouragement of poaching on their land.

The most significant hunting activity is shooting. Organised shoots typically take place in February, at the end of the pheasant shooting season. Stoate & Tapper (1993) recorded between 28 and 69% of populations were removed by such activity. They also argued that organised shoots tend to have a density-dependent property: because shoots often have the intent of reducing crop damage by hares, farmers are more likely to organise intensive shoots when hare densities are high. Hence, at lower densities, not only will fewer hares be shot, but a smaller proportion of the population would be removed. There is no clear-cut trend for this in the data for six shoots presented by Stoate & Tapper (1993), although the densities concerned ranged from relatively high (13.6 hares per km²) to very high (55.5 hares per km²) and thus lacked the lower densities where the effect is most likely to be observed. According to the National Game Bag Census Data at least 200,000-300,000 hares are currently shot each year (Macdonald *et al.* 2000). In addition to organised game shoots, unknown numbers of hares are shot by landowners and farmers because of concerns associated with damage to agricultural interests. White *et al.* (2003) derived a figure of 6.17 per km² for the maximum culling rate per year of hares from their survey of land managers. Hare populations can apparently sustain such high levels of culling both in the UK and elsewhere (e.g. France - Pepin 1987). However, some models, such as that given by Marboutin *et al.* (2003), suggest that the sustainable harvest rate (i.e. the proportion that can be killed without causing the intrinsic population growth rate to fall below 1) of hare populations is around 30%, although small populations may only sustain $\leq 20\%$ harvest rates. However, shoots tend to take place where hares are abundant and are localised, so it has been argued that immigration as well as production allows populations to recover rapidly (Stoate & Tapper 1993). These authors also suggest that because hare shoots generally take place in localised areas managed for game, with associated habitat management and predator control, conditions are suited to the rapid recovery of the population. The resilience of such populations is reflected in the matrix population model developed by Macdonald *et al.*

(2000), in which long term population reduction becomes virtually impossible if culling is restricted to adults, as is essentially the case for driven shoots in February. However, some have questioned the sustainability of such intensive culling even with active management to assist population recovery, as occurs on game estates. Hutchins & Harris (1996) suggest that game estates act as population sinks whereby favourable habitat in terms of cover, created by the game interest, and abundant food, arising from intensive culling, attract substantial numbers of animals in from neighbouring areas, with implied adverse consequences in terms of hare densities in these implicitly more marginal habitats. However, it is recognised that post-culling hare densities on game estates of 6.4-18 per km² (Macdonald *et al.* 2000) are still higher than the average densities of hares currently found in Britain (2.8-4.9 per km²; unpublished data quoted in White *et al.* 2000) and close to or above the 7.12 per km² average reported by Hutchings & Harris (1996) for arable land. There is thus the possibility that shooting estates, rather than acting as population sinks, could be potential sources for populating surrounding areas, especially if steps are taken to improve habitat quality in such areas to match that on game estates. In the survey reported by Hutchings & Harris (1996), some game estates in the southwest have stopped driven shoots due to low hare numbers, and some in East Anglia have cancelled or postponed shoots. Nevertheless, there is no evidence that low hare abundance in these was generated by hunting; rather the shooting pressure responded, in a density-dependent manner, to hare densities that had declined for other reasons.

Habitat requirements

In intensive agricultural habitats, with relatively limited plant diversity, hares are likely to encounter seasonal gaps in the availability of high quality food (Frylestam 1980, 1986). However, Frylestam (1992) demonstrated that planting green fodder strips, each 3m wide and comprising a range of grasses and herbs, can offer valuable feeding refuges for hares that ensure continuity of food supply in habitats dominated by cereal, oilseed rape and sugar beet crops. Tapper & Barnes (1986) concluded that hares select areas where they have access to a range of crops and other food, and that home ranges expand to include this diversity. Quality of cover is also particularly important in terms of protecting leverets from predation (e.g. Pepin 1989, Goszczynski & Wasilewski 1992, Reynolds & Tapper 1995b). However, there is an upper energetic limit on the extent of range expansion possible. Some authors have thus suggested that small field sizes are generally favourable for hares (e.g. Meriggi & Alieri 1989, Lewandowski & Nowakowski 1993). There may, however, be a trade-off for optimal field size between meeting food requirements, which may be difficult to attain in large monocultures, and minimising predation risk, especially from foxes hunting in field margins alongside woods (e.g. Bresinski 1983). As Goszczynski & Wasilewski (1992) pointed out, hares may lose their speed advantage over foxes when away from open fields. Tapper & Barnes (1986) also showed how hares shift their activities between fields according to crop development and also how daytime refuges can lie outside night-time foraging ranges. Similarly complex spatial and temporal patterns of space use in agricultural landscapes were observed

in France by Reitz & Leonard (1994). There thus may be no simple answer as to what constitutes optimal hare habitat. Instead food and cover requirements can perhaps be met in a variety of ways. A number of authors have suggested that these conditions are most likely to be met in habitats that are relatively diverse (e.g. Tapper & Barnes 1986, Lewandowski & Nowakowski 1993, Vaughan *et al.* 2003). However, others have found no positive relationship between hare abundance and diversity (Meriggi & Alieri 1989, Marboutin & Aebischer 1996). Hutchins & Harris (1996) emphasise the importance of habitat richness, i.e. the number of different habitats present rather than the diversity of those habitats. This is in direct contrast with the findings of Vaughan *et al.* (2003) who observed a negative relationship with habitat density. A plausible explanation for these differences is interaction between key parameters of habitat density, habitat diversity and field size (Vaughan *et al.* 2003). These authors make some initial recommendations for habitat management aimed at encouraging hares. However, defining the optima for the key parameters remains elusive. For instance, adult hares from arable landscapes are in better condition than those from pastoral landscapes but this does not reflect differences in dietary quality or foraging habitat quality (University of Bristol 2003).

Despite the above uncertainty, it has been clearly demonstrated that landscape management can increase hare densities in the UK. Brockless (1995) reported an increase in hare density from 5 per km² to 65 per km² over three years following both habitat management and predator removal. The habitat management consisted of maintaining field sizes at 8-10ha, increasing the number of crop types and restoration of hedgerows along with the provision of field boundary strips, beetle banks and conservation headlands (Tapper 1999). The raised hare densities were maintained throughout the 1990s (Boatman *et al.* 2000). Stoate *et al.* (1994) suggested that fox control is required to reap the full benefits of habitat improvement in terms of increased hare densities. This view is contentious, despite the circumstantial evidence of links between hare densities and fox predation. Hare densities are, in general, substantially higher on kept game estates than elsewhere but this does not necessarily reflect the consequences of reduced predation pressure due to fox control. In pastoral landscapes, no benefit of the presence of a gamekeeper is apparent for hare densities, once habitat richness is taken into account (Hutchings & Harris 1996). Hence, this offers no evidence of a direct effect of predator control, and it is possible that increased habitat richness, and hence enhanced hare densities, reflect habitat management designed to promote game interests. In arable areas, the presence of gamekeepers is positively related to hare densities, once habitat richness is accounted for (Hutchings & Harris 1996). Nevertheless, the authors dispute that this reflects positive benefits of predator control, suggesting instead that hares on farms without keepers, particularly those in the arable landscapes of eastern England, are heavily culled to reduce poaching and illegal coursing. However, there are no data suggesting that such culling has any greater impact on hare numbers than the organised shoots typical of game estates that remove up to 69% of adult populations (Stoate & Tapper 1993). Hence, the more parsimonious explanation is that predator control in these landscapes is beneficial for hare numbers.

One approach to dealing with the apparent complexity of interactions underlying hare population ecology would be to use the currently available data to develop a spatially explicit model of hare metapopulation biology. This would be used to predict long-term population trends for the complex mosaic of patches of optimal habitats, sometimes offering predator control for game interests, potentially acting as sinks for more extensive sub-optimal habitats with low hare density, no predator control and limited culling. The responses, at the metapopulation level, to different forms of habitat management, could then be simulated to refine recommendations for hare conservation under various stewardship schemes.

Population trends

Data on changes in actual population size for hares are limited. However, because hares are hunted as game, there are extensive records for game bags, which represent valuable information on trends in relative abundance. In the UK these show a clear decline from the early 1960s and through the 1970s (Tapper & Parsons 1984). Similar declines have been observed throughout Europe, including Poland (Pielowski & Raczynski 1976), Sweden (Frylestam 1979), Denmark (Strandgaard & Asferg 1980), Hungary (Kovacs & Heltay 1981), Netherlands (Broekhuizen 1982), Germany (Spittler 1992) and Croatia (Sostaric *et al.* 1991). Game bag records offer an index of abundance whose relationship to actual numbers may be influenced by a number of factors such as weather, habitat characteristics and, in particular, hunting effort. For instance, it is known that the proportion of the actual population killed by shooting varies substantially (28% to 69% of population present in the data presented by Stoate & Tapper 1993). There is also the possibility that the proportion shot increases with actual density, as more intensive shoots are likely to be organised when hares are abundant than when they are sparse (Tapper 1987b). Nevertheless, despite such systematic biases, that might exaggerate the apparent trends in game bag records, the broad agreement across data sets suggest that the general decline across Europe has been real. There is some evidence that game bag records and sightings for the British Field Sports Society's survey have stabilised since the mid-1980s in the UK (Stoate 1993). Similarly Newsome & Noble (2003) showed no overall change in hare presence recorded during Breeding Bird Surveys between 1995 and 2000, although there was a significant decline in the southwest. What this means in terms of numbers is unclear, however, because elsewhere there are indications that the decline has not only been halted but reversed. For instance, spring counts in Bavaria have steadily increased in recent years (Kilias & Ackermann 2001).

There have been a number of estimates made of hare population densities to quantify what the observed trends mean for the total number of hares in Britain. Tapper & Stoate (1992) estimated that the pre-breeding adult population was approximately 1 million based on an estimated annual game bag of 390,000 hares assuming that this represented, on average, 40% of the total population. Hutchings & Harris (1976) suggested, using these data but

making alternative assumptions regarding the proportion of hares killed and density estimates, that the February population in the early 1990s was approximately 425,000. Robertson *et al.* (1989) derived estimates based on hare density, using Barnes & Tapper's (1985) night count methodology, in areas with and without gamekeepers. They suggested estimates of between 1,250,000 and 1,900,000 hares overwinter in Britain, the range reflecting assumptions about the impact of game keeping on hare densities. Hutchings & Harris (1996) point out that such estimates are based on a small number of sampled sites, all in England and with areas of low hare densities probably under represented. The 1991-1993 National Hare Survey was thus undertaken using the line transect approach described by Langbein *et al.* (1996) with a stratified random sampling process applied to the ITE land classification scheme. This generated a broadly accepted estimate of 817,520 ($\pm 95\%$ confidence interval of 137,251) hares present overwinter in Britain (Hutchings & Harris 1996). The survey was repeated during the winters of 1997-1999. This was briefly reported by White *et al.* (2000) who quoted an estimate of 752,608 \pm 37,697 hares. ***There thus appears to have been no statistically significant overall change in hare numbers in Britain during the 1990s, although White et al. (2000) state that there were significant reductions in arable areas in southern England, northeast England and eastern Scotland.*** It should also be recognised that any comparison between two data points (i.e. the 1991-1993 estimate and that for 1997-1999) needs to be treated with caution, especially given that hares can be vulnerable to severe overwinter weather (e.g. Bresinski 1976). However, because each national hare survey has carried out over two successive winters, such variation will have been smoothed.

Factors influencing hare population trends

i. Disease

There has been speculation that disease, notably EBHS, could have led to declines in hare densities (e.g. Sostaric *et al.* 1991). However, although epidemics can cause substantial local population reductions, there is no strong evidence that the disease has made any significant contributions to the long-term pan-European population declines (Gavier-Widen & Morner 1993, Frolich *et al.* 1996, 2001).

ii. Predation

There has been a steady increase in the numbers of foxes killed on game estates since the 1980s (Tapper 1992, 1999). It is unclear how this relates to actual fox densities, especially as game estates cover only approximately 12% of the land area. However, White *et al.* 2000 agree that fox populations are increasing in East Anglia, parts of Wales, the Pennines and eastern Scotland. There have been suggestions that increased predation has contributed to some hare population declines (e.g. Tapper & Stoate 1994). However, as Hutchings & Harris (1996) point out, increases in the numbers of foxes culled have coincided with a period over which hare numbers have remained relatively stable on game estates (Stoate 1993). Nevertheless,

increased predation could be one mechanism underlying reduced hare densities, especially if this is linked to habitat changes that reduce the effectiveness of the hare's well-developed antipredator strategies. Furthermore, hare populations on game estates may be buffered, by the activities of gamekeepers, against general increases in fox abundance. Fox densities are unlikely to be determined by hare abundance given the range of alternative prey generally available. This lack of density-dependence suggests that the impact of fox predation may be proportionately greater at low hare densities and thereby constrain population recovery.

iii. Habitat quality

It is widely considered across Europe that agricultural intensification is the generic cause of declines in hare populations (e.g. Broekhuizen 1976, Strandgaard & Asferg 1980). However, the specific changes in agricultural practices generating such consequences remain unclear. In open agricultural habitats in Hungary, hare ranges are influenced by strong preferences for small fields of alfalfa and pasture (Kovacs & Buza 1992). The authors thus suggest that the decline in hare populations in Hungary, apparent from game bag records during the 1960s (Kovacs & Heltay 1981), arises from increases in mean field size with consequent declines in total field edge length. However, optimum field size for hares is a complex issue. Although small field sizes potentially offer greater habitat richness, thus increasing the prospect of year round food availability, they may not offer the optimum open aspect for adult hares to detect and avoid slower predators such as foxes (e.g. Hewson 1977, Meriggi & Verri 1990).

In the UK high densities of hares can still be maintained in arable landscapes, typical of eastern England, and here the decline in numbers, during the last century, has been less marked than in the pastoral areas of west and south-west England where hare densities are now, in general, low (Hutchings & Harris 1996). Thus there may be different ecological processes occurring in these contrasting landscapes. The relatively low numbers of hares in pastoral landscapes might appear to contradict the origins of the species in open steppe grassland habitats and the importance of grass in their typical diet (e.g. Homolka 1982, Frylestam 1986). McLaren *et al.* (1997) suggested that habitat fragmentation may be an important contributor to the decline in pastoral landscapes; pockets of good quality habitat becoming isolated oases in a generally hostile environment. The authors suggest, along with Hutchings & Harris (1996), that patches of arable land may be important for retaining hare populations but their absence appears an unlikely cause of the decline. Instead it seems more probable that the majority of the pastoral landscape has become less hospitable. Possible causes for the impoverishment of the pastoral landscape include grassland improvements leading to increased domestic stocking rates, given that hares are reported to avoid fields with livestock (e.g. Barnes *et al.* 1983). A potentially important factor has been the substantial increase in grass grown for silage rather than hay. The consequent repeated cutting from May onwards could substantially reduce leveret survival, just as the reproductive success of ground nesting birds such as lapwings has declined (e.g. O'Connor & Shrubbs 1989). Tapper & Barnes

(1986) suggest that in arable landscapes, reduced diversity through increasing cereal monoculture may limit food supply once the crop has grown away and become too fibrous to be palatable. This is considered a possible reason for the decline in hares in these areas (e.g. Hutchings & Harris 1996). ***However, the decline of hare populations in arable landscapes has been less marked than in pastoral areas. Perhaps the substantial increases in the planting of winter rather than spring cereals, especially of barley (Robinson & Sutherland 2002), has been beneficial by providing food for early born leverets which are then subject to limited disturbance from agricultural practices (Pepin 1989). Another major change in farmland landscapes since the 1960s is the reduction in hedgerows. In some cases this could prove beneficial to hares in terms of predator avoidance. Could it be that major changes in the agronomy of cereal production over the last 40 years have buffered some of the negative effects of other factors? Commensurate with this hypothesis are the unpublished data, quoted by White et al. (2000), showing relatively high leveret survival in East Anglia amongst those born between January and March. Comparison with similar data on leveret survival in the currently less favourable pastoral landscapes would inform management actions. This might, for instance, precipitate recommendations that where possible some winter cereal is included in the land use mosaic.***

Nevertheless, if the 1997-1999 National Hare Survey survey does reveal an ongoing and significant decline of hare density in some arable dominated areas in England, as suggested by White *et al.* (2000), the causes will need to be understood and remedies implemented.

It is clear that hare populations can be maintained despite very substantial hunting pressure (e.g. Pepin 1987 & 1989, Stoate & Tapper 1993). Thus some have suggested that there must be compensatory population processes operating, perhaps reflecting density-dependent productivity and recruitment (Broekhuizen 1979, Frylestam 1980). However, as Marboutin & Peroux (1995) point out, if ecological processes involving habitat quality reduce recruitment, populations may become more sensitive to additional sources of mortality such as predation, disease or hunting. It is against this background that we need to seek specific habitat related answers for the pan-European population trends over the past 40 years that can be turned into management plans to conserve hare numbers.

Pest status

The hare is generally considered a relatively minor problem species in terms of damage to agricultural and forestry interests. However, there are very limited data available regarding such damage. Hares will forage on a wide range of crops and, when available, will spend much of the late winter-feeding on winter cereals (Tapper & Barnes 1986). Crawley (1989) showed that rabbit grazing on winter wheat has a cumulative negative effect on yield, for which subsequent regrowth does not compensate, while McKillop *et al.* (1996) estimated losses for winter wheat to be 1% per rabbit per ha. The high hare

densities reported on game estates (e.g. 13.6-55.5 per km² Stoate & Tapper 1993, 65 per km² Brockless 1995), particularly if concentrated on the available cereal fields overwinter, indicate that hares can potentially be sufficiently locally abundant to cause economic loss, bearing in mind that an adult hare is approximately twice the weight of an adult rabbit. Control may thus be economically justified in some circumstances and 15% of the 106 farmers surveyed by White *et al.* (2000) considered the hare to be a pest. Similarly, White *et al.* (2003) reported that 27% of land managers regarded the brown hare as a pest. Eighty five percent of these gave the reason for this pest status as being agricultural or forestry crop loss.

Hares can also cause damage to forestry interests especially to young trees, which may be killed. Wray & Harris (1994) surveyed foresters by questionnaire. Hares were most common and apparently caused most damage in eastern England. However, there is some evidence that trees damaged early in their lives can recover losses by extra subsequent growth.

Conservation status

Primarily because, for the past forty years, hare populations have been in decline across much of Europe, the species was included in the UK Biodiversity Action Plan (Anon. 1995). The species is not threatened; indeed it is more abundant than a number of truly native mammal species not included in the BAP. However, it can be regarded as an important indicator species for the general quality of lowland agricultural habitats. Furthermore, promoting biodiversity is not simply about saving rare species but also ensuring that common species remain common (Tapper 2000). The key target for the plan is doubling the spring population by the year 2010. There is no biological basis for choosing this challenging target but Tapper (1999) suggests ways of approaching this through habitat management in the context of current game keeping practices. It is envisaged that agr-environment schemes will be the main tools by which the target will be met. Tapper (1999) argues that the species must remain a game animal because this encourages its conservation. It is certainly true that hare densities are high on game estates and that this partly reflects habitat management to promote game interests in general. The role of predator control is more controversial. White *et al.* (2000) point out that Reynolds & Tapper (1995b) showed mean hare densities were 15 per km² in an area without intensive predator control, compared to densities as high as 60 per km² in a comparable area with intensive predator control. Average hare densities, even in arable landscapes, are less than half of 15 per km². Since the aim of the Biodiversity Action Plan is to double spring hare numbers, there is clearly scope for hares to exist at double the current densities without the need for intensive predator control. White *et al.* (2000) thus contend that “the available data suggest that predator control is not essential for the conservation of hares, but it is to produce a large shootable surplus.” In any case, encouraging such high hare densities, across large tracts of arable land outside game estates, might lead to hares being considered to cause widespread, rather than just local, damage to cereals and to increase concerns regarding illegal poaching.

The low densities in pastoral landscapes compared to levels before the 1960s, especially in western England, suggests that these offer the greatest scope for increasing densities and, hence, it is here that conservation efforts should be focussed. University of Bristol (2003) recommends that enhancing survival should be targeted, based on a model that suggests raising adult survival has a proportionately greater impact on population growth than does increasing survival of other age classes. The sensitivity analysis of their population model showed that a five per cent change in adult survival had a greater impact on annual population growth rate than the same percentage change for any other parameter. However, variation in survival rates is greater for leverets than for adults (see description of Population Biology above). The absolute effect of leveret survival may thus be as or more important than adult survival and, hence, could also be a key target for action. Marboutin *et al.* (2003) have demonstrated that leveret survival is more important than any other demographic parameter for population growth rate in French hares. Their analyses taking into account the observed empirical variation in each parameter, as advocated by Haydon *et al.* (1999). Similarly, differences in hare densities between habitats in Austria are explained by differences in juvenile survival rates (Hackländer *et al.* 2004). Furthermore, leveret survival is known to be relatively variable between habitats, contrasting with the stability, even for declining populations, of productivity (e.g. Broekhuizen & Maaskamp 1981) and adult survival (e.g. Marboutin & Peroux 1995). Populations experiencing poor leveret survival between March and August can persist, and may even appear to be stable, as in the model developed by White *et al.* (2000). However, these populations are also highly sensitive to changes in leveret survivorship. This model also suggests that current hare populations are not necessarily producing large surpluses of animals to buffer hunted populations (White *et al.* 2000). ***Perhaps leveret survival should be a specific target for conservation action. Unfortunately comparative data are lacking on this population parameter across habitats where hare densities vary. Hence, as yet we do not have enough information to design habitat management to specifically enhance leveret survival.*** The relatively high hare densities in areas where predator control is carried out suggest that this might be beneficial in some circumstances but, as White *et al.* (2000) point out, perhaps not essential. ***An alternative approach to reducing predation is to enable hares to exploit fully their natural anti-predator strategies of avoiding detection (e.g. Broekhuizen & Maaskamp 1980) or escaping (e.g. Hewson 1977, Holley 1993, Hutchings & Harris 1995) as shaped by evolution. We might do this by managing habitats such that they offer the appropriate combination of cover, open aspects and food availability. The approach is to influence the predator-prey relationships through habitat modification to increase the numbers of prey (Schneider 2001, Vaughan *et al.* 2003).*** However, this will need to complement management for other biodiversity initiatives and be agronomically viable. For instance, the availability of some large winter cereal fields seems an important component of the matrix of habitat richness required to maximise hare density. The provision of such fields might conflict with optimal action plans for other species, although other initiatives such as the provision of some woodland and fallow land would not (Vaughan *et al.* 2003). Nevertheless, there are encouraging signs emerging from the pilot

Arable Stewardship Scheme, where brown hares densities have increased significantly on participating farms in comparison to nearby non-agreement farms (Browne 2004). Hence, extension of these measures nationally, for instance, as Arable Options under the Countryside Stewardship Scheme or as part of Entry Level Stewardship, could have a substantial positive effect on hare numbers.

An action for the Biodiversity Action Plan (Anon. 1995) is to “Review the use of legislation pertaining to shooting and selling of hares in the light of research findings on the seasonality of reproduction.” This is action for CCW, DOE, EN, JNCC, SNH, SOAEFD and WO under item 5.1.4 of the plan in relation to policy and legislation. Intensive annual culls by driven shoots, generally in February, can have enormous impacts on local hare populations, as shown by the model developed by White *et al.* (2000). This model does not allow for immigration. However, the areas hunted are normally small in size, and so immigration from surrounding populations can, given adequate productivity, usually buffer hunted hare populations. With reduced densities arising from reduced habitat quality, surrounding populations may be less able to produce the surplus animals required to achieve this. White *et al.* (2000) nevertheless conclude that “.....**a close season would be unlikely to have a large impact on the hare population since brown hares grow fast and, from October onwards, many of the surviving recruits would also be killed during the open season**”. Furthermore, any impact of a close season would probably be particularly limited in areas, such as western England, where organised hunting has already declined in response to reduced hare numbers. It is also clear that declines in hare abundance have occurred elsewhere in Europe, despite the putatively greater protection afforded by close seasons on hunting.

Although the introduction of a close season currently seems unlikely to offer significant benefits in terms of conservation it could be argued that animal welfare would be enhanced. This would be in terms of reducing the number of female hares killed when nursing wholly dependent young. The data on pregnancy, gestation length and weaning indicate that the period when the majority of females would have litters that were currently reliant on them would last from around mid-March through to mid-October. Females do become pregnant in January so a close season beginning in mid-February might be more appropriate. Attaining virtually complete prevention of nursing hares being killed would require an open season lasting only from mid-December through to the end of January. However, consideration would need to be given to allowing landowners and farmers the opportunity to cull hares during the close season in relation to crop and forestry damage, especially in eastern England. This is the case elsewhere in Europe, for instance, in Denmark where licences can be issued for this purpose. The extensive organised hare shoots that currently take place in February are considered by many participants to have a pest control as well as sporting context (Stoate & Tapper 1993). **Hence, the introduction of a close season for hunting hares might have more limited overall benefit, in terms of welfare, than anticipated.** Indeed most culling that currently takes place from March onwards is likely to be in the context of pest control, except for illegal

poaching activities. Culling of hares in order to reduce illegal poaching and coursing, as is apparently common practice in eastern England, will also often take place during any proposed close season. This would offer further ambiguity with regard to welfare issues. In this context, the negative welfare consequences of culling potentially lactating hares would need to be set against possible gains in terms of reducing the use of the less humane methods associated with illegal activities.

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