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Do voles make agricultural habitat attractive to Montagu's Harrier *Circus pygargus*?

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Loss and degradation of habitat threatens many bird populations. Recent rural land-use changes in the Netherlands have led to a shift in habitat use by breeding Montagu's Harriers *Circus pygargus*. Since the 1990s, unprecedented numbers of this species have bred in farmland compared with numbers in natural habitat. Destruction of nests by agricultural operations, however, compromises breeding success. Between 1992 and 2005, the number of breeding pairs in the northeastern Netherlands was positively, though weakly, correlated with previous-year estimated abundance of voles, mostly *Microtus arvalis*. In good vole years, the onset of laying was earlier and mean clutch size was larger. Vole abundance was relatively higher in set-aside land and in high and dense vegetation. We suggest that agri-environmental schemes aimed at increasing the availability of voles in agricultural breeding areas may be an effective management tool for the conservation of Montagu's Harriers in the northeastern Netherlands.

In recent decades, many bird populations have declined in Europe and worldwide (Tucker & Heath 1994, Norris & Pain 2002). One of the principal causes of these declines has been habitat loss (e.g. Owens & Bennett 2000, Bruford 2002, Newton 2004). Large areas of natural habitat have been lost from Europe, where many bird species have become increasingly reliant on farmland habitats (Tucker 1997). One such species is Montagu's Harrier *Circus pygargus* (Arroyo *et al.* 2002), the conservation status of which is vulnerable because more than half of its global population is found in Europe (Burfield & Van Bommel 2004). Montagu's Harrier is included in Annex I of the European Birds Directive (79/409/EEC), which lists species that are classified as particularly threatened and in need of special conservation measures.

European Montagu's Harriers are long-distance Palearctic migrants, traditionally breeding in lowland heaths, dunes, hay-meadows and (pseudo-) steppes (Clarke 1996, Leroux 2004). Since the 1990s, 70–90%

of breeding pairs in Western Europe have bred in agricultural habitats (Arroyo *et al.* 2002). With intensification of land use, the percentage of Harriers breeding in farmland is also expected to increase in Eastern Europe. Montagu's Harriers are opportunistic predators (Arroyo 1997) and, in vole-rich habitats, feed mainly on voles. Up to 90% of their diet in Western France (Butet & Leroux 1993, Salamolard *et al.* 2000) and around 60% in Dutch farmland consisted of voles (Koks *et al.* 2005).

Montagu's Harriers breeding in farmland, however, may experience lower breeding success than those in more natural habitats. Between 20 and 70% of nests of this ground-nesting species can be destroyed during harvesting activities (Corbacho *et al.* 1997, Koks *et al.* 2001, Millon *et al.* 2002). In the Netherlands, lucerne (alfalfa) is mown repeatedly and early in the season (starting in May–June), which means that clutches in this crop do not survive and even breeding females can be killed during the harvest. Nests in early harvested winter barley and winter wheat are at risk as well. In the Netherlands, nests are protected by leaving a 10 × 10-m unharvested area around nests and placing electric fences around the remaining vegetation to exclude terrestrial predators.

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Nest protection in the Netherlands has proven to be successful (Koks & Visser 2002), and farmers are willing to participate without financial compensation. Nest protection, however, is still very resource-consuming in terms of time, manpower and equipment (Arroyo *et al.* 2002).

Montagu's Harriers were widespread and numerous (500–1000 pairs) in the Netherlands until the beginning of the 20th century (Zijlstra & Hustings 1992). The Dutch population originally nested in natural vegetation and, during the 1970s and 1980s, in deciduous tree plantations (Fig. 1). By 1987, the population had declined to near extinction (Fig. 1; Zijlstra & Hustings 1992). In the early 1990s, however, Montagu's Harriers were observed regularly in agricultural habitat in the eastern part of the province of Groningen (northeastern Netherlands). During this period, vole numbers in farmland in East Groningen increased rapidly, following increases in agricultural set-aside. In 1988, 10–20% of farmland in this area was set aside according to European agricultural policy (Koks & Van Scharenburg 1997, Robson 1997). Numbers of Common Voles *Microtus arvalis* in the resulting fallow grassland increased rapidly, and vole-eating raptors such as Hen Harrier *Circus cyaneus*, Montagu's Harrier, Common Kestrel *Falco tinnunculus* and Short-eared Owl *Asio flammeus* settled in East Groningen (Koks & Van Scharenburg 1997).

This study presents information derived from the East Groningen population. Ecological information and knowledge of population trends is crucial for

effective conservation management (e.g. Green 2002, Underhill & Gibbons 2002, Komdeur & Pels 2005, Whittingham *et al.* 2005), and for the development of conservation strategies required by EU agri-environmental policy (Ormerod & Watkinson 2000, Fox 2004). We investigated (1) the relationship of vole abundance with the number of Harrier pairs present in the study area and Harrier breeding parameters, (2) the importance of voles in the Harrier diet and (3) the relationship between vegetation characteristics and vole abundance. This information can be used to determine which vegetation types support high densities of Montagu's Harrier prey, and as a result, may attract higher numbers of Harriers and sustain better breeding performance than other vegetation types. Management of Harrier prey populations via habitat management may be an alternative conservation strategy to intensive nest protection.

METHODS

Study area and study population

The study site was located in the eastern part of the province of Groningen, northeastern Netherlands (53°11'N, 7°4'E, surface area of *c.* 650 km²). The relatively uniform, flat and open polder landscape of East Groningen is mainly used for cultivation of winter wheat but also for other land uses including pasture and cultivation of lucerne, sugar beet, oilseed rape and winter barley.

Montagu's Harriers in East Groningen constituted about two-thirds of the Dutch population between 2000 and 2005 (172 out of the total 229 pair-years, Dutch Montagu's Harrier Foundation unpubl. data). The remaining pairs were located in the province of Flevoland (29 pair-years, also in agricultural breeding habitat), the Lauwersmeer nature reserve (26 pair-years) and in other areas (2 pair-years).

Harrier pairs and nests were located each year (1990–2005) through observation of birds showing territorial, mating or nesting behaviour. The total number of pairs present in the study area was divided into pairs that bred (successfully or not), pairs that were territorial but did not breed and pairs of unknown breeding status. A minority of males were bigamous, e.g. three out of 27 males (11%) in East Groningen in 2005. Monogamous and bigamous pairs were treated in the same way for the analyses, because the breeding parameters we used were measured per nest, not per individual. Individual birds were distinguished by colour rings and plumage

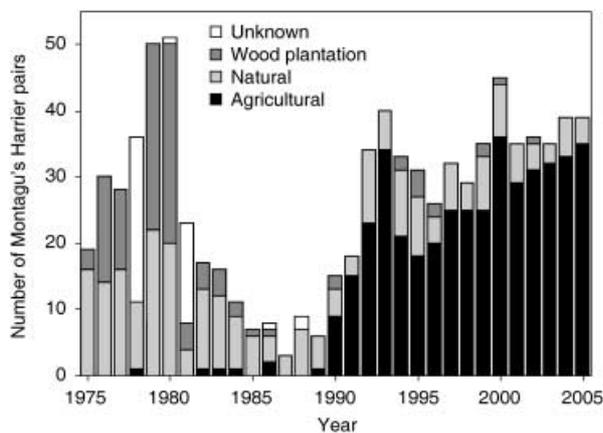


Figure 1. Total number of Montagu's Harrier pairs in different breeding habitats in the Netherlands, 1975–2005 ($n = 836$) (Zijlstra & Hustings 1992, Bijlsma 1994, Dutch Montagu's Harrier Foundation unpubl. data).

characteristics. The annual finite population growth rate λ was calculated according to the formula $\lambda = n_{t+1}/n_t$ (Sibly *et al.* 2003), where n_{t+1} was the total number of pairs in the following year and n_t was the total number of pairs in a given year. Linear regressions were calculated using SPSS version 12.0.1 (SPSS Inc.).

Known nests were visited on average three times during a breeding season (May–July). The purpose of the first visit was to find the nest, the second visit was made in order to check the number of young, and the third visit was made to ring the young and measure them (weight, wing length, claw with and without nail, eye colour, number of fault bars). The estimated clutch size at laying was a minimum, as we could not exclude the possibility of partial predation. If the clutch was incomplete during the first visit, laying date could be back-calculated assuming eggs had been laid every second day (Clarke 1996). For nests which were first visited in the nestling phase, nestling growth curves were used to calculate the age of the young and to back-calculate approximate laying dates (Bijlsma 1998). Means are denoted \pm se.

Clutches in fields that were harvested before the fledging of the young were protected. An electric fence prevented terrestrial predators from entering the nest patch. Additional nest visits were made to check the battery of the protection fence. Protected clutches that would have been destroyed without intervention had the same probability of producing at least one young as clutches that did not require protection (probability of 63% (56/89) vs. 60% (164/274), Dutch Montagu's Harrier Foundation unpubl. data).

Precautions were taken to minimize any risk of desertion and exposure to predation due to nest visits. Nests were only visited in the early stages of nesting when this was necessary in order to protect them. Care was taken not to leave a trail in the crop. Nest desertion caused by our visits was only observed in four pairs out of 172 pair-years in East Groningen (1990–2005). These were nests in lucerne that had to be visited at a very early stage to prevent destruction by harvesting activities. In two cases, the nest was empty (before the start of laying) and in the other two, the nest contained one egg.

We used laying date and clutch size as measures of adult reproductive performance. In raptors, earlier laid clutches have a higher chance of producing young, and larger clutches can produce more young (e.g. Daan *et al.* 1990). Laying date affects the chances that young will be produced, regardless of additional effects of nest protection and predation.

Clutch size reflects the investment of the female in egg production, and the investment both parents will have to make to rear the young. In this study (investigating the relationship between reproductive performance and food supply), fledging success is not a useful measure: the number of fledglings produced not only depends on the available food, but also on nest protection and predation.

Vole abundance and vegetation measures

Each year from 1992 to 2005 (except in 2002), the abundance of small mammals during the first week of August was estimated. The missing abundance in 2002 was estimated from the regression equation of vole index vs. proportion of small mammals in pellets based on biomass (1994, 1996–2001, 2003–05). The proportion of small mammals in pellets was arcsine square-root transformed before regression with the vole index (regression line: $y = 0.72 + 0.03 \cdot \text{vole index}$; $F = 3.2$, $df = 1$, $P = 0.1$). Although the relationship between vole index and the proportion of small mammals in pellets was a statistically non-significant trend, we assume it represents a biologically meaningful way to produce an estimate for the 2002 vole abundance, especially as 2002 was a year with a low proportion of small mammals in pellets and had the lowest estimated vole index (according to the above model). In order to ensure that our estimated value did not overly influence the results, analyses involving vole index were also performed without the 2002 data. Results were broadly similar, in terms both of significance levels and of parameter estimates in the regression equations.

Small mammals were trapped according to a standard protocol (Dijkstra *et al.* 1995, Hörnfeldt 2004): five snap traps were baited with carrots and arranged in a circle of diameter 4 m, if present near vole runways or burrows, forming one station. One transect comprised ten stations spaced 10 m apart. On average, 14 ± 1 transects were checked annually on three consecutive days. If transect vegetation type had not changed, the same transect was measured in consecutive years; otherwise, new transects were chosen. Transects were located in different habitats, grouped in two categories. Category one included non-fallow vegetation types, i.e. roadsides, ditch edges, wood plantations and plantation edges, cereals (wheat, barley), grassland, grass seed, old dyke used as pasture, lucerne, grassy path, and small sample sizes of grazed nature reserve and sugar beet.

Category two included fallow vegetation types, i.e. set-aside land under different management regimes. This category comprised whole set-aside fields (remaining fallow for more than 5 years) and field margins, which were managed according to agri-environmental schemes. Margins set aside under these schemes remain fallow for 6 years, and must comply with set mowing, fertilizer and pesticide/herbicide restrictions.

Almost all small mammals trapped (1845/1866) were identified to species level. Of these ($n = 1845$), 92% were Common Voles (other species trapped: 4% *Apodemus sylvaticus*, 3% *Sorex araneus*, 1% *Micromys minutus*, 1% *Clethrionomys glareolus*, and < 1% *Microtus agrestis* and *Mus musculus*). As most small mammals trapped were voles, 'small mammals' are hereafter referred to as 'voles'.

To produce a vole index, a multilevel logistic regression model with a logit link function (Quinn & Keough 2002, Rasbash *et al.* 2004) was fitted to the vole capture success data (average value over 50 traps and three trap nights for each transect in each year, $n = 177$), using the program MLwiN version 2.02 (Multilevel Models Project, Institute of Education, University of London). The estimation method was second-order penalized quasi-likelihood (PQL) and parameter estimates were calculated by Residual Iterated Generalized Least Squares (RIGLS; Snijders & Bosker 1999). Level one represented the observations, level two years (1992–2005) and level three unique transect numbers. Year was also added as a fixed effect (categorical variable). The second fixed effect tested was habitat type (fallow or non-fallow). Statistical significance of the effects was determined by Wald tests (the Wald statistic follows a χ^2 distribution). Trapping probabilities were calculated from the model including year as well as habitat type. These probabilities were multiplied by 100 to derive a vole index, i.e. an estimate of the number of voles trapped in 100 trap nights.

We tested whether sampling the same transect in multiple years affected the number of voles trapped. For this, we used a similar multilevel logistic regression model as for the vole index. This model contained two explanatory variables: habitat type ($\beta = 0.77 \pm 0.21$, Wald statistic = 13.4, $df = 1$, $P = 0.0002$) and the number of years an individual plot was sampled (1–12 years, $\beta = 0.006 \pm 0.04$, Wald statistic = 0.02, $df = 1$, $P = 0.8$). There was no negative effect of the number of years a transect was sampled on the number of voles trapped, indicating that the data were not biased by destructive sampling.

In 2003–05, vegetation height and cover of all vole trapping transects were measured. Vegetation height was measured by dropping a polystyrene disc (diameter 45 cm, height 1.5 cm) on the vegetation, along a tubing which was calibrated with a centimetre scale. Vegetation cover was assessed visually over a 20×20 -cm square as the percentage of the area that was covered by live or dead vegetation. Vegetation height and cover were measured ten times at random locations within each transect. To establish the effects of vegetation height and cover on trapping probabilities, a multilevel model was fitted to the subset of data ($n = 52$) for which information on vegetation structure was available (2003–05). The model fitted was two-level (level 1, observation; level 2, year) because sample sizes were too small to include transect number as a third level.

Harrier diet

During each week of each breeding season (end of April until beginning of August, 1992–2005), perch posts, field margins and paths along ditches near nest-sites were checked for pellets. Pellet sample size differed between years, so in order to exclude the confounding effect of sample size, we included data only from years with sample sizes of at least 150 pellets in our analyses (1994, 1996–2005). Pellets were stored (dry) and processed at the end of the season. The minimum number of individual prey per pellet was counted. All prey individuals present in pellets were assigned to prey categories (according to taxon) and, if possible, species and age class, using characteristics of fur, teeth, feathers and other remains with the help of identification literature (Jenni & Winkler 1994, Lange *et al.* 1994, Kapteyn 1999) and reference collections. For the resulting 97 taxon, species and age categories, an average mass was available (data from Schipper 1973, Arroyo 1997 and Dutch Montagu's Harrier Foundation unpubl.). Prey numbers in each category were multiplied by average biomass of the category to calculate its proportion of total biomass.

Five main categories of prey in pellets ($n_{\text{pellets}} = 3353$) were distinguished: 'small mammals', 'larger mammals', 'birds', 'eggs' and 'invertebrates'. Of the 'small mammals' category, 1917 out of 3128 prey items were sorted into taxonomic groups: voles made up 95%, mice 4% and shrews 1%. Of items identified to species level in this category, 95% were Common Voles (1539/1620) and 5% belonged to other species (3% *Micromys minutus*, 1% *Apodemus sylvaticus*, and (all < 1%) *Sorex araneus*, *Mus musculus*,

Clethrionomys glareolus, *Microtus agrestis* and *Sorex minutus*). In the 'larger mammals' category, 145 out of 169 items were identified to species level, of which 70% were Brown Hares *Lepus europaeus*, 15% Rabbits *Oryctolagus cuniculus*, 14% Moles *Talpa europaea* and 1% Brown Rats *Rattus norvegicus*. From 960 prey items categorized as 'birds', 88% were passerines (mostly Yellow Wagtails *Motacilla flava*, Meadow Pipits *Anthus pratensis* and Skylarks *Alauda arvensis*) and 22% were other birds, such as Northern Lapwings *Vanellus vanellus* and Quails *Coturnix coturnix*. The remaining categories were 'eggs' (of passerines and other bird species) and 'invertebrates' (mostly Coleoptera, Orthoptera and Odonata spp.).

In 2003, prey delivery was observed at one nest. The nest was located in lucerne and protected. A hide was placed outside the nest protection fence at 6 m from the nest. Observations were conducted by one observer (C.T.) during the nestling phase (10 July–2 August). A total of 13 observations were made, with an average duration of 8.5 h. Prey delivered by the parents was filmed with a video camera and analysed subsequently. To test whether diet revealed by pellet analysis reflected diet as shown by video

tape, the results of the video analysis were compared with prey items identified from pellets collected on the same nest in the same period.

RESULTS

Vole abundance, Harrier population growth and breeding parameters

Annual differences in vole index were statistically significant (Table 1). The vole index showed two major peaks, in 1992 and 2004 (Fig. 2a). The total number of Montagu's Harrier pairs in the study area increased steeply up to 1993, decreased between 1993 and 1996, and increased more or less steadily after this time (Fig. 2a). Most of these pairs were breeding pairs (Fig. 2b). Vole index in year t was not significantly correlated with the total number of Harrier pairs, the number of breeding pairs or the number of non-breeding pairs in the same year (Linear regression, total number: $F = 0.02$, $df = 1$, $P = 0.90$; breeding: $F = 0.72$, $df = 1$, $P = 0.4$; non-breeding: $F = 0.08$, $df = 1$, $P = 0.8$). However, the relationship between vole index in year t and the total number of

Table 1. Multilevel logistic regression model for average vole capture success per transect per year ($n = 177$). Predictions of the model multiplied by 100 produced the vole index (estimated vole number trapped per 100 trap nights).

Explanatory variable	n (for year: transects, for habitat type: transect-years)	β (se)		Wald statistic	df	P	Vole index (voles/100 nights)
		β	(se)				
Fixed part							
Intercept		-2.12	(0.38)	30.39	1	< 0.0001	
Year				97.37	12	< 0.0001	
1992	10	Reference					17.83
1993	14	-2.46	(0.47)				2.03
1994	12	-2.53	(0.50)				1.83
1995	12	-2.40	(0.50)				1.96
1996	11	-2.14	(0.50)				2.28
1997	11	-2.67	(0.51)				1.36
1998	13	-1.53	(0.47)				4.11
1999	13	-1.36	(0.46)				4.82
2000	10	-1.89	(0.51)				2.75
2001	13	-3.30	(0.52)				0.77
2003	19	-1.22	(0.43)				5.54
2004	21	-0.51	(0.41)				11.04
2005	18	-2.21	(0.49)				2.21
Habitat type				12.29	1	0.0005	
Non-fallow	84	Reference					2.81
Fallow	93	0.88	(0.25)				6.31
Random part							
Year level		0.79	(0.14)	31.29	1	< 0.0001	
Transect level		0.34	(0.15)	4.98	1	0.03	

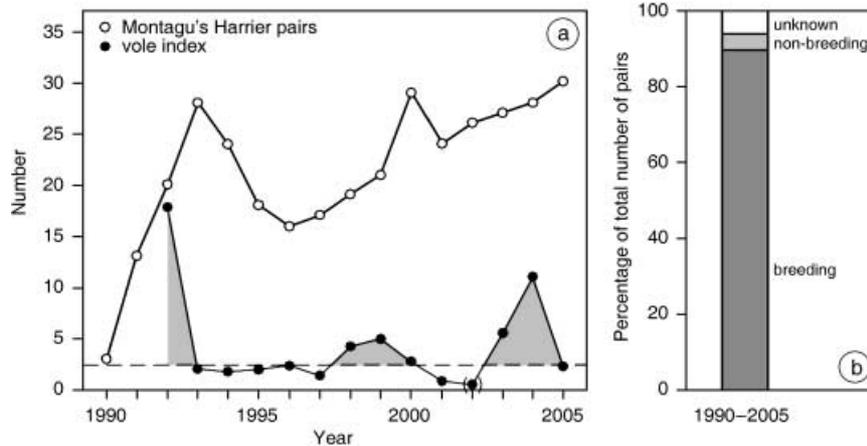


Figure 2. (a) Number of Montagu's Harrier pairs (including non-breeding pairs and pairs of unknown breeding status) in East Groningen, Netherlands. Vole index (no. trapped/100 nights) in East Groningen (1992–2001, 2003–05) with estimated vole index of 2002 (closed circle in parenthesis). The dashed line indicates the threshold value (2.3) of vole index above which population growth was predicted to be positive ($\lambda > 1$) (Fig. 3a). The grey surface indicates vole indices above this line (years relatively rich in voles). (b) Percentages of breeding pairs, non-breeding pairs and pairs of unknown breeding status of the total number of Montagu's Harrier pairs in East Groningen (1990–2005).

pairs in year $t + 1$ approached statistical significance ($F = 3.8$, $df = 1$, $P = 0.08$). Furthermore, the annual finite population growth rate λ from year t to year $t + 1$ (based on the total number of pairs) was positively correlated with vole index in year t (Fig. 3a). Above a threshold vole index of 2.3 in year t , population growth was predicted to be positive ($\lambda > 1$). The relationship of λ with vole abundance in year $t - 1$ was not significant ($F = 0.7$, $df = 1$, $P = 0.4$); the relationship between λ and the vole index in year $t + 1$ approached statistical significance ($F = 4.5$, $df = 1$, $P = 0.06$).

Clutches were laid significantly earlier in years with a high vole index (Fig. 3b) and clutches were significantly larger in years with a high vole index (Fig. 3c). Clutch size at laying was significantly negatively correlated with laying date ($n = 144$, $F = 74.8$, $df = 1$, $P < 0.0001$).

Voies in Harrier diet

In terms of both numbers and biomass, small mammals were the most important prey category found in pellets (Fig. 4a & b). The average percentage of small mammals in the diet, based on numbers found in the pellets of adults, was $61 \pm 4\%$ (1994, 1996–2005) with a range of 41% (1994) to 78% (1998). The average percentage of small mammals based on biomass was $52 \pm 4\%$ with a range of 30% (1994) to 75% (1998). Larger mammals were more important in terms of biomass (on average $23 \pm 2\%$) than in

terms of numbers ($4 \pm 1\%$). On average, birds constituted $21 \pm 2\%$ of items found and $22 \pm 3\%$ of biomass. Smaller prey categories (eggs and invertebrates) were less important, especially in terms of biomass. Video observations at one nest ($n = 78$ items identified) suggested that small mammals made up 83% of ingested biomass of juveniles, compared with 55% biomass as assessed from pellets of juveniles ($n = 35$ items identified, Fig. 5). Larger mammals were not observed from video playback but accounted for 21% of biomass (1/35 items) as assessed from pellets. Birds constituted 17% of biomass based on video observations and 24% based on pellet analysis. Invertebrates were a minor dietary component according to data from both video and pellets, especially in terms of biomass (both less than 1%). The number and biomass of small mammals estimated from video observation was higher than from pellet analysis, and larger mammals and birds were more often recorded in pellets. Small mammals were, as for adults, the most important diet component.

Vole abundance, vegetation type and vegetation structure

The vole index was more than twice as high in fallow habitat types as in non-fallow types (Table 1). Additionally, significantly larger numbers of voles were trapped both in higher and in more dense vegetation, even when controlling for vegetation type (Table 2). Vegetation height and cover were

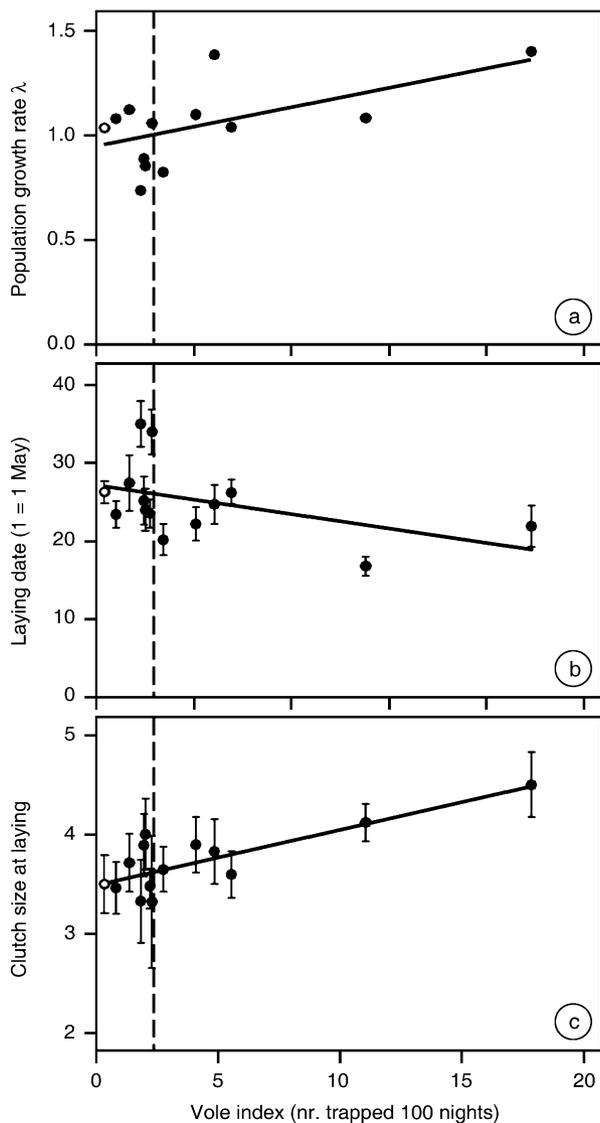


Figure 3. (a) Annual finite population growth rate λ ($\lambda = n_{t+1}/n_t$) based on the total number of Montagu's Harrier pairs, $n = 13$) vs. vole index (v_i , no. trapped/100 nights) at time t (1992–2004). $\lambda = 0.9 + 0.02 \cdot v_i$; $F = 5.7$, $df = 1$, $P = 0.04$. Dashed line indicates threshold value of vole index ($v_i = 2.3$) above which population growth was predicted to be positive ($\lambda > 1$). (b) Annual average laying date (ld) expressed as day number starting at 1 May vs. vole index at time t (1992–2005). Linear regression analysis on individual laying dates ($n = 204$): $ld = 26.2 - 0.5 \cdot v_i$; $F = 13.0$, $df = 1$, $P < 0.0001$. (c) Annual average clutch size (cs) at laying vs. vole index at time t (1992–2005). Linear regression analysis on individual clutch sizes ($n = 168$): $cs = 3.5 + 0.06 \cdot v_i$; $F = 13.6$, $df = 1$, $P < 0.0001$. Open circles are values for 2002 based on estimated vole index.

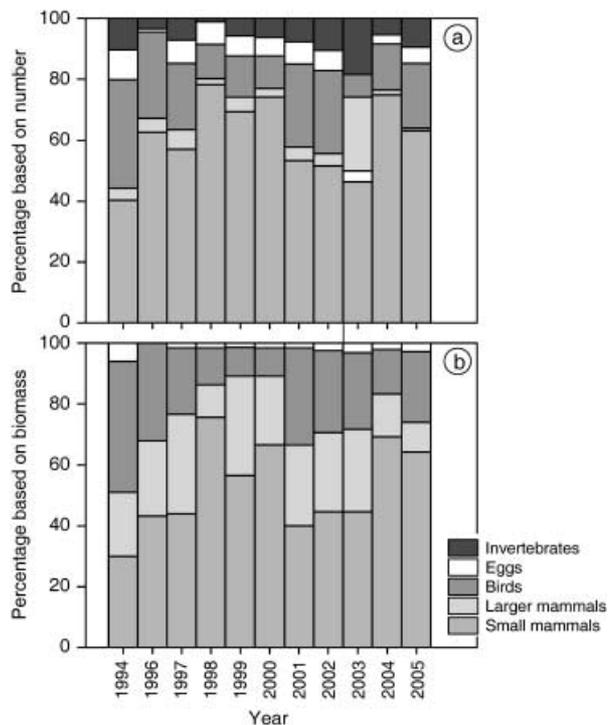


Figure 4. Diet of adult Montagu's Harriers: (a) prey categories in pellets (1994, 1996–2005) as percentage based on numbers and (b) based on biomass.

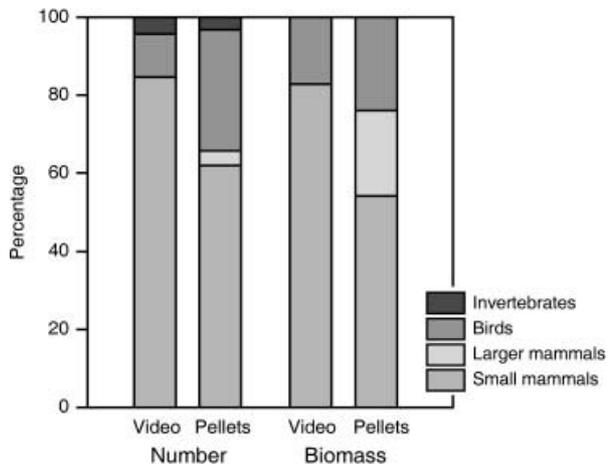


Figure 5. Diet of Montagu's Harrier nestlings: prey categories as percentages based on numbers and biomass recorded on video at the nest ($n = 78$ prey items) and found in pellets collected on the same nest during the same period ($n = 35$ prey items).

Explanatory variable	<i>n</i> (transect-years)	β	(se)	Wald statistic	<i>df</i>	<i>P</i>
Fixed part						
Intercept		-3.78	(0.30)	156.20	1	< 0.0001
Habitat type				8.72	1	0.003
Non-fallow	25	Reference				
Fallow	27	0.42	(0.14)			
Vegetation height		0.03	(0.004)	36.93	1	< 0.0001
Vegetation cover		0.01	(0.003)	5.25	1	0.02
Random part						
Year level		0.89	(0.22)	16.97	1	< 0.0001

Table 2. Multilevel logistic regression model for average vole capture success per transect per year ($n = 52$) for transects with known vegetation structure (2003–05).

significantly correlated ($F = 6.9$, $df = 1$, $P = 0.01$). Percentage cover was variable in short vegetation, but was consistently high in tall vegetation.

DISCUSSION

Fluctuations in vole abundance

No regular vole cycles could be distinguished in East Groningen (1992–2005), in contrast to observations of vole cycles in (semi-)natural areas in the Netherlands (e.g. Dijkstra *et al.* 1988, Beemster & Dijkstra 1991, Bijlsma 2005). Agricultural management may have interfered with natural fluctuations of vole abundance in the study area: from 1992 onwards, long-term, large-scale fallow land disappeared, and short-term, small-scale set-aside land increased due to new agri-environmental schemes realized after the MacSharry reform of the European Common Agricultural Policy.

Harrier population growth in relation to vole abundance

We found no relationship between Montagu's Harrier numbers and vole abundance in the same year. Such a relationship has been observed for Montagu's Harrier in western France (Salamolard *et al.* 2000), for other vole-eating raptors, such as Hen Harrier (Hamerstrom 1979, Redpath *et al.* 2002) and Common Kestrel (Village 1990), and for various owl species (Village 1981, 1987, Korpimäki 1985, Hörnfeldt *et al.* 1990, Taylor 1994). The growth rate of the Harrier population from year t to year $t + 1$, however, was positively though weakly correlated with the vole index in year t . This cannot be explained by an increase in recruits born in year t as Montagu's

Harriers only rarely return to the breeding grounds in their second calendar year, and usually start breeding in their third calendar year (Clarke 1996). In the East Groningen population, only one second calendar year bird (a female) was observed to breed. An increase in population size from locally born recruits might be expected 2 years after a good vole year, but we found no evidence of a relationship between λ and vole index in year $t - 1$. This is probably due to the low philopatry of the species (Arroyo *et al.* 2004), including the East Groningen population. Despite the fact that all young fledged from known nests since 1999 have been colour ringed, birds known to be of local provenance comprise a relatively small proportion of breeders in East Groningen (e.g. 13% (5/38) in 2005). This suggests that we are not dealing with a closed population in East Groningen, and that there is movement to and from adjacent subpopulations of the northwestern European Montagu's Harrier population in northern Germany (Lower Saxony, Schleswig-Holstein) and southern Denmark. This is confirmed both by the rapid increase of Montagu's Harrier pairs in East Groningen from three pairs in 1990 to 20 pairs in 1992 (many of these birds must have come from outside the Netherlands, as by 1987 the Dutch population was virtually extinct), and by ring recoveries and resightings of Dutch birds breeding in Germany and German birds breeding in the Netherlands (Koks & Visser 2002, Trierweiler *et al.* 2006b).

The relationship between the number of Harrier pairs and the vole index of the previous year suggests that Montagu's Harriers can use information on vole abundance from the previous year when deciding where to settle and breed after returning from their West African wintering grounds in spring. Harriers could be attracted to the area when food conditions

were good in the previous year, but settle in another subpopulation when food conditions were poor, as annual vole densities tend to vary synchronously over relatively large areas (Newton 1998). Harriers could also be attracted to areas where conspecific reproductive success was high the previous year (Arroyo *et al.* 2002), as a result of 'public information' (Valone & Templeton 2002). During a satellite telemetry study, two Dutch Montagu's Harrier females have been observed passing through breeding areas of neighbouring Harrier populations during autumn migration, which could be a mechanism of 'prospecting' (Trierweiler *et al.* 2006a). Finally, adult survival could be positively related to vole abundance, with lower survival and fewer returning adults in years following poor vole years.

Harrier breeding parameters in relation to vole abundance

Vole numbers in summer can be considerably higher than at the time when Montagu's Harrier breeding territories are established (Dijkstra *et al.* 1988). It has been shown that spring vole abundance is positively correlated with summer vole abundance of the same year (Butet & Leroux 2001). We assume that our summer estimates can be used to indicate food availability some months earlier, when laying date and clutch size are determined.

The onset of laying was earlier in good vole years, a relationship that has also been observed in other vole-eating raptors, such as Hen Harrier (Simmons *et al.* 1986), Common Kestrel (Meijer *et al.* 1988) and several owl species (Wijnandts 1984, Hörnfeldt *et al.* 1990, Taylor 1994). Clutches laid earlier in the season tended to be larger, as was observed in a Montagu's Harrier population in northeastern France (Millon *et al.* 2002) and in other raptor species (Wijnandts 1984, Village 1990, Taylor 1994, Dijkstra & Zijlstra 1997). Consequently, clutches were larger in good vole years, as has been found for Montagu's Harriers in western France (Salamolard *et al.* 2000, Butet & Leroux 2001) and Hen Harriers in southern Scotland (Redpath *et al.* 2002). In Common Kestrels, both laying date and clutch size correlate with measures of adult fitness (Daan *et al.* 1990). Vole abundance affected both laying date and clutch size in our study population, so if these variables are also related to fitness in Montagu's Harrier, creating good vole habitats may have a positive impact on numbers of this species. However, Harrier productivity is also affected by other factors, such as agricultural

practices, nest protection, predation and weather conditions. In summary, our data indicate that annual vole abundance can affect timing (laying date) and effort (clutch size) of Montagu's Harrier reproduction and perhaps influence local settlement in the following year.

Voles as vital food source

The influence of vole abundance on Montagu's Harrier reproduction is probably due to the importance of voles in the diet. The results of video analysis, which found that voles constitute up to 85% of nestling diet, are comparable with those of a similar study on a population in cultivated land in southern France, where voles made up 72% of nestling diet (Maurel & Poustomis 2001). Although the results of pellet analysis suggest a lower proportion of voles in the diet (55%), both analyses confirm the importance of voles to nestlings in the East Groningen population. In the 1960s and 1970s, Schipper (1973) found that small mammals made up only 5–29% of prey items identified from nests in natural habitat, where the diet was dominated by birds. Differences between the diets of these Harriers and Harriers in East Groningen are likely to reflect differences in prey availability. Only two decades after Schipper's study, Dutch Montagu's Harriers mostly chose not only different breeding habitats, but also different prey.

Agri-environmental schemes: possibilities for management of Harrier food supply

Set-aside habitats in East Groningen were generally more vole-rich than non-fallow types, as was found in western France (Butet & Leroux 1989). Certain types of set-aside can constitute very high-quality habitat for Common Voles (Jacob 2003, Briner *et al.* 2005). Positive effects of set-aside land on biodiversity and abundance of different taxa can be reinforced by increasing the area set aside and the duration for which it is left fallow (Van Buskirk & Willi 2004). These and other characteristics of set-aside land such as vegetation height, mowing regime and the seed mixtures with which it is sown can be manipulated through appropriate agri-environment schemes.

Vole abundance is highest in tall, dense vegetation, but voles in such cover are less available to hunting harriers (Simmons 2000, Vulink 2001). Vole availability to harriers could be increased through appropriate mowing management. Mowing does not

in itself lower vole survival significantly, but by reducing cover, it makes the voles more vulnerable to predators (Jacob 2003). Regular partial mowing schemes could be employed to increase the availability of voles to hunting harriers.

Harrier conservation in the agricultural landscape

Agricultural habitat is attractive for Montagu's Harriers as an alternative to degraded or lost natural breeding habitat. We suggest that creating conditions that favour high vole abundance, by expanding and optimizing certain agri-environmental schemes, could improve Harrier food availability and thereby positively influence their reproductive performance. The decrease of prey abundance in intensively used agricultural landscapes (Arroyo *et al.* 2002) could be halted. Set-aside land not only supports high vole densities, but also high densities of farmland birds such as Skylark (Boatman *et al.* 1999, Donald 2004), which are prey species of Montagu's Harrier, and an important component of farmland biodiversity. Montagu's Harrier conservation could be used to promote the positive perception of agricultural landscapes as bird habitats, and to prioritize farmland bird conservation in general.

If management of food supply in agricultural breeding habitat proves to be successful, it might be considered as an alternative to nest protection, which is resource- and time-consuming. Higher prey abundance could attract more Harrier pairs and increase Harrier fledgling production. An increase in the numbers of Harriers breeding in farmland could make the Dutch population less susceptible to the effects of short-term decreases in food supply, or to losses caused by agricultural practices.

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