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Variation in demography, condition and dietary quality of hares *Lepus europaeus* from high-density and low-density populations

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Numbers of European hares *Lepus europaeus* have declined throughout Europe due to agricultural intensification. However, hares are more common in intensive arable areas than in pastural areas. To identify factors limiting populations, functional explanations for differences in density of hares were sought. We compared demography (litter size, prenatal mortality and participation in breeding by females), body condition (urinary and serum nitrogen, kidney fat, bone marrow fat, skeletal size and body weight), and dietary quality of hares from parts of England and Wales where they are present at relatively high densities (arable habitats) and at relatively low densities (pastural habitats). In pastural areas a lower proportion of adult females were lactating in late winter than in arable areas. Recruitment was therefore lower in pastural than in arable habitats. Hares from pastural areas were smaller, lighter and had less fat than those from arable areas, but dietary quality was similar. Thus hares in low-density populations from pastural areas were able to obtain a good-quality diet, but expended more energy and were unable to maintain body condition as well as those from arable areas. Pastural habitat, which in England and Wales is relatively warm and wet, is suboptimal for hares. The reduced recruitment and chance of survival of hares in the pastural habitats we describe may explain the differences in density of hares in arable and pastural habitats. Efforts to conserve the hare should focus on the reduction of predation and exposure to unfavourable weather by the provision of year-round vegetative cover (such as fallow land, rough grassland and shelterbelts), to increase the chances of survival of leverets and adult hares.

Key words: Biodiversity Action Plan, climate, conservation, game, nutrition, predation, reproduction

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The European hare *Lepus europaeus* is protected under the Bern Convention (Anon. 1979). It is classed as a 'priority species of conservation concern' by the UK government, and so has a Biodiversity Action Plan (BAP) to increase numbers of hares (Anon. 1995). Records of hares shot suggest that numbers have declined in recent decades throughout Europe (Pielowski & Pucek 1976, Tapper 1992), and agricultural intensification has been blamed for the decline (Tapper & Barnes 1986, Slamečka 1991). Populations of hares decline if agriculture becomes very intensive (Tapper & Barnes 1986, Slamečka 1991, Panek & Kamieniarz 1999). However, throughout Europe, the hare is more common in intensively farmed arable areas than in pasture and other non-arable areas (Hutchings & Harris 1996, Vaughan et al. 2003, Smith et al. 2005).

It is unclear what limits populations of hares, although nutrition (Frylestam 1980a, Hackländer et al. 2002b), predation (Lindström et al. 1994), and exposure to unfavourable weather conditions (Hackländer et al. 2002a) have been suggested, and may affect recruitment and survival. A high-fat diet increases female reproductive rate (Hackländer et al. 2002b). Hares in mainly pastural areas of low habitat diversity have higher mortality rates and lower body weights than hares in diverse arable landscapes (Frylestam 1980a). Increased numbers of hares have resulted both from improving habitat quality without manipulation of predator numbers (Slamečka 1991), and from removal of red foxes *Vulpes vulpes* (the main predator) without any change in habitat (Lindström et al. 1994). Climate is correlated with numbers of hares (precipitation negatively and temperature positively; Smith et al. 2005).

In this paper, we seek functional explanations of variations in abundance of hares through measurement of selected demographic and other parameters, as advocated by Marboutin & Péroux (1995) and Vaughan et al. (2003). We quantify pre-breeding population age structure, litter size, incidence of prenatal mortality, and for females, percentage of young and adult hares breeding. We also quantify potential covariates of demographic parameters: body condition, skeletal size and body weight (Frylestam 1980a, Marboutin et al. 1990), and describe dietary quality. We compare these parameters for hares from relatively high-density populations in cool and dry arable areas (in the east of England; mean January temperature: 3-4°C, mean annual precipitation: 466-740 mm) with those for hares from relatively low-density populations in warm and wet pastural areas (in the west; mean January temperature: 4-8°C, mean annual precipitation: 741-4,577 mm; averages for 1971-2000, UK Meteorological Office; www.met-office.gov.uk). We also quantify the weather conditions experienced by hares in the locations and years in which we sampled them.

We test the hypothesis that pastural habitats support relatively low densities of hares because they are suboptimal in terms of nutrition. We expect hares from pastural areas to have poor quality diets, poor body condition, and to perform badly in terms of reproduction compared with hares from arable areas. If nutrition is important in limiting the growth of populations of hares in pastural areas, habitat management could benefit populations and help conservation targets to be reached. We evaluate the likely effectiveness of farmland habitat management for increasing numbers of hares.

Material and methods

Study animals

We collected 920 carcasses from 125 locations (Fig. 1) in 1998-2001 (all habitats sampled in each year); 774 were from 26 shooting estates, and the remaining 146 had mainly been killed by cars.

Age determination

We estimated the ages in days of animals ≤ 454 days old from mean eye lens weights (Suchentrunk et al. 1991). Mean weights were repeatable ($r_I = 0.999$, $F_{19,40} = 3602$, $P < 0.0001$).

The mandibles of hares for which no eye lenses were available, and of those estimated from the eye lens weight to be > 454 days old, were cleaned and dried for 48 hours at 60°C (Hearson oven). We carried out age analysis (to the nearest year) from adhesion lines in periosteal tissue (Frylestam & von Schantz 1977).

The presence of an epiphyseal protusion at the lateral ulnar knob ('Stroh's sign'; Stroh 1931) indicated animals

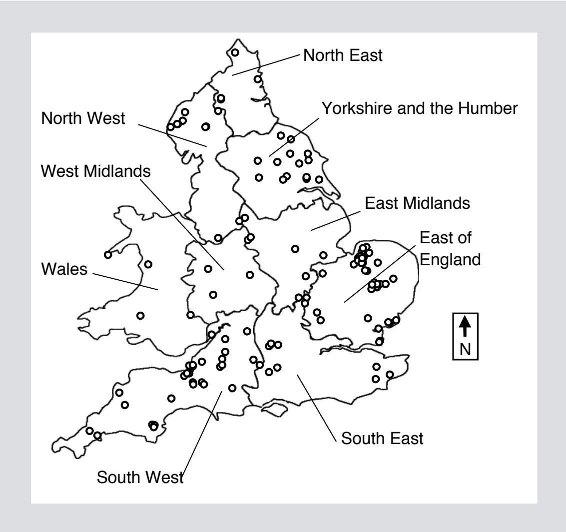

Figure 1. Location (○) in England and Wales of the 125 sites from each of which 1-57 hares were included in the analysis.

aged ≤ 234 days (~ 7.7 months). At this age, 50% of hares aged by eye lens weights had lost their protusion (Suchentrunk et al. 1991).

Of the 920 hares, the ages of 892 (97%) were determined using eye lens weights and/or adhesion lines in mandibles. When more than one method was used, results were consistent.

The youngest hare in our sample was three months old and therefore independent (Broekhuizen & Maaskamp 1980). Hares were defined as 'adult' if > 7.7 months (i.e. sexually mature; Raczyński 1964, Broekhuizen & Maaskamp 1981, and fully grown; Stroh 1931) and as 'young' if aged < 7.7 months. Depending on their time of year of birth, hares may breed as young as four months, but all hares aged ca eight months can breed (Broekhuizen & Maaskamp 1981).

Reproduction in females

We noted signs of lactation. Since milk is present in the mammary glands of rabbits *Oryctolagus cuniculus* in the last days of pregnancy (Brambell 1942), we did not class female hares as lactating if their embryos were near full-term (≥ 38 days since conception based on embryo weight; Broekhuizen & Martinet 1979). Females were classed as pregnant if embryos were visible. In rabbits, blastocysts are undetectable macroscopically for the first 10% of the gestation period (Brambell 1942). If pregnancy in hares is similar, we missed all pre-implantation pregnancies in the first 4.3 days (10% of pregnancies; the gestation period is ca 43 days; Stavy & Terkel 1992).

The uteri of non-pregnant females were examined for uterine scars (Bray et al. 2003). We used scars classed as < 48 days old, found only in lactating females, to determine the number of leverets in the litter currently sucking (Bray et al. 2003). From scars, we calculated the six-week 'season' of birth (defined as: early spring = 22 March-6 May, late spring = 7 May-21 June, early summer = 22 June-7 August, late summer = 8 August-23 September, early autumn = 24 September-7 November, late autumn = 8 November-21 December, early winter = 22 December-3 February, and late winter = 4 February-21 March) for sucking litters by assuming they had been born 15 days before (i.e. were half-way through the suckling period of ca 30 days).

We counted numbers of viable and resorbing embryos in the uteri of pregnant females (Raczyński 1964). We were able to quantify post-implantation resorption. We may have missed very early resorption if the female was killed much later in the pregnancy, and any resorption which may have occurred had the female not been killed. We aged embryos (N = 359) to the day of gestation (Broekhuizen & Martinet 1979) and predicted the season of birth.

Seasons of birth of litters were predicted from pregnancies and from uterine scars, but not from both for the same female. In females which were pregnant and lactating, we calculated the season of birth from pregnancy. Females carrying resorbing embryos could be pregnant (if the litter included viable embryos), but were classed as non-pregnant if carrying only resorbing embryos.

Body condition

We used several methods to quantify body condition in adult hares (Henke & Demarais 1990).

The urinary urea nitrogen (mg/dl) to creatinine (mg/dl) ratio (UN:C) and the serum urea nitrogen concentration both provide a snapshot view of the quality of the diet. We quantified UN:C in urine samples. More urea nitrogen is found in urine as protein intake increases. It is standardised with respect to creatinine, because while urine concentration varies, creatinine is excreted at a constant rate (Villafuerte et al. 1997). We measured urea and creatinine spectrophotometrically in diluted urine samples by using reagent kits and an autoanalyser (Konelab 30i; Konelab Corporation, Ruukintie, Finland). As urine was not available from all hares, we took blood samples (ca 5 ml) within three hours of death. We measured levels of serum urea (mMol/l) spectrophotometrically (see above), and converted them to serum nitrogen (mg/dl; SUN).

The kidney fat score reflects the nutritional status of the hare in the medium term (< ca 2 weeks; Henke &

Demarais 1990). Nancy Jennings estimated perirenal fat on a scale of 0-8.

The bone marrow fat index provides a long-term indication of body condition (Henke & Demarais 1990). Bone marrow fat is mobilised after several weeks on a restricted diet (in cottontail rabbits *Sylvilagus floridanus*; Warren & Kirkpatrick 1978). We removed marrow (0.5-1.5g wet weight) from each femur. Marrow was weighed using an Oertling R20 balance with an accuracy of 0.0001 g, dried to constant weight for 72 hours at 70°C in a Hearson oven, and then reweighed. We calculated the bone marrow fat index as the mass of dried marrow as a percentage of its original fresh weight (Keith et al. 1984).

The skeletal size and cleaned weight provide long-term indicators of body condition; body size reflects food availability during skeletal growth (i.e. the first ca eight months of life). To quantify skeletal size, Nancy Jennings measured the hind foot with an accuracy of 0.1 cm. Lengths were repeatable ($r_I = 0.948$, $F_{9,20} = 55.7$, $P < 0.0001$). We took body weights and cleaned weights (weight after removal of liver, reproductive tract and digestive tract from below the diaphragm) using a Salter 235 6S scale with an accuracy of 10 g.

Dietary quality

We weighed stomachs full and empty of contents. Contents were oven-dried for 72 hours at 60°C, milled to 1-mm fragments (Culatti mill), mixed and analysed for % dry matter, % ash, % crude protein, % crude fat, % crude fibre, and % carbohydrate content. We calculated the dry weight of the stomach contents from the % dry matter and the total wet weight. Energy content of stomach contents was calculated using Atwater factors; the digestible energy of fat, protein and carbohydrates were assumed to be 37.7, 16.7 and 16.7 kJ g^{-1}, respectively (see Hackländer et al. 2002b).

Allocation of hares to arable or pastural habitats, and climatic data

The location of origin for each hare was represented by an Ordnance Survey grid reference. For the 2,500-ha square which contained each grid reference, we obtained mean annual precipitation (in mm) and mean January temperature (in °C) for the years 1997-2000 from the UK Meteorological Office (see www.met-office.gov.uk). We included data for 1997 since many of our hares were killed in February 1998. We obtained data on the habitat at each grid reference from the land classification database (Centre for Ecology and Hydrology (CEH); Bunce et al. 1996), and from the annual agricultural census database for 1999 ('June census') held by the UK government's Department for Environment, Food and Rural Affairs (Defra) and the Geographical Information (GI) Services Branch of the National Assembly for Wales. Allocation to a land class is based on geology and soil type. The June census data reflect crops grown and can therefore be altered through land management, although the distribution of arable and pastural land changes little from year to year.

Table 1. Sample sizes (expressed as numbers of adult carcasses; total N = 808) among three landscape and two farmland types. Percentages are of total number shown; levels of variables from which < 5% of hares originated are not shown.

Landscape type	Arable a	209	(27%)
	Arable b	502	(64%)
	Pastural	72	(9%)
Farmland type	Arable	676	(86%)
	Pastural	107	(14%)

Data from the land class database

We allocated the 100-ha square represented by each grid reference to levels of CEH's land classification system (i.e. the 'landscape types': arable a, arable b, arable c, pastural and marginal upland; Bunce et al. 1996; Table 1). Less than 5% of hares were from arable c and marginal upland landscape types. Densities of hares in the remaining landscape types, surveyed during 1991-1993, were: arable a: 3.3 hares 100 ha^{-1}, arable b: 9.0 hares 100 ha^{-1}, pastural: 3.0 hares 100 ha^{-1} (Hutchings & Harris 1996). Arable a and b landscape types are similar, but arable a occurs in southern England and arable b in eastern and central England. The pastural landscape type occurs mainly in the west of England and in Wales (Bunce et al. 1996).

Data from the June census

Our June census data were pooled for parish groups. In England there were 1,263 parish groups, which had a mean area of 10,526 ha of agricultural land (range: 0.9-77,804 ha). In Wales, the 'small area', of which there were 235, is comparable. The 'farmland type' in the parish group (or small area) of origin of each hare was derived from the total area of land in agricultural use and areas used for crops and set-aside, and pasture (see Table 1). If > 50% of the area was a certain farmland type, it was allocated to that type. Hares are much more common in arable farmland types than in pastural farmland types (Vaughan et al. 2003).

Paired sampling

For some analyses, particularly when sample sizes were small, a precise and powerful comparison between hares from areas which support high and low densities of hares was desirable. Therefore, and since the arable b landscape type supports high densities of hares while pastural and marginal upland landscape types support similar and much lower densities of hares, hares from arable b were chosen at random from all suitable hares to form matched pairs with hares from the pastural (64 pairs) and marginal upland landscape types (16 pairs). Marginal upland supports ca 2.50 hares 100 ha^{-1} (Hutchings & Harris 1996), and is mostly pasture (Bunce et al. 1996). Pairs (78 in total; 41 adult male pairs and 37 adult female pairs) were matched with regard to gender, time of year of death, and cause of death. The time of day of death was not always known, but was matched as far as possible, since the cause of death was matched within pairs. The mean number of days between the deaths of members of the pairs was 10 (range: 0-29).

Statistical analysis

We used SPSS 10 (Field 2000), with a significance level (α) of 0.05 unless stated otherwise, and examined samples blind. We compared parameters between hares allocated to landscape types and farmland types (see Table 1). In χ^2 analysis, levels were omitted if their inclusion resulted in an average expected frequency of < 6.

For body condition, size and weight variables, we developed a separate logistic regression model for each gender. Collinearity existed between body weight and cleaned weight, so we excluded body weight. We carried out simple analyses with the dependent variables landscape type and farmland type, to select variables for inclusion in the final models. We included variables with significant log-likelihood tests in final models ($\alpha = 0.1$; Hosmer & Lemeshow 2000). The significance of the final models was tested by the log-likelihood test; overall fit was quantified by the deviance goodness-of-fit test (Hosmer & Lemeshow 2000).

We analysed paired samples by means of repeated-measures analyses of variance (ANOVAs), in which habitat was a within-pair factor and gender was a between-pair factor. We checked for sphericity and for homogeneity of variances (Field 2000) and transformed variables if necessary to conform to the assumptions of ANOVA.

Since hares were rarely shot except in February, sample sizes from other times of year were often too small for comparison. Also, not all parameters could be measured from each carcass, so sample sizes varied between analyses. Statistical analysis is limited to seasons and age classes of hares for which the sample size was considered large enough.

Table 2. Percentages of young female hares killed in winter pregnant and/or lactating in three landscape and two farmland types. Sample sizes are expressed as total number of hares for which information about reproduction is available.

Landscape type	Arable a	90%	(N = 10)
	Arable b	62%	(N = 21)
	Pastural	100%	(N = 1)
Farmland type	Arable	75%	(N = 28)
	Pastural	29%	(N = 7)

Results

Of the 920 hares, 418 were adult males, 390 were adult females, 61 were young males, and 51 were young females; 67 were killed in spring, 35 in summer, 47 in autumn, and 768 in winter. Of the 156 paired hares, 32 were killed in spring, 10 in summer, 18 in autumn, and 96 in winter.

Demography

Population age structure, litter size and prenatal mortality

Of males and females killed in winter (pre-breeding), ca 30% were < 1 year old (males: 32%, total N = 397; females: 29%, total N = 361), and 6% of males and 15% of females were > 3 years old. We found no effect of landscape or farmland type on pre-breeding age structure.

Median litter size in adult females was 1 (range: 1-4; N = 151) in late winter, and 2 (range: 1-5; N = 54) in early spring. Kruskal-Wallis and Mann-Whitney tests were used to compare litter sizes between the landscape and farmland types, but no significant differences were found.

We examined 318 embryos in females killed in late winter, and 14% of these were resorbing. Of the 206 litters examined, 11% contained at least one viable and

Table 3. Percentages of adult females pregnant (A) and lactating (B) in late winter. Sample sizes are expressed as numbers for which data on pregnancy or lactation are available. Overall in late winter, 41 adult females were both pregnant and lactating.

A) Pregnant			
Landscape type	Arable a	69%	(N = 89)
	Arable b	63%	(N = 207)
	Pastural	40%	(N = 10)
Farmland type	Arable	65%	(N = 279)
	Pastural	53%	(N = 19)
B) Lactating			
Landscape type	Arable a	62%	(N = 50)
	Arable b	27%	(N = 146)
	Pastural	13%	(N = 8)
Farmland type	Arable	37%	(N = 182)
	Pastural	0%	(N = 15)

Table 4. Descriptive statistics of body condition, size and weight variables for adult male and female hares killed in winter. UN:C = urinary urea nitrogen to creatinine ratio; SUM = serum urea nitrogen (mg/dl).

	Males			Females		
	Mean	(min-max)	N	Mean	(min-max)	N
UN:C	29.2	(3.6-162.0)	202	19.2	(3.3- 53.7)	70
SUN	32.8	(7.8- 70.0)	111	29.7	(2.8- 84.3)	112
Kidney fat score	3.0	(0- 7)	348	4.1	(0- 8)	329
Bone marrow fat index	47.0	(33.9- 61.8)	40	43.5	(17.4- 61.2)	49
Hind foot length (in cm)	14.4	(12.1- 15.7)	352	14.5	(12.4- 15.7)	332
Cleaned weight (in kg)	2.6	(1.4- 3.4)	350	2.9	(1.4- 3.8)	330
Body weight (in kg)	3.2	(2.0- 4.1)	349	3.6	(1.8- 4.6)	331

one resorbing embryo, and 6% contained only resorbing embryos. These figures were consistent across landscape and farmland types. We found no resorption at other times of year (41 embryos in 19 litters examined).

Percentage of young females breeding

Of 35 young females killed in winter, 60% were pregnant and 9% were lactating. In winter, more young females than expected were breeding in the arable farmland type, and fewer than expected were breeding in the pastural farmland type (χ^2 = 5.358, df = 1, P = 0.020; Table 2). No significant difference in participation in breeding by young females due to landscape type was found.

Percentage of adult females breeding

Of adult females in spring, 50% were pregnant (total N = 22) and 71% (N = 17) were lactating; in summer, 19% were pregnant (N = 16) and 47% were lactating (N = 15); in autumn, 10% were pregnant (N = 10) and 11% were lactating (N = 9); in winter, 61% were pregnant (N = 331) and 32% were lactating (N = 225). Since there was a large increase in participation in breeding in winter (17% pregnant in early winter and 64% pregnant in late winter), we compared numbers of adult females pregnant and lactating in late winter in landscape and farmland types (Table 3), but found no significant differences in incidence of pregnancy. Incidence of lactation was higher than expected in arable a and lower than expected in arable b and pastural landscape types (χ^2 = 22.265, df = 2, P = 0.000). Adult females from pastural farmland types were also less likely to be lactating than those from arable farmland types (χ^2 = 8.368, df = 1, P = 0.004).

Body condition

We collected body condition data for adult hares (Table 4). Of hares killed in winter, both males and females from arable landscape types were significantly larger and heavier than those from pastural landscape types. Differences between hares from different farmland types were less clear, but the directionality of responses was highly consistent. Hares from areas where hare density is high (i.e. arable areas) were heavier than hares from areas of low density (Table 5).

Table 5. Final binary or nominal logistic regression models of body condition variables on the dependent variables landscape type and farmland type. Only variables which were significant at the simple level were included in the final model. Variables which were significant at the simple level but not in the final model are shown. In all cases the directionality of simple effects was as expected, i.e. hares from high density areas were in better condition than those from low density areas. In the final models, the reference event is always the level with the lower hare density, so a positive coefficient (± SE) indicates an effect as expected. Log-likelihood tests and goodness-of-fit tests are shown for the final models. Odds ratios (95% CI) are the odds of change in the dependent variable from the reference event for a one-step increase in the independent variable; fat score = kidney fat score; HFL = hind foot length (in cm); CW = cleaned weight (in kg); Aa = arable a, Ab = arable b, P = pastural landscape types; A = arable, P = pastural farmland types.

Dependent variable, gender	Independent variable	Levels of dependent variables	Coeff. ± SE	Z, P	Odds ratio		Var. sign. at simple level
Landscape	CW	Aa vs P (ref event)	1.64 ± 0.98	1.7, 0.094	5.1	(0.8- 34.9)	fat score, HFL
Males	CW	Ab vs P (ref event)	2.40 ± 0.98	2.4, 0.015	11.0	(1.6- 75.2)	
Δd_6 = 25.6, P = 0.000 Deviance goodness-of-fit P = 1.00							
Landscape	CW	Aa vs P (ref event)	2.54 ± 1.26	2.0, 0.043	12.7	(1.1-149.0)	fat score, HFL
Females	CW	Ab vs P (ref event)	2.67 ± 1.23	2.2, 0.030	14.4	(1.3-159.2)	
Δd_6 = 26.6, P = 0.000 Deviance goodness-of-fit P = 1.00							
Farmland	CW	A vs P (ref event)	1.26 ± 0.62	2.1, 0.040	3.5	(1.1- 11.8)	-
Females	Δd_1 = 4.0, P = 0.045 Deviance goodness-of-fit P = 0.99						

Table 6. Repeated-measures ANOVAs on body condition and size parameters for within-pair factor: habitat (arable and pastural) and between-pair factor: gender. Source = source of variation, df = degrees of freedom, MS = mean square, x = interaction term.

Parameter	Source	df	MS	F	P
Kidney fat score	Habitat	1	29.58	8.79	0.004
	Habitat x gender	1	3.73	1.11	0.296
	Error (habitat)	61	3.36		
	Gender	1	14.48	3.10	0.083
	Error (gender)	61	4.67		
Bone marrow fat index	Habitat	1	91.67	1.40	0.245
	Habitat x gender	1	34.08	0.52	0.475
	Error (habitat)	31	65.29		
	Gender	1	353.50	2.54	0.121
	Error (gender)	31	138.99		
Hind foot length (in cm)	Habitat	1	1.93	5.71	0.019
	Habitat x gender	1	0.03	0.08	0.776
	Error (habitat)	73	0.34		
	Gender	1	0.29	0.66	0.420
	Error (gender)	73	0.45		
Cleaned weight (in kg)	Habitat	1	142.03	4.54	0.037
(Box-Cox transformed;	Habitat x gender	1	0.07	0.0	0.960
λ = 2.697)	Error (habitat)	61	31.28		
	Gender	1	86.98	3.15	0.081
	Error (gender)	61	27.60		

Comparison of body condition in 78 matched pairs of hares (Table 6) revealed effects of habitat on kidney fat score, hind foot length and cleaned weight. Hares from arable areas were fatter (median fat score = 3 for arable and 2 for pastural hares), bigger (mean hind foot length = 14.3 cm for arable and 14.1 cm for pastural hares), and heavier (mean cleaned weight = 2.7 kg for arable and 2.5 kg for pastural hares) than hares from pastural areas (see Table 6).

Dietary quality

Analysis of dietary quality for 40 matched pairs of hares (18 male pairs and 22 female pairs; Table 7) revealed significant effects of habitat on % ash (higher in arable hares than in pastural hares), % fibre (lower in arable than in pastural hares), and % carbohydrates (lower in arable than in pastural hares). Effects of gender occurred in % protein (higher in males than in females) and % fibre (lower in males than in females; Table 8). There is no evidence to suggest that hares in arable areas are able to obtain a better quality diet than hares in pastural areas.

Climate

We found a significant difference in mean annual precipitation due to landscape type; mean annual precipitation was significantly lower in arable b (734 mm) than in arable a (899 mm) and in pastural landscape types (1,011 mm; oneway ANOVA: $F_2 = 30.74$, $P = 0.000$). A significant difference was also found due to farmland type; mean annual precipitation was lower in the arable farmland type (736 mm) than in the pastural landscape type (1,173 mm; oneway ANOVA: $F_1 = 86.24$, $P = 0.000$). In the years in which sampling for hares took place, in the locations from which our hares originated, wetter conditions were experienced in pastural landscape types and farmland types than in arable areas.

We found a significant difference in mean January temperature due to landscape type; mean January temperature was similar in arable a (4.1°C) and arable b (4.2°C), and significantly higher in the pastural landscape type (4.7°C; oneway ANOVA: $F_2 = 13.12$, $P = 0.000$). Mean January temperature in arable (4.1°C) and pastural farmland types (4.4°C) was similar (oneway ANOVA: $F_1 = 3.21$, $P = 0.076$).

Table 7. Descriptive statistics of dietary quality of paired hares. Only pairs in which the variable could be measured in both hares are included.

		Males			Females		
Dietary component		Mean	(min-max)	N	Mean	(min-max)	N
% ash	Arable	14.6	(8.2- 28.8)	18	16.4	(3.0- 46.9)	22
	Pastural	9.3	(4.9- 17.7)	18	11.5	(4.7- 37.6)	22
% protein	Arable	32.8	(17.1- 44.0)	18	28.9	(15.3- 38.7)	22
	Pastural	32.8	(26.1- 50.3)	18	28.6	(20.6- 35.3)	22
% fat	Arable	6.1	(3.0- 10.4)	18	5.8	(1.7- 8.7)	22
	Pastural	6.0	(4.4- 8.8)	18	6.0	(1.7- 8.7)	22
% fibre	Arable	14.4	(10.4- 22.6)	18	19.2	(10.7- 27.5)	22
	Pastural	17.7	(4.8- 28.1)	18	22.2	(11.9- 26.1)	22
% carbohydrates	Arable	32.2	(22.3- 54.9)	18	29.7	(10.3- 46.1)	22
	Pastural	34.2	(30.5- 39.1)	18	33.7	(20.8- 42.6)	22
Total dry weight (g)	Arable	9.4	(5.0- 16.9)	15	10.2	(4.3- 21.8)	17
	Pastural	10.2	(5.1- 19.0)	15	9.5	(5.6- 14.7)	17
Total energy (kJ)	Arable	121.6	(61.2-193.6)	15	122.4	(46.1-259.8)	17
	Pastural	139.1	(70.4-276.9)	15	120.1	(75.4-191.8)	17

Table 8. Repeated-measures ANOVAs on dietary quality parameters for within-pair factor: habitat (arable and pastural) and between-pair factor: gender. Source = source of variation, df = degrees of freedom, MS = mean square, x = interaction term.

Parameter	Source	df	MS	F	P
Log (% ash+1)	Habitat	1	0.48	9.82	0.003
	Habitat x gender	1	0.00	0.04	0.852
	Error (habitat)	38	0.05		
	Gender	1	0.02	0.62	0.435
	Error (gender)	38	0.03		
% protein	Habitat	1	0.42	0.03	0.870
	Habitat x gender	1	0.55	0.04	0.852
	Error (habitat)	38	15.41		
	Gender	1	318.74	5.99	0.019
	Error (gender)	38	53.19		
% fat	Habitat	1	0.09	0.04	0.851
	Habitat x gender	1	0.58	0.24	0.629
	Error (habitat)	38	2.44		
	Gender	1	0.45	0.17	0.686
	Error (gender)	38	2.68		
% fibre	Habitat	1	92.23	6.73	0.013
	Habitat x gender	1	25.31	1.85	0.182
	Error (habitat)	38	13.71		
	Gender	1	262.38	11.20	0.002
	Error (gender)	38	23.43		
% carbohydrates	Habitat	1	184.07	4.92	0.033
	Habitat x gender	1	19.59	0.52	0.474
	Error (habitat)	38	37.44		
	Gender	1	43.44	1.04	0.315
	Error (gender)	38	41.96		
Total dry weight (in g)	Habitat	1	0.01	0.00	0.980
	Habitat x gender	1	8.75	0.77	0.388
	Error (habitat)	30	11.43		
	Gender	1	0.16	0.01	0.922
	Error (gender)	30	16.33		
Total energy (in kJ)	Habitat	1	927.76	0.46	0.503
	Habitat x gender	1	1563.61	0.78	0.386
	Error (habitat)	30	2016.52		
	Gender	1	1329.51	0.45	0.506
	Error (gender)	30	2938.17		

Discussion

Demography

Litter size and prenatal mortality

Litter sizes given here for late winter and early spring are not directly comparable with those in the literature, since we used predicted season of birth. Litter size is unrelated to habitat, and to nutrition (Hackländer et al. 2002b), but is related to weather conditions (Hewson & Taylor 1975).

We found typical rates of prenatal mortality for late winter (14% of embryos): in the east of England, 14% of litters were resorbed (Lloyd 1968), and in the Russian Federation, 24% of females pregnant in January had resorbing embryos (Kolosov 1941). In Poland, 6-10% of embryos were resorbed in February-April, whereas in January 80% of embryos were resorbed (Raczyński 1964).

Percentage of females breeding

The percentage of young females we found breeding in winter differed between farmland types. In the east of England 4% (Lincoln 1974), and in France about 14% (Bray 1998) of females breed in their year of birth. Lloyd (1968) found 37% of young females killed in winter in the east of England to be pregnant; we found 60%.

Although we found no effect of landscape type or farmland type on percentage of adult females pregnant, the incidence of pregnancy we found in late winter, spring and summer was low compared to that found by others using similar methods to define pregnancy (60-100% in Scotland, Hewson 1964; ca 80% in the Netherlands, Broekhuizen & Maaskamp 1981). Pregnancy rate in arable areas in Poland differed between consecutive Februaries (44 and 85%; Raczyński 1964). Variation in participation in breeding is typical of the hare and may be due to intrinsic factors and/or variation in climate (Marboutin et al. 2003, Smith et al. 2005).

We found a low incidence of lactation in pastural habitats, but incidence of pregnancy and litter size was similar in arable and pastural habitats. This suggests that either survival of leverets is lower in pastural than in arable areas, or females suckle for shorter periods of time, perhaps because they are in poor condition and cannot continue to produce milk. Both would result in reduced survival of leverets or juveniles. Leveret and juvenile survival is estimated at 0.25-0.50 in an arable area (Pépin 1989), 0.23 in a mixed agricultural area and 0.18 in a mainly pastural area (Frylestam 1980b).

Body condition and dietary quality

The snapshot views of body condition provided by UN: C and SUN, and of dietary quality provided by the analysis of stomach contents, were similar in hares from arable and pastural habitats, suggesting that in both habitats hares can fulfil their short-term nutritional needs. Our values for the bone marrow index are similar in both habitats, and similar to those in other lagomorphs (Warren & Kirkpatrick 1978, Henke & Demarais 1990).

The difference we found in kidney fat index and body size suggests that energy expenditure is higher in pastural areas than in arable areas, perhaps due to climatic differences, such as those we demonstrate. Relatively wet conditions in pastural areas could lead to high energy demands. Body condition is often correlated with nutritional quality and is therefore a measure of habitat quality (Villafuerte et al. 1997), but body condition in snowshoe hares *Lepus americanus* improves if predators are removed as well as if diets are supplemented (Hodges et al. 1999). As well as nutritional quality, foraging behaviour and predation risk determine body condition (Villafuerte et al. 1997).

We expected body condition and dietary quality to be low in pastural areas where the density of hares is relatively low. However, compared with those from arable areas, hares from pastural areas in our study were able to obtain a similar quality diet, but were unable to maintain as good body condition.

Conclusions

We present differences in demography which help to explain the differences in density of hares in arable and pastural areas. Pasture is a suboptimal habitat for hares, where energy expenditure is relatively high, body condition is relatively poor, incidence of lactation in late winter and thus recruitment is reduced, but food quality is similar to that in arable areas. Reduced survival of leverets to weaning in pastural areas, coupled with a prebreeding age structure which is similar in arable and pastural areas, suggest that post-weaning juvenile survival is lower in arable areas than in pastural areas. Also, adult survival may be relatively low in pastural areas, due to relatively poor body condition. Our data confirm that pastural landscape types are on average warmer than arable landscape types (Bunce et al. 1996) and experience more precipitation. Unfavourable climatic conditions are therefore associated with pastural habitats, and climatic differences may be related to the differences in demography and body condition we observe (Smith et al. 2005). High precipitation results in mortality in leverets (Hackländer et al. 2002a), and high winter temperatures result in high levels of recruitment, but also in high levels of mortality through increased transmission of disease (Hewson & Taylor 1975, Hackländer et al. 2002a). Pastural areas also support higher numbers of foxes than arable areas (as indicated by numbers shot; (Tapper 1992), and by faecal counts (Webbon et al. 2004)).

Implications

Research into the conservation of hares needs to focus on determining their causes of death. Although foxes are common in areas where hares are rare (Vaughan et al. 2003) and predator removal may help to increase hare populations (Lindström et al. 1994), the provision of permanent cover alone can result in increased numbers of hares (Slamečka 1991). Conservation efforts should therefore concentrate not only on the provision of year-round forage (Panek & Kamieniarz 1999, Vaughan et al. 2003) and on the inclusion of some arable land in mainly pastural habitats (Vaughan et al. 2003), but also on the reduction of predation and exposure to unfavourable weather by the provision of year-round vegetative cover (Smith et al. in 2004). Suitable cover is provided by fallow land (Vaughan et al. 2003), rough grass margins (Panek & Kamieniarz 1999), and shelterbelts, woodland and hedges (Tapper & Barnes 1986, Slamečka 1991). Efforts to conserve the hare in accordance with the Bern Convention (Anon. 1979) or to achieve the aims of the BAP (Anon. 1995) need to focus on increasing the survival of leverets and adult hares (Smith et al. submitted).

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