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Predation by foxes *Vulpes vulpes* on brown hares *Lepus europaeus* in central southern England, and its potential impact on annual population growth

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A computer model was used to simulate processes of reproduction, growth and loss occurring during twelve months within a real-world brown hare *Lepus europaeus* L. population in a mixed farming area of central southern England. Model parameters representing hare density, and the density and diet of foxes *Vulpes vulpes* L., were derived from field studies, whereas likely values for other parameters were set on the basis of studies performed elsewhere. Simulations were created to represent a) the hare population on an area of 11 km^2 comprising several fox territories; and b) the hare population on individual fox territories. In the larger-scale simulations (a), the number of hares eaten by foxes easily exceeded their breeding density and amounted to 76-100% of annual production. The hare population could not have withstood more than a very low additional mortality without declining. When fox predation was set to zero, the final density of hares in the model was 3 to 6 times that produced when fox predation occurred. Simulations for individual fox territories (b) suggested that variation in territory size and social group composition of foxes introduced significant local variation within this overall picture. We conclude that the hares eaten by foxes were a substantial loss relative to productivity. This conclusion was robust in the face of estimation errors or changes in underlying assumptions of the model. This study describes the extent of fox predation on hares and its potential impact on hare population growth. Because the degree of compensation between mortality factors was unknown, the study does not show that fox predation *per se* limited the hare population. Nevertheless, our findings are a necessary adjunct to experimental evidence and population studies which suggest that red foxes play a major role in hare population dynamics in many environments.

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The role of predators in the demography of their prey is a subject of abiding interest in ecology, but progress in understanding it has been impeded by semantic confusion and by the difficulty of acquiring incisive evidence. The question of whether predation limits or regulates a prey population can be answered only through careful experimental design (Sinclair 1991, Boutin 1992).

For predation in terrestrial vertebrate communities, the commonest type of experiment has been the predator removal experiment, in which predators are removed from

a treatment area, while prey population dynamics are monitored both on that area and on an unmanipulated control area (e.g. Chesness et al. 1968, Balser et al. 1968, Trautmann et al. 1973, Duebbert & Lokemoen 1980, Parker 1984, Marcström et al. 1988, 1989, Tapper et al. 1991, 1993, and in press). Typically prey productivity is greater when predation is reduced; in some of the studies cited breeding density also fluctuated around a higher mean level. Such results demonstrate limitation, but to infer population regulation it is necessary to demonstrate full reversibility of treatment effects (e.g. Tapper et al. *op.cit.*) or at least to obtain additional evidence of density-dependence (Sinclair 1991, Boutin 1992).

Although predator-removal experiments can demonstrate that a prey population is limited or regulated, they can still be misleading, and for several reasons other kinds of evidence are a necessary adjunct to experimentation. Without elaborate and unwieldy designs, predator-removal cannot usually dissociate the roles of individual predator species, since removing only one or two species may facilitate increased (compensatory) predation by those remaining (e.g. Trautmann et al. 1973, Parker 1984). If this is the case, the usual extent of predation in the intact system by the species removed will be underestimated, and this may also lead to incorrect conclusions about their impact in the absence of competitors. Furthermore, the degree of limitation revealed depends on the effectiveness of the predator removal, which has rarely been assessed. Both of these shortcomings could lead to incorrect management decisions.

An obvious precaution is to quantify the consumption of prey by predators and compare this with the size of the prey population. However, if a prey population is very productive it is quite feasible for the annual consumption of prey to exceed its pre-breeding density (Reynolds & Tapper 1995), and even its post-breeding density. A comparison of consumption by predators with the standing population of prey at yearly intervals then becomes meaningless. It is better to compare consumption with the estimated productivity of the prey (e.g. Erlinge et al. 1984), but the timing of predation also determines its impact on productivity.

A solution to this problem is to construct a sequential model of prey numbers where production of young and loss through predation are implemented at shorter, more biologically meaningful time intervals. Since any process defined in the model - such as predation by foxes *Vulpes vulpes* - can be altered or switched on and off at will, it is possible to compare the dynamics of the modelled prey population under a variety of conditions, which would be impracticable or very expensive to contrive in the field. Such a simulation does not test any hypothesis, but it is a valuable tool to understand whether and how quantitative data on predation are consistent with experimental results.

We studied the density and diet of foxes in central southern England, and simultaneously monitored the numbers of the small game species that formed the basis of their diet (Reynolds & Tapper 1995). In the present paper we focus on one of those species, the brown hare *Lepus europaeus*, and use a simulation model of the kind just described to assess the extent and potential impact of fox predation on the hare population.

Methods

Study site and field estimates

The 11 km² study site, centered around West Woodyates in northeast Dorset (50°55'N, 1°55'W), is described by Reynolds & Tapper (1995). During 1985-87, fox territory boundaries, fox social group size, and fox diet were determined as described in Reynolds & Tapper (*op.cit.*). Hares were counted at night, field by field, using a spotlamp technique based on Barnes & Tapper (1985). Counts were made in February-April, while crops were still sufficiently short, and again after harvest in October-December. The precise dates depended on farm work and weather conditions.

No hares were deliberately killed by man within the study area. Besides foxes, other hare predators were present, notably buzzards *Buteo buteo* L., crows *Corvus corone* L., stoats *Mustela erminea* L., and cats *Felis catus* L. Regular predator culling - affecting foxes, crows, and stoats - was practised on only one 4.75 km² farm. This was suspended at our request during 1987.

Basic design of the model

The hare population model proceeded through monthly iterations from January to December inclusive (Fig. 1). For each month, production of leverets was estimated from the current population of adult females and the leveret production rate for that month. Each monthly cohort of leverets was tracked separately through the model, implementing monthly growth rates, non-fox mortality and fox predation, in that order.

The hare population and associated parameters were expressed in real numbers. Effectively this described a homogeneous, unbounded hare population, which was less susceptible to extinction at low densities than a model working in integers.

Wherever possible, model parameters were estimated values derived from field and laboratory work. Other values and relationships were based on literature published by other authors (Table 1). Where choices had to be made, we adopted a conservative policy, selecting as starting points (default values) parameters and relationships that would minimise the apparent impact of fox predation on hare numbers within the model (see Appendix).

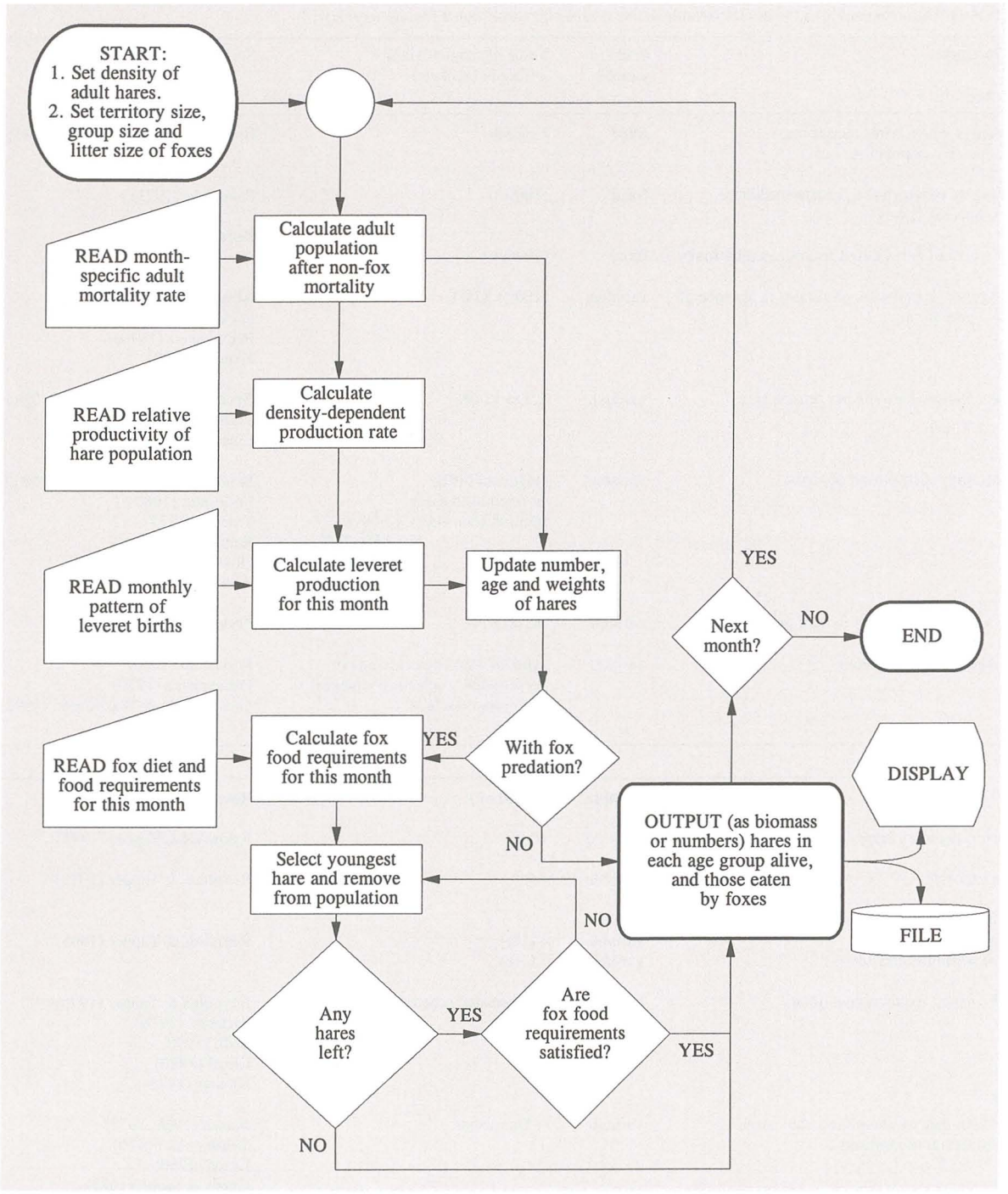

Figure 1. Main processes in the computer model. The modelled hare and fox populations are initialised in January with figures based on field study. For each month from January to September, the numbers and biomass of hares in each monthly age class are updated from estimates of leveret production, leveret growth, consumption by foxes, and other mortality.

Use of the model

The model was initialised with a starting population so that numbers matched those estimated at the date of the late-winter hare count (usually early February). It was then run with the default values listed in Table 1 and the output at the appropriate date was compared with the end-of-year hare count (usually early December). Model pa-

Table 1. Parameters used in the model, default settings, variability and source literature reviewed.

Parameter	Fixed or variable	Value or range (default setting in brackets)	Source or relevant literature
Hares			
Age at which hares recruit into countable population	fixed	1 month	Broekhuizen & Maaskamp (1981)
Degree to which fox predation additive to non-fox losses	fixed	(100%)	Pielowski (1971) Petrusewicz (1970)
Percent of hares killed and/or eaten by foxes	fixed	(100%)	
Age/sex-specific survival rates in absence of fox predation	variable	(100 to 87%)	Abildgård et al. (1972) Frylestam (1980) Petrusewicz (1970) Hansen (1992)
Annual productivity per female hare	variable	2.3 to 12 (9)	Broekhuizen & Maaskamp (1981) Frylestam (1980) Lincoln (1974)
Monthly distribution of births	variable	staggered births or fixed birth dates (default four litters: 1 March 22% 1 May 33% 1 July 33% 1 September 12%	Broekhuizen & Maaskamp (1981) Frylestam (1980) Lincoln (1974) Raczynski (1964) Hewson & Taylor (1975) Abildgård et al. (1972)
Density-dependence in hare production	variable	on/off (on)	Frylestam (1980)
Age-specific predation	variable	random with respect to age or preferentially selecting youngest individuals (selective)	Frylestam (1980) Petrusewicz (1970) Goszczynski & Wasilewski (1992)
Foxes			
Territory size	variable	(2.72 km^2)	Reynolds & Tapper (1995)
Non-breeding adults per territory	variable	(0.5)	Reynolds & Tapper (1995)
Litter size	variable	(4)	Reynolds & Tapper (1995)
Proportion of hare in fox diet: a) cubs b) subadults and adults	 variable variable	 (11%) (17%)	Reynolds & Tapper (1995)
Fox food requirements (total)	fixed	(age-related schedule)	Reynolds & Tapper (1995) Sargeant (1978) Stahl (1990) Lloyd (1980) Kleiber (1975)
Mean date of unreplaced cub losses (dispersal or mortality)	variable	1 December	Jensen (1968, 1973) Storm et al. (1976) Lloyd (1980) Harris & Smith (1987) Trewhella et al. (1988)

rameters were then constrained until the output matched the count. This was done by altering either hare birth rate, non-predation loss rate, or the date of fox cub dispersal; all of these were variables that we were unable to measure in our field study. Having produced one or more plausible simulations, the next stage was to eliminate the loss of hares due to fox predation from each one, and re-run the model. The difference in outcome with and without fox predation illustrates the potential impact of fox predation.

We could simulate either the hare population in the entire 11 km² area, or the local population within a single fox territory. Inevitably, there is a trade-off between precision and generality. Local simulations are more specific, but the fox diet parameters and hare counts had wider errors attached because of smaller sample sizes; estimates of hare numbers at this scale may also be more influenced by local movements of hares. The larger-scale simulation is less influenced by estimation errors or hare movements, but requires interpolation to produce mean estimates of hare numbers, fox numbers, diet, etc. for the entire area and study period. The smaller territory-specific simulations were based on territories investigated during 1987, when predator control was suspended and fox family groups remained unchanged throughout the period considered.

The effect of uncertainty in model parameters was studied through a form of sensitivity analysis, varying each key relationship or parameter in turn, and measuring its effect on conclusions.

Results

Large-scale simulation

Starting values (Table 2) for the large-scale simulation (representing the entire 11 km²) were based on average values of hare density, fox density, and fox diet for the entire study. The target hare density was set to equal the starting density. Using these data, and adopting the conservative default settings, the model hare population grew to exceed the target by 21 hares/ha at the end of the year (2.4 times the starting density). The model could be constrained to fit the target density in various ways: by reducing the reproductive rate of hares (simulation 1, Table 2); by increasing the non-fox mortality of hares (simulation 2); or by delaying the dispersal of fox cubs (and fine-tuning the model through adjustment of the hares' reproductive rate - simulation 3). These options all represent plausible alternative simulations of the field situation though the field situation is most likely to have been a hybrid of all three scenarios. If we had overestimated fox density and predation, still greater constraints on production and survival would have been necessary to fit the model to the field counts. None of the variants involved adopting unrealistic values for any parameter. The relative merits of each are considered below.

Simulation 1: Hansen (1992) has shown that in a modern farming system leveret production can be as low 4 to 6 leverets/ adult female, 33% to 50% of physiological maximum in the terms of our model. Arable crop production at Woodyates was intensive, so the production rate of 47% adopted in this simulation is not unlikely. In Hansen's study, this low productivity went hand-in-hand with a very low leveret survival rate of 66% to 75% per month, whereas simulation 1 assumes no mortality of hares except through fox predation.

Table 2: Large-scale simulations of hare population dynamics on the entire 11 km² study area. Initial settings of model parameters were adjusted individually to create plausible simulations 1 to 3, in each of which final hare density equals the starting density. For each simulation, the difference in outcome when fox predation terms are dropped from the model represents the impact of fox predation. See text for further details and compare with Appendix Table I.

	Simulation 1	Simulation 2	Simulation 3
Main settings (other values as in text)			
initial hare density (hares/km²) on 1 January	15.0	15.0	15.0
productivity (% of physiological maximum)	47	75	68
monthly adult hare survival (%)	100	97	100
monthly leveret survival (%)	100	93	100
fox-cub dispersal (100% by 1st of month)	SEP	SEP	JAN
Model outcome 1 (with predation by foxes)			
leverets produced (individuals/km²)	37.1	53.1	54.9
total number of hares eaten (individuals/km²)	37.1	40.1	55.3
total hare biomass eaten (kg/km²)	46.6	46.6	78.8
final hare density (individuals/km²) on 31 December	15.0	14.7	14.6
final hare biomass (kg/km²) on 31 December	41.9	41.2	38.9
Model outcome 2 (without predation by foxes)			
leverets produced (individuals/km²)	39.0	56.2	57.9
final hare density (individuals/km²) on 31 December	54.0	43.5	72.9
final hare biomass (kg/km²) on 31 December	150.5	120.5	202.8
Difference in final population (outcome 2 - outcome 1)			
number of hares (individuals/km²)	39.0	28.8	58.3
hare biomass (kg/km²)	108.6	79.3	163.9

Table 3: In all simulations, consumption of hares by foxes was estimated from field measures of fox density and diet. In simulation 2, model output was brought in line with field estimates of hare abundance at each end of the year by introducing additional mortality. This table shows the relative contributions of hares eaten by foxes and the additional mortality to the dynamics of the modelled population. The population could not have withstood much non-fox mortality without declining.

	Weighted* mean monthly mortality (in %)	
	Percent eaten by foxes	Percent additional mortality
Adult females	1	3
Adult males	1	3
March-born leverets	8	7
May-born leverets	64	7
July-born leverets	60	7
September-born leverets	25	7
All leverets	31	7

* weighted by the number of hares in each age group at the beginning of the month

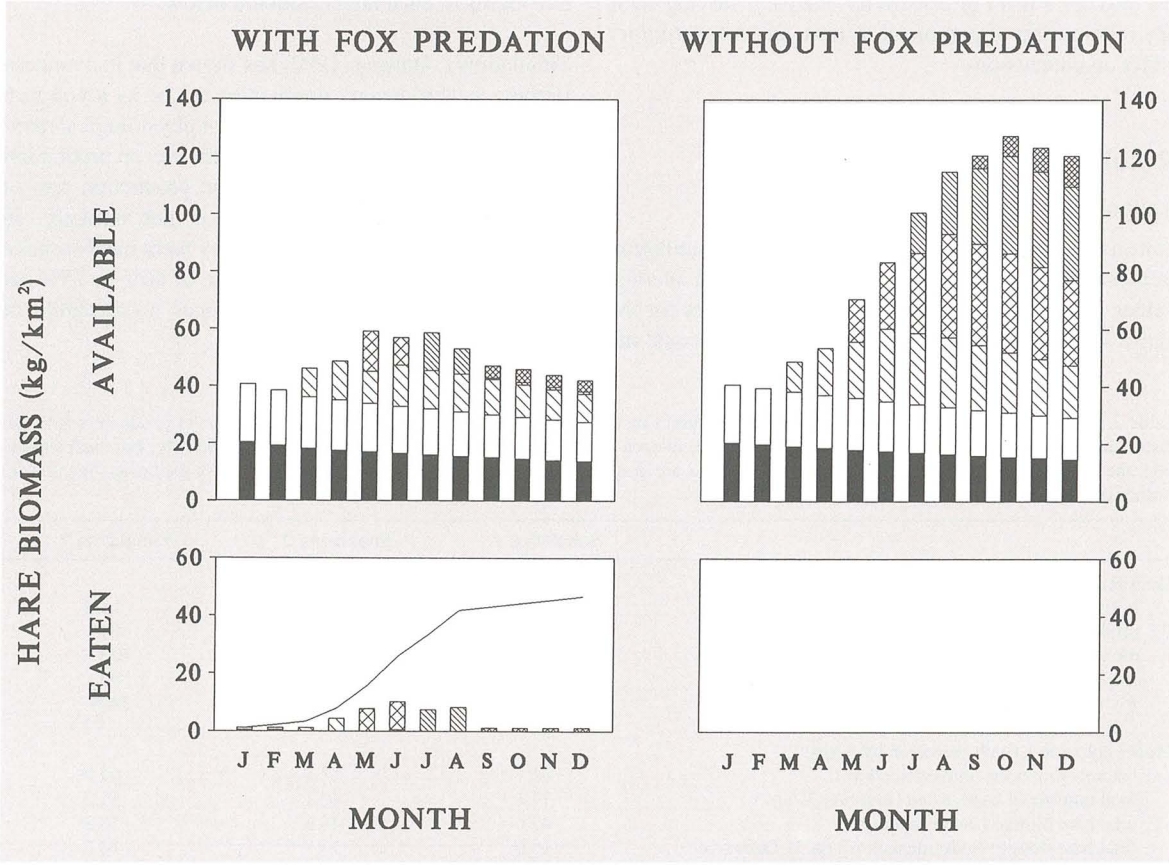

Figure 2. Example of outputs from the model for one simulation (i.e. large-scale simulation 2, Table 2). Each side of the figure represents hare biomass dynamics within a single year, either with (left) or without (right) fox predation. In the left-hand simulation, hare productivity is set at 75% (the maximum likely mean level), and by introducing additive non-fox mortality the model is constrained to return to its initial level of 15 hares/km^2: this corresponds to a plausible simulation of field events. The right-hand simulation retains the same settings, except that fox predation is disabled. The difference between right and left-hand parts of the figure indicates the impact of that predation on population dynamics of the hare within the year. The upper histograms represent the biomass of hares available for fox predation each month after other forms of mortality have taken place. Adult male and female hares are represented by filled and open bars respectively, and each successive cohort of leverets (born March, May, July, September) by a different hatch-pattern. The biomass available to foxes simultaneously increases through reproduction and growth, and decreases through fox predation and (in this simulation) additive non-fox mortality. The lower histograms show the biomass of each age-class of hares actually eaten by foxes, the line showing the cumulative total.

Simulation 2: To match output with target hare density, it was necessary to raise monthly non-fox mortality rates to 3% for adults and 7% for leverets. This corresponds to 69% annual survival for adults, and 74% survival over a 6 month growth period for leverets, similar to survival figures obtained by Abildgård et al. (1972) for hares on an island without foxes. This non-fox mortality was very small compared with the consumption by foxes (Table 3), suggesting that the hare population would actually support very little additive non-fox mortality without declining.

Survival of leverets varied with birth-date (Table 3), largely because of the seasonal pattern of food requirements for a breeding fox group, but also because of our assumption that young leverets were more vulnerable than older ones. On average, hares consumed in this simulation weighed only 1.162 kg.

Simulation 3: It is unlikely that all fox cub dispersal took place as early as 1 September, since tagged male cubs were observed on the area up to late November. In Bristol, although male cubs were twice as likely to disperse as females, only 87% of male cubs dispersing in their first winter had done so by 31 December (Harris & Trewhella 1988). Also, since we do not believe the Woodyates area to have been any more productive of foxes than surrounding land, we might expect that outward dispersal was partially offset by the temporary presence of other itinerant juveniles throughout the winter period.

The result of eliminating fox predation from the model

In these simulations of the entire study area, fox predation accounted for 76% to 100% of the annual production of hares, and in all cases it exceeded the initial breeding density by July. When fox predation was dropped from any of the simulations the change in model outcome was considerable, the final density of hares (44 to 92/km^2) being 3 to 6 times that produced when fox predation took place (Table 2, Fig. 2). Because of the lost reproduction and growth of the hares eaten by foxes, this potential increase in the hare population amounted to 0.71 to 1.3 times the number of hares consumed by foxes, 1.7 to 2.5 times in terms of biomass.

Small-scale simulations of individual fox territories

Figure 3 a), CRU. This was a large (3.6 km^2) territory occupied by a dog-fox, vixen, and litter of four cubs. No other adults were thought to be present. This family group had access to a hare population numbering 61 in February and 76 by December. Such a low end-of-year population could only be simulated if we assumed productivity to be as low as 37% of physiological maximum (sim-

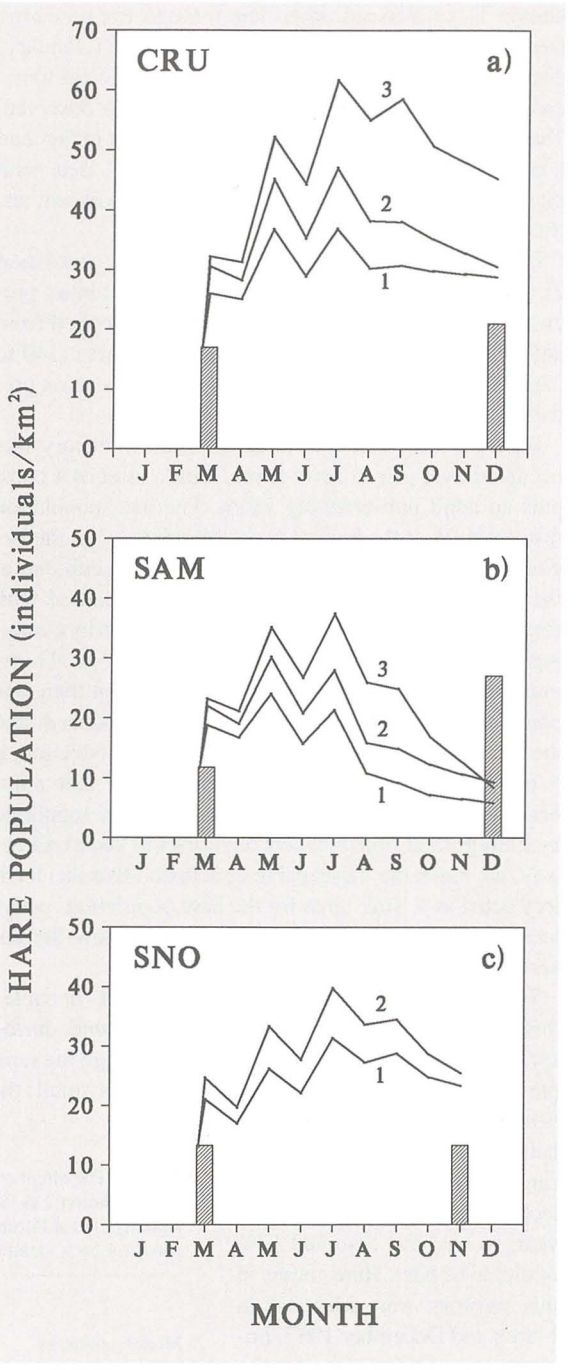

Figure 3. Results of applying simulations of the large-scale model to each of three fox territories, CRU, SAM, SNO. Bars indicate known numbers of hares within each territory and lines 1-3 indicate simulations based on Table 2 parameters. In a) and c) hare numbers counted at the end of year were lower than predicted by the large scale model; in b) there were more hares left at the end of year than predicted. a) and c) represent source areas of hares, and b) a predation 'sink'.

ulation 1); or if losses other than through fox predation were locally very high (simulation 2). Late (1 January) dispersal of cubs (simulation 3) was not sufficient to account for the low December hare population observed. The most plausible scenario was that the area in fact had a normal production rate but was a 'source' area, with many hares dispersing outwards, e.g. to the adjacent territory (b).

Even with productivity set as high as 75% (simulation 2), fox predation accounted for 51% of the annual production of hares. When fox predation was dropped from any of the simulations the final density of hares (140 to 220 hares) was 2 to 3 times that produced when fox predation took place.

Figure 3 b), SAM. This small (2.2 km^2) territory was occupied by a pair of adult foxes, with a litter of 4 cubs, plus an adult non-breeding vixen. The hare population rose from 26 at the beginning of March to 61 at the beginning of December. Hares formed 11% of cub diet at the earth. A satisfactory simulation which tallied with these field observations could only be achieved by assuming that hare productivity was 87% of physiological maximum and that hare survival was 100%. Even then, fox predation accounted for 82% of leverets produced, and the loss of 198 kg/km^2 of potential biomass production. It is more likely that the substantial increase of hare numbers observed in this fox territory was actually supported by immigration from adjacent territories a) and c). Either way, we reach the inescapable conclusion that this territory acted as a 'sink' area for the hare population, where local hare production was insufficient to allow the observed level of predation by foxes.

Figure 3 c), SNO. Unusually, the vixen SNO occupied this very small home-range (0.75 km^2) alone during spring and summer, and did not breed. Although the sample of scats collected from this territory was small, the percentage of scats containing hare remains was not significantly different from those collected elsewhere in the same year, so we have assumed 10% of diet to be hare. Hare counts in this territory were identical in March and December 1987, implying no net increase despite the light fox predation pressure. This situation could be simulated only by assuming a very low productivity (18% of maximum) or a very high non-fox mortality of hares (10% of adults and 16% of leverets per month). Hare consumption for the year by this single vixen barely equalled the spring breeding density of hares. It seems probable that because of the light fox predation this small area acted as a 'source' of hare production, for example to the adjacent territory described in b) above.

Sensitivity analysis of the general model

To assess the relative influence of individual model parameters on our conclusions, we varied key assumptions and parameters in large-scale simulation 2 described above, and tested their effects on our prediction that in the absence of fox predation the end-of-year hare density would have been three times larger. The effect of these was compared by looking at the main conclusion of our study, that in the absence of fox predation, or any mortality that compensated for it, the end-of-year hare density would have been three times as large as when fox predation took place. Table 4 ranks the key model parameters in increasing order of importance.

Of all parameters, fox territory size and cub dispersal had the greatest influence on model outcome. In fact there was impressively little overlap in movements of neighbouring foxes (Reynolds & Tapper 1995), and we were confident that territory size was accurately determined. On the other hand, we had little information about the timing of cub dispersal. Late cub dispersal had a substantial influence on the outcome of the model through depletion of the adult hare stock in late winter. Even when births of leverets in the model were staggered throughout the breeding season, leveret production in the early months of the year was very small. If it was insufficient to meet the food requirements of foxes in the model, the adult breeding stock was depleted, severely reducing the growth potential of the hare population. In the absence of specific data our conservative policy favoured 1 September as the earliest date by which net cub loss could be

Table 4: The effect of variation in model parameters on the main conclusion of this study. Using simulation 2 as the starting point, processes and parameters in the model were varied individually. The difference between the model outcome with and without fox predation was compared for each variant.

Model parameter	Relative increase in final hare density when fox predation is disabled
Simulation 2 (see Table 2)	(x) 3.00
No density-dependent relationship in leveret production	2.82
Staggered births of leverets (from Broekhuizen & Maaskamp 1979)	3.07
No non-breeding vixens in fox territorial groups	2.65
25% variation of fox litter size	2.23 - 3.66
25% variation of % hare in cub diet	2.56 - 3.30
25% variation of % hare in both adult fox and cub diet	2.10 - 3.72
25% variation in fox territory size	2.13 - 5.37
Mean cub dispersal date delayed to 1 February	6.12

complete (see Appendix). Thus based on dispersal, fox predation could have been greater than suggested by our simulations, but not less.

Discussion

The extent of fox predation relative to hare population growth

In the public domain it is common to undervalue the extent and impact of predation on prey species that form only a small fraction of predator diet, though in reality it can be very significant, dependant on the relative density of predators and prey. In the scientific literature this point is by no means new. For example, Sargeant (1978) found that, even though ducks formed less than 4% of breeding season food intake for a typical fox family, this predation accounted for 18% of incubating female mallards, besides 5% of males. It does not follow, however, that the impact of predation at low prey densities is always negligible, as this would depend on the relative density of predators and prey.

In the present study, we have simulated fox and hare populations at unexceptional densities in a situation typical of lowland agricultural Britain. Even using a conservative approach in choosing parameters, these simulations suggest that consumption of hares by foxes was substantial relative to the maximum productivity of the hare population, and that the hare population could not have withstood much additive mortality without declining.

The full extent of predation by foxes is greater than the number or biomass of hares killed, because of the lost potential for reproduction by adults and growth by juveniles. In the various simulations, the full extent of predation by foxes was 0.9 to 4.1 times the breeding density, or 12 to 59 hares/km^2. Clearly this level of predation could be sustained only by a vigorously reproducing hare population. Indeed, to explain field counts of hares in one fox territory, all female hares must have been reproducing close to their physiological maximum, or else the hare population was supported by immigration from outside the study area.

This difference between consumption and its effect on population growth reflects the difference between the yield of the hare population to a predator operating throughout the breeding season of the hare (like the fox), and one that defers harvest until most production and growth is complete (such as man). Overall, foxes in our simulations consumed 75 to 100% of leveret production, depending on the relative values of hare productivity and additive non-fox mortality (Table 2). This predation amounted to 47 to 87 kg/km^2/year, and there was effectively no post-production 'surplus' available for human hunters. If there had been no fox predation or other compensatory mortality, the hare population might have supported a harvest of up to 29 to 77 hares/km^2/year, or 79 to 213 kg/km^2/year. Thus, because foxes harvest hare production at an earlier date, they are superior competitors, but less efficient exploiters of the hare population.

The extent of fox predation suggested by our analysis is greater than that estimated by Erlinge et al. (1984) for the Revinge military training area in southern Sweden, which at the time was among the highest recorded. The hare population density at Revinge was 14-15/km^2 in 1975-76 (Frylestam 1980) and thus similar to that in this study (approximately 15/km^2). Fox density at Revinge (von Schantz 1980) was also similar to those in our study (at Revinge: 1 litter/2.25 km^2, mean 3.8 cubs/litter, 0.78 adults/km^2; at Woodyates 1 litter/2.6 km^2, mean 4 cubs/litter, 0.96 adults/km^2). To understand the difference in impact, we have used these and other parameters published by Erlinge's team to simulate the Revinge situation using our own model. We estimated the effect of hare consumption by foxes at Revinge to be 10% more in hare biomass, i.e. 17% more in numbers of hares than did Erlinge et al. This difference in interpretation of the Revinge data arises because our method assesses the potential for production and growth of the hares eaten by foxes, whereas Erlinge et al. simply compared consumption by foxes with estimates of the production of hares and their size at death. However, this discrepancy is small compared with the difference in potential impact of fox predation between the Revinge study and ours at West Woodyates. Although foxes were the most significant predator of hares at Revinge, they accounted for only 40% of annual hare production, compared with 76 to 100% at Woodyates. This is largely because hares formed only 3% of annual fox diet at Revinge, but 10% of fox diet at Woodyates. Later, in 1988, we studied fox diet on Salisbury Plain military training area, 35 km northeast of Woodyates, where hare density was about 1.5 times that at Woodyates; here hares formed 30% of fox diet (Reynolds & Tapper, unpubl.). Studies in Poland have found hares to form 12-46% of fox diet (Pielowski 1976, Goszczynski & Wasilewski 1992).

The potential impact of fox predation on hare population growth

Long-term trends in brown hare abundance in Britain and elsewhere result from changes in agricultural practices (Frylestam 1979, Tapper & Barnes 1986) and competition (Barnes & Tapper 1986), whereas year-to-year changes in hare density result particularly from variations in weather (Hewson & Taylor 1975, Bresinski 1976). However, any factor that limits hare production must restrict the ability of the hare population to respond to improvement in these conditions, and must therefore depress the mean long-term hare density.

Many studies have found a response in hunting bags or population density of hares (*Lepus europaeus*, *L. timidus* L., *L. americanus* Erxleben, and *L. arcticus* L.) where fox density has been substantially reduced through rabies (Spittler 1974, Pegel 1986), mange (Swedish mainland: Lindström & Mörner 1985, Danell & Hörnfeldt 1987, Bornholm: H.H.Dietz, pers.comm.), or control by man (Jensen et al. 1970, Marcström et al. 1989, Tapper et al. 1993, Small & Keith 1992). On islands without foxes both maximum and mean densities of brown hares can be substantially higher than on the mainland (e.g. 186/km^2 - Abildgård et al. 1972, 162/km^2 - Frylestam 1980). This is also the case for *L. timidus* (Angerbjörn 1977, Häkkinen & Jokinen 1981, Lindlöf & Lemnell 1981), whose island populations can apparently become limited by predation if foxes reach the islands (Nyholm 1971, Angerbjörn 1989). Hearn et al. (1987) concluded that fox predation limited population growth of *L. arcticus* in the coastal barrens of Newfoundland. Of all these studies, only those by Marcström et al. and Tapper et al. describe controlled experiments monitored by field counts of hares rather than hunting statistics; both these experimental studies involved the removal of other predators besides foxes. Also, the impossibility of dispersal rather than lack of predation may explain high island hare densities. Nevertheless together this body of literature forms persuasive evidence that predation by foxes can severely limit hare population growth and density in a variety of systems from the arctic to temperate agricultural regions.

This interpretation is stengthened by our findings. In a man-made agricultural habitat with unremarkable densities of both foxes and hares, the loss of hares consumed by foxes in our study was large enough to limit hare population growth significantly. Such a result is necessary if the interpretation given above is to be plausible. Nevertheless, we cannot conclude that fox predation *per se* limited the hare population, because we knew nothing of the relationship between fox predation and other causes of mortality. If compensation between fox predation and other forms of mortality were pronounced, the impact of the fox on hare productivity and population dynamics would be smaller than suggested by the model.

So, is a substantial degree of compensation likely, or is fox predation sufficiently additive to limit hare density? Predator control (i.e. predator culling with the intention of reducing predator density) is a traditional management tool for small game in Britain, and we knew from earlier work (Barnes & Tapper, unpubl.) that whereas mean breeding densities of hares were just 15/km^2 in the present study, on similar agricultural land with intensive predator control they can be as high as 60/km^2. Stoate et al. (1995) report preliminary findings from 23 sites suggesting that habitat improvement increases hare density only if fox density is also suppressed. Brockless (1995) reported an increase of hare density from 5/km^2 to 65/km^2 in three years under a regime of combined habitat improvement and predator control, compared with no increase on a nearby area without such management. The experimental predator removal study of Tapper et al. (1993) showed that control of several common predator species without habitat improvement increased winter hare density; in other words, although compensation amongst all the predator species removed remained possible, compensation between predation and other factors (e.g. dispersal, disease, reproductive inhibition) was insufficient to prevent the substantial experimental outcome. Lindström et al. (1994) showed that reduction of red fox density alone increased mountain hare *Lepus timidus* density. The present study shows that predation by foxes can certainly be extensive enough potentially to achieve a similar impact on brown hares.

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References

Abildgård, F., Andersen, J. & Barndorff-Nielsen, O. 1972: The hare population (Lepus europaeus Pallas) of Illumø Island, Denmark. A report on the analysis of the data from 1957-1970. - Danish Review of Game Biology 6(5), 32 pp.

Aebischer, N.J. & Coulson, J.C. 1990: Survival of the kittiwake in relation to sex, breeding experience and position in the colony. - Journal of Animal Ecology 59: 1063-1071.

Angerbjörn, A.1977: En studie av en extremt tät population av skogshare (Lepus timidus) på en västkustö. (In Swedish with English summary: A study on an extremely dense population of mountain hare (Lepus timidus) on a west coast island) - Zoologisk Revy 4: 119-130.

Angerbjörn, A. 1989: Mountain hare populations on islands: effects of predation by red fox. - Oecologia 81: 335-340.

Balser D.S., Dill, H.H. & Nelson, H.K. 1968: Effect of predator reduction on waterfowl nesting success. - Journal of Wildlife Management 32: 669-682.

Barnes, R.F.W. & Tapper, S.C. 1985: A method for counting hares by spotlight. - Journal of Zoology 206: 273-276.

Barnes, R.F.W. & Tapper, S.C. 1986: Consequences of the myxomatosis epidemic in Britain's rabbit (Oryctolagus cuniculus L.) population on the numbers of Brown hares (Lepus europaeus Pallas). - Mammal Review 16: 111-116.

Boutin, S. 1992: Predation and moose population dynamics: a critique. - Journal of Wildlife Management 56: 116-127.

Bresinski, K. 1976: Agrarian structure vs. the European hare population density. - In: Pielowski, Z. & Pucek, Z. (eds.); Ecology and management of European hare populations, Polish Hunting Association, Warsaw, pp. 195-197.

Brockless, M. 1995: Game and shooting at Loddington. - The Game Conservancy Review 26: 67-68.

Broekhuizen, S. & Maaskamp, F. 1979: Age determination in the European hare (Lepus europaeus Pallas) in the Netherlands. - Zeitschrift für Saugertierkunde 44: 162-175.

Broekhuizen, S. & Maaskamp, F. 1981: Annual production of young in European hares (Lepus europaeus) in the Netherlands. - Journal of Zoology, London 193: 499-516.

Chesness, R.A., Nelson, M.M. & Longley, W.H. 1968: The effect of predator removal on pheasant reproductive success. - Journal of Wildlife Management 32: 683-697.

Danell, K. & Hörnfeldt, B. 1987: Numerical responses by populations of red fox and mountain hare during an outbreak of sarcoptic mange. - Oecologia 73: 533-536.

Duebbert, H.F. & Lokemoen, J.T. 1980: High duck nesting success in a predator-reduced environment. - Journal of Wildlife Management 44: 428-437.

Erlinge, S., Frylestam, B., Göransson, G., Högstedt, G., Liberg, O., Loman, J., Nilsson, I.N., von Schantz, T. & Sylvén, M. 1984: Predation on brown hare and ring-necked pheasant populations in southern Sweden. - Holarctic Ecology 7: 300-304.

Frylestam, B. 1979: Structure, size, and dynamics of three European hare populations in southern Sweden. - Acta Theriologica 24: 449-464.

Frylestam, B. 1980: Reproduction in the European hare in southern Sweden. - Holarctic Ecology 3: 74-80.

Goszczynski, J. & Wasilewski, M. 1992: Predation of foxes on a hare population in central Poland. - Acta Theriologica 37(4): 329-338.

Häkkinen, I. & Jokinen, M. 1981: Population dynamics of the mountain hare on an island in the outer archipelago of SW Finland. - In: Myers, K. & MacInnes, C.D. (eds.); Proceedings of the World Lagomorph Conference, Guelph, 12-16 Aug. 1979. University of Guelph, Guelph, Ontario, pp. 469-477.

Hansen, K. 1992: Reproduction in European hare in a Danish farmland. - Acta Theriologica 37: 27-40.

Harris, S. & Smith, G.C. 1987: Demography of two urban fox (Vulpes vulpes) populations. - Journal of Applied Ecology 24: 75-86.

Harris, S. & Trewhella, W.J. 1988: An analysis of some of the factors affecting dispersal in an urban fox (Vulpes vulpes) population. - Journal of Applied Ecology 25: 409-422.

Hearn, B.J., Keith, L.B. & Rongstad, O.J. 1987: Demography and ecology of the arctic hare (Lepus arcticus) in southwestern Newfoundland. - Canadian Journal of Zoology 65: 852-861.

Hewson, R. & Taylor, M. 1975: Embryo counts and length of the breeding season in European hares in Scotland from 1960-1972. - Acta Theriologica 20(19): 247-254.

Jensen, B. 1968: Preliminary results from the marking of foxes (Vulpes vulpes L.) in Denmark. - Danish Review of Game Biology 5: 1-8.

Jensen, B. 1970: Effect of a fox control programme on the bag of some other game species. - Transactions of the International Congress of Game Biologists, Moscow 9: 480.

Jensen, B. 1973: Movements of the red fox (Vulpes vulpes) in Denmark investigated by marking and recovery. - Danish Review of Game Biology 8: 1-20.

Kleiber, M. 1975: The fire of life: an introduction to animal energetics. - Wiley, New York, 475 pp.

Lincoln, G.A. 1974: Reproduction and »March madness« in the brown hare, Lepus europaeus. - Journal of Zoology 174: 1-14.

Lindlöf, B. & Lemnell, P.A. 1981: Differences in island and mainland populations of mountain hare. - Proceedings of the World Lagomorph Conference, Guelph 1: 478-485.

Lindström, E. & Mörner, T. 1985: The spreading of sarcoptic mange among Swedish red foxes (Vulpes vulpes L.) in relation to fox population dynamics. - Revue d'Écologie (La Terre et la Vie) 40: 211-216.

Lindström, E.R., Andrén, H., Angelstam, P., Cederlund, G., Hornfeldt, B., Jäderberg, L., Lemnell, P.A., Martinsson, B., Sköld, K. & Swenson, J.E. 1994: Disease reveals the predator: sarcoptic mange, red fox predation, and prey populations. - Ecology 75: 1042-1049.

Lloyd, H.G. 1980: The red fox. - B.T.Batsford, London, 320 pp.

Marcström, V., Keith, L.B., Engrén, E. & Cary, J.R. 1989: Demographic responses of arctic hares (Lepus timidus) to experimental reductions of red foxes (Vulpes vulpes) and martens (Martes martes). - Canadian Journal of Zoology 67: 658-668.

Marcström, V., Kenward, R.E. & Engrén, E. 1988: The impact of predation on boreal tetraonids during vole cycles: an experimental study. - Journal of Animal Ecology 57: 859-872.

Nyholm, E.S. 1971: Ekologisia havaintoja jäniksestä in Krunnien saarilla sekä Kuusamossa. (In Finnish with English summary: Ecological observations on the snow hare (Lepus timidus L.) on the islands of Krunnit and Kuusamo) - Suomen Riista 20: 15-31.

Parker, H. 1984: Effect of corvid removal on reproduction of willow ptarmigan and black grouse. - Journal of Wildlife Management 48: 1197-1205.

Pegel, M. 1986: Der Feldhase (Lepus europaeus Pallas) im Beziehungsgefüge seiner Um- und Mitweltfaktoren. - Schriften des Arbeitskreises Wildbiologie und Jagdwissenschaft an der Justus-Liebig-Universität Gießen 16: 224 pp. (In German).

Petrusewicz, K. 1970: Dynamics and production of the hare population in Poland. - Acta Theriologica 15: 413-445.

Pielowski, Z. 1971: Length of life of the hare. - Acta Theriologica 16: 89-94.

Pielowski, Z. 1976: The role of foxes in the European hare population. - In: Pielowski, Z. & Pucek, Z. (eds.); Ecology and management of European hare populations, Polish Hunting Association, Warsaw, pp. 135-148.

Raczynski, J. 1964: Studies on the European hare. V. Reproduction. - Acta Theriologica 9: 305-352.

Reynolds, J.C. & Aebischer, N.J. 1991: Comparison and quantification of carnivore diet by faecal analysis: a critique, with recommendations, based on a study of the fox Vulpes vulpes. - Mammal Review 21: 97-122.

Reynolds, J.C. & Tapper, S.C. 1995: The ecology of the red fox (Vulpes vulpes) in relation to small game in rural southern England. - Wildlife Biology 1: 105-119.

Sargeant, A.B. 1978: Red fox prey demands and implications to prairie duck production. - Journal of Wildlife Management 36: 225-236.

Sinclair, A.R.E. 1991: Science and the practice of wildlife management. - Journal of Wildlife Management 55: 767-773.

Small, R.J. & Keith, L.B. 1992: An experimental study of red fox predation on arctic and snowshoe hares. - Canadian Journal of Zoology 70: 1614-1621.

Spittler, H. 1974: Zur Populationsdynamik des Fuchses (Vulpes vulpes L.) in Nordrhein-Westfalen. (In German with English summary: About the population-dynamics of the red fox in Nordrhein-Westfalen) - Transactions of the International Congress of Game Biologists 11: 167-174.

Stahl, P. 1990: Influence of age-related changes in prey consumption on correction factors established for important prey of the red

fox (Vulpes vulpes). - Gibier Faune Sauvage 7: 107-125.
Stoate, C., Wakeham-Dawson, A. & Tapper, S.C. 1995: Hares, farming and foxes. - The Game Conservancy Review 26:108-110.
Storm, G.L., Andrews, R.D., Phillips, R.L., Bishop, R.A., Siniff, D.B. & Tester, J.R. 1976: Morphology, reproduction, dispersal and mortality of midwestern red fox populations. - Wildlife Monographs 49: 82 pp.
Tapper, S.C. & Barnes, R.F.W. 1986: Influence of farming practice on the ecology of the brown hare (Lepus europaeus). - Journal of Applied Ecology 23: 39-52.
Tapper, S.C., Brockless, M. & Potts, G.R. 1991: The effect of predator control on populations of grey partridge Perdix perdix. - In: Csanyi, S. & Ernharft, J. (eds.); Transactions of the Congress of the International Union of Game Biologists. Gödöllö, Hungary 20: 398-403.
Tapper, S.C., Brockless, M. & Potts, G.R. 1993: Effet d'une réduction expérimentale des prédateurs sur l'abondance du petit gibier. - In: Migot, P. & Stahl, P. (eds.); Actes du colloque: Prédation et gestion des prédateurs - Dourdan 1-2 December 1992, Office National de la Chasse, Paris, pp. 37-44. (In French).
Tapper, S.C., Potts, G.R. & Brockless, M.H. (in press): The effect of an experimental reduction in predation pressure on the breeding success and population density of grey partridges (Perdix perdix). - Journal of Applied Ecology.
Trautmann, C.G., Fredrickson, L.F. & Carter, A.V. 1973: Relationship of red foxes and other predators to populations of ring-necked pheasants and other prey, South Dakota. - Proceedings of the North American Wildlife Conference 39: 241-253.
Trewhella, W.J. & Harris, S. 1988: A simulation model of the pattern of dispersal in urban fox (Vulpes vulpes) populations and its application for rabies control. - Journal of Applied Ecology 25: 435-450.
von Schantz, T. 1980: Prey consumption of a red fox population in southern Sweden. - Biogeographica 18: 53-64.
Wasilewski, M. 1991: Population dynamics of the European hare Lepus europaeus Pallas, 1778 in central Poland. - Acta Theriologica 36: 267-274.

Appendix

Model parameters: Hares

Population density

Leverets were assumed to recruit into the countable hare population at one month of age: at this age all leverets are weaned and moving around to feed (Broekhuizen & Maaskamp 1979). Since hare counts were made on a field-by-field basis, we could describe the hare population on specific parts of the study site as well as the entire study area.

Fox predation and other causes of mortality

In this paper we assume that all hares eaten by foxes were killed by foxes, and divide hare mortality into 'fox predation' and additive 'non-fox loss'. In the model, non-fox loss represent emigration as well as death and was assumed to take place before fox predation at each monthly update. Initially non-fox loss was set at zero, but was then increased to fit the model to the target.

Some conception of realistic levels of non-fox loss can be gleaned from the literature. In most published studies of brown hares, mortality estimates include predation losses. However, Abildgård et al. (1972) and Frylestam (1980) studied brown hare populations on islands which lacked wild mammalian predators, and estimates of survival were derived from these. We reanalysed the published data of Abildgård et al. (*op.cit.*) using a generalised linear model with logistic link function, after the method of Aebischer & Coulson (1990, Appendix Table 1).

The data from Abildgård et al. (1972) indicate that on Illumø during October and November leverets had lower survival than did adult hares. During the winter period December to March there was no difference in survival rate between young and adult hares, a conclusion supported by Petrusewicz (1970) for hares in Poland. During the summer period, March-October, survival of adult female hares was significantly higher than that of adult males, but in other seasons male and female survival was similar within each age group.

Hansen's (1992) study of hares in a modern agricultural system was particularly relevant to the agricultural landscape of our study site. The very high mortality he described translates to monthly survival figures of only 66.4% to 75.2%, but these include predation losses.

Annual reproductive output

The annual reproductive output of hares ranges from 2.3 to 12 leverets per female (Broekhuizen & Maaskamp

Appendix Table I. Monthly survival rates of hares in the absence of foxes on Illumø, Denmark, derived from Abildgård et al. (1972). Allowance has been made for a 4% capture mortality.

	Monthly survival rates		
Age of hares/Periods	October-December	December-March	March-October
Young < 9 months old	86.6%	92.3%	
Adults > 9 months old	96.3%	94.7%	
Males > 9 months old			98.3%
Females > 9 months old			95.9%

1981), and is clearly related to both latitude (Broekhuizen & Maaskamp *op.cit.*) and spring density (Frylestam 1980). We have taken 12 leverets/female/year to be the physiological maximum, and 9 (i.e. 75% of maximum) as the mean at very low densities, as in Frylestam (*op.cit.*). Hares were assumed not to breed in their year of birth (Lincoln 1974).

Monthly distribution of births

The timing of births within the year is obviously important to the outcome of the model. In all European studies reviewed, males were largely sexually inactive during October, November and much of December (Broekhuizen & Maaskamp 1981, Frylestam 1980, Lincoln 1974, Raczynski 1964), and leveret production in these months was essentially zero. The onset of breeding was not simultaneous in all females. Since we did not have specific information about leveret production in our study population during the years in question, we adopted a simple schedule of birth-dates based on comparable studies, in which all female hares produced 4 litters simultaneously on four birth dates (1st of March, May, July, September) each year, representing 22%, 33%, 33% and 12% respectively of annual production.

In reality, although the onset of breeding each year is relatively synchronised (Hewson & Taylor 1975), successive litters become progressively out of step, resulting in a wide distribution of births within each year. This distribution has been calculated in a number of studies (Broekhuizen & Maaskamp 1981, Frylestam 1980, Hewson & Taylor 1975, Lincoln 1974, Raczynski 1964), and clearly differs substantially between years and localities. The default schedule of leveret production in our model could be readily substituted by the shape of one of these real distributions to test the sensitivity of model output to this feature.

Weather has clear effects on the length of breeding season and litter size (Hewson & Taylor 1975), leading to a threefold difference in productivity between good and bad years. On top of this there is also weather-related variation in leveret survival (Abildgård et al. 1972). Without specific information about hares on our study site in the years in question, we could not take this into account; but by varying annual reproductive output and birth schedules in the model we could nevertheless consider the effects of variation in productivity on our conclusions.

Density-dependence in hare production

From placental scar counts, Frylestam (1980) found that leveret production per female was inversely related to hare density in spring by the following linear relationship derived from Figure 2 in Frylestam *op cit.*:

leverets per female = 9.004 - 0.058 (adult females per km^2)

It may be incorrect to assume that this relationship holds for all hare populations, and arguably it makes the model simpler to omit density-dependence. However the simpler model is no more likely to be realistic, and we opted to include Frylestam's relationship in the model, with the usual facility to switch it on or off. Thus our model modified leveret production each month according to the current density of adult female hares, using the slope of this line but with the intercept set at some fraction of the physiological maximum of 12, as described earlier. If productivity was set at 75%, the intercept would be 9 and the relationship would be identical to Frylestam's; a setting of 100% would give, at each hare density, the maximum productivity possible on physiological grounds.

Age-specific predation

We assumed that fox predation each month began with the youngest cohort of leverets and then progressed through cohorts of increasing age until either predation demands were met or the hare population was extinct. This assumption results in a conservative estimate of the impact of fox predation.

Foxes unquestionably do kill adult brown hares (Reynolds, pers.obs., Petrusewicz 1970, Goszczynski & Wasilewski 1992), but Frylestam (1979) found a considerably lower survival of leverets in summer compared with adult hares. Furthermore, leveret survival was considerably lower on mainland sites with numerous predator species than on the island of Ven, which had only domestic cats and a sparse crow population, implying that at least part of the difference between leveret and adult summer survival on the mainland was attributable to predation.

Model parameters: Foxes

Fox density

For the large-scale simulation, fox density was set at the mean value observed during our field study. Territory size was calculated as the mean of seven territories determined by radio-tracking. Each territory was held by a dog-fox and one breeding vixen, with half the territories having one additional, non-breeding adult vixen. Each vixen was assumed to wean four cubs, the size of virtually all litters observed during our study. For simplicity, all cubs were assumed to be born on 1 April (as in von Schantz 1980, Harris & Smith 1987).

In small-scale simulations describing a single fox-territory in a specific year, territory size, fox numbers and litter size were substituted directly from field observations.

Fox diet

The proportion of hare in the diet of foxes was determined

by our analysis of fox faeces (Reynolds & Aebischer 1991, Reynolds & Tapper 1995). Although this differed significantly both between seasons and between subunits of the study area, these factors were interrelated and we could not determine a clear seasonal trend which applied uniformly over the entire study area. Thus in large-scale simulations we have assumed that hare formed a constant fraction of fox diet away from cubbing earths; for territory-specific simulations local and seasonal variations were specified, but these variations were actually small relative to estimation errors.

The diet of cubs at the earth differed significantly from that of free-ranging adult and sub-adult foxes. In particular, cub diet contained a higher proportion of medium-sized prey such as rabbits, hares, and pheasants. In the model therefore, cub diet between 1 April and 30 June differed from adult diet; outside this period cub and adult diets were assumed identical. Because fox cubs are less efficient at ingesting and digesting large hares (Stahl 1990), the estimated proportion of hare in cub diet depends on an unavoidable assumption about whether the hares eaten were adults (estimate 36% in diet) or leverets (estimate 17%). In the model, the least impact of foxes on hares - both in terms of biomass killed and impact on the population - arises if we assume that cubs ate only young leverets, and this is the option we have adopted.

Fox food requirements

Food requirements for adult foxes and cubs were based on a combination of data from Sargeant et al. (1978) and Stahl (1990). The daily feeding of cubs by Stahl more closely mimicked the provision of food by adult foxes at the den than Sargeant's more frugal regime, and resulted in less efficient use of each prey item. Also, because European foxes are larger and roughly 25% heavier than those in central North America (Sargeant *op.cit.*, Lloyd 1980), Stahl's data should be the more relevant to our situation. However, Sargeant's data allow a more detailed temporal breakdown of food requirements in relation to cub growth, and a more parsimonious estimate of hare consumption. We have therefore used Sargeant's estimates of minimum food requirements, expressed per kilogram fox body weight. For adult foxes, these were scaled for the mean adult body weights observed in our study (6.5 kg for males, 5.5 kg for females) raised to the power of 0.75 (Kleiber 1975).

To estimate cub food requirements we extrapolated the consumption/time curve given by Sargeant, with food requirements per cub peaking at 1.3 times mean adult levels at 28 weeks *post partum*, and falling back to mean adult levels by 12 months of age.

Dispersal of cubs

Typically, cubs disperse at some time between September and February (Jensen 1968, 1973, Storm et al. 1976, Lloyd 1980, Harris & Smith 1987, Trewhella et al. 1988), though some - mainly female cubs - may remain to recruit into the local population. Since the food requirements of cubs are at a maximum by mid-winter, the actual timing of dispersal can be expected to have a major impact on the outcome of the model. As we had no means of estimating dispersal dates in our field study, we created a third set of simulations by varying mean dispersal date between 1 September and 1 March.

Although dispersing cubs have a high mortality rate, they obviously do not die as soon as they disperse, and the area may contain itinerant cubs for some time; so the parameter modelled here is really the net (unreplaced) cub loss.