Vole abundance in the Montagu's harrier breeding area in Eastern-Groningen and how this affects male hunting habitat selection

By Marycha Franken 3044203
Supervised by Ben Koks, Almut Schlaich and Raymond Klaassen

Abstract
After set-aside habitat was introduced in the Netherlands to compensate for over-reproduction of wheat in 1988, farmland vole population increased and Montagu's harriers started nesting in agricultural habitat. Upcoming farming intensification led to decline in plant and animal species richness and impoverished food supplies reduced Montagu's harrier breeding density and reproductive success. Set-aside habitats have been shown to contain higher numbers of several prey species and are now used to create habitats that favour higher vole abundance. In this study fieldwork data was combined with data collected by male Montagu's harriers with UvA-BiTS GPS loggers to investigate vole abundance in the Montagu's harrier breeding area in Eastern-Groningen and how prey densities influence male hunting habitat selection. Vole abundance was higher in fields adjacent to set-aside habitat and vole dispersal from high quality habitat resulted in higher vole densities at the edges of fields compared to the middle. Despite presumed lower vole abundances compared to set-aside habitat, Montagu's harrier males hunted on freshly mown grassland and harvested wheat, preferably fields bordering fallow habitat. Accessibility of prey was more important than absolute prey numbers. Montagu's harrier males do not forage on mown fields with high prey availability more than 3500 m away from the nest on a single foraging trip. Energetic costs of flying over long distances appear high and make hunting on mown grasslands with low prey availability close to the nest more profitable. We suggest a combination of refuge areas with high vole abundance and adjacent a mosaic of freshly mown grasslands, managed within close distance of nesting habitat. The results of this study show the value of GPS logger use in habitat studies and how, in combination with fieldwork, this data can provide valuable insights necessary for efficient and sustainable conservation.

Introduction
European Montagu's harriers are long-distance Palearctic migrants, traditionally breeding in open landscapes in places characterized by dense and tall herbaceous or chamaephytic plant communities (Koks et al. 2007, Butet and Leroux 2001). Over the past few decades, large areas of natural breeding habitat have been lost or degraded in many European countries forcing Montagu's harriers to breed in farmland habitats (Koks et al. 2001, Koks et al. 2007, Trierweiler and Koks 2009). Winter cereal fields (wheat and barley) and sometimes rye-grass or alfalfa now appear to be the most common nesting habitat of this ground-nesting species in Western Europe (Arroyo et al., 2002). This shift in breeding habitat has caused great conservational concern as dependency on a man-made environment makes the Montagu's harriers particularly exposed to all changes occurring in this habitat (Arroyo et al. 2002, Bourrioux et al. 2002, Millon et al. 2002).

The late breeding phenology of Montagu's harriers nesting in farmland elicits large-scale nest failure because chicks fledge at harvesting time and are killed by farming machines (Koks et al. 2001, Millon et al. 2002). Advanced timing of crop harvesting in Western Europe reduces nest survival even further (Trierweiler and Koks 2009, Terraube and Arroyo, 2011). Without intervention, between 50% and 90% of the nests would be destroyed each year (Arroyo et al. 2002, Bourrioux et al. 2002, Koks and Visser 2002, Trierweiler and Koks 2009). The loss of clutches and broods during harvest operations makes population persistence in farmland unsustainable in the absence of conservation measures (Arroyo et al. 2002, Koks and Visser 2002, Millon et al. 2002). As a result, most conservation programmes in Western European countries focus on protection of nests and nesting habitats. Each year, the human effort and the amount of economic resources involved in nest protection are significant. Despite this massive involvement, observed Montagu's harrier population trends suggest stability or decline (Millon er al. 2002, Trierweiler and Koks 2009) and alternative conservation measures appear necessary to improve future perspectives.

As opportunistic predators, Montagu's harriers feed on a variety of prey types, including mammals, birds and insects (Arroyo 1997, Koks et al. 2001, Koks et al. 2007). Farming intensification, both in terms of cultivation practices and increased use of pesticides and fertilisers, has led to a dramatic decline in plant and animal species richness in the agricultural landscape (Arroyo et al. 2002, Arlettaz et al. 2010). In European industrialised farmland where nest protection increases nest survival, impoverished food supplies can reduce breeding density and reproductive success (Arroyo 1998, Arroyo et al. 2002, Millon et al. 2002, Koks et al. 2007). Nest protection should therefore be merged with management of harrier prey populations via habitat management (Arroyo et al. 2002, Trierweiler and Koks 2009, Guix and Arroyo 2010, Liminãna et al. 2011). Several European countries have adopted agri-environmental schemes to promote biodiversity and abundance of insects, mammals and birds in farmland areas. Set-aside habitats and extensified borders of farmland parcels have indeed been shown to have a higher biodiversity and contain higher numbers of several prey species (Aschwanden 2005, Aschwanden et al. 2007, Renwick and Lambin, 2011).

In the Netherlands, set-aside habitat was introduced as a measure to counteract over-production in agriculture from 1988 onwards (Koks et al. 2000, Trierweiler and Koks 2009). In the eastern part of the province of Groningen (north-eastern Netherlands) this resulted in rapid growth of farmland vole populations (Koks and Van Scharenburg 1997, Koks et al. 2000, Koks and Visser 2002). Montagu's harriers and other vole-eating predators started nesting in agricultural habitat in response to the introduction of set-aside habitat. Due to intensive nest protection and improved agri-environmental schemes, the Montagu's harrier population in the Netherlands has grown from only two breeding pairs in 1990 to around 60 pairs today (Koks and Van Scharenburg 1997, Trierweiler et al. 2008, Trierweiler and Koks 2009).

Voles still constitute the most important part of the Montagu's harrier diet in the Netherlands (Koks et al. 2001, Koks et al. 2007, Trierweiler et al. 2008). Current Montagu's harrier conservation activities mainly focus on expanding and optimizing fallow field margins to create habitats that favour high vole abundance. Fallow field margins like wild flower and herbaceous strips provide food and cover and serve as a refuge for voles during harvest of adjacent agricultural fields (Aschwanden et al. 2005, Aschwanden 2007). The tall and dense vegetation however, makes it difficult for harriers to detect and capture voles (Aschwanden et al. 2005). So even though vole abundance might be high in fallow habitat strips, voles in such vegetated habitat might be less available for hunting harriers (Aschwanden 2005, Bretagnolle et al. 2011).

The availability of voles in fallow habitats could be improved by mowing, since mowing decreases both vegetation height and cover (Jacob 2003, Koks et al. 2007, Whittingham and Devereux 2008). Voles in agricultural fields also become more available after vegetation cover is reduced by mowing or harvesting. Especially grassland and lucerne appear important hunting sites as these fields are mown several times during the breeding season and cover a much larger surface than small set-aside strips (Aschwanden 2005). A mosaic of various habitat types with both undisturbed strips and mown surfaces could be suggested as a good approach to enhance available food for vole hunters (Aschwanden et al. 2005, Whittingham and Devereux 2008, Aschwanden 2007, Koks et al. 2007, Bretagnolle et al. 2011 Garratt et al. 2011, Peggie et al. 2011).

In this study, we quantified local vole population densities within the Montagu's harrier breeding area in Eastern-Groningen. Vole densities and the main factors influencing vole numbers are then used to study hunting habitat selection by Montagu's harriers. Vole densities in the breeding area are determined by vole-hole transect counts in potential hunting habitat. Detailed information on habitat use is provided by six Montagu's harrier males equipped with UvA BiTS GPS loggers. Some additional data on prey availability and prey choice are collected by snap-trap transects and pellet analysis. Mowing dates of grasslands and lucerne fields were also recorded in the area.

By gaining insight in prey abundance and availability and how this affects Montagu's harriers hunting site selection, conservation schemes could be improved in order to attract more harrier pairs and increase harrier breeding success.

Materials and methods

Study area and study population

Field work was carried out throughout the Montagu's harrier's breeding season (end of April until beginning of August 2011). The study area is located in the eastern part of the province of Groningen, North-eastern Netherlands (53°11 'N, 7°4E). Habitat types in the relatively flat and open polder landscape of Eastern-Groningen were crop fields (e.g. cereals, potatoes, beetroots, and onions), grassland and meadows, lucerne, set-aside, agri-environmental schemes and grassy paths and ditch edges.

Montagu's harriers in Eastern-Groningen constitute about two-third of the Dutch population. During this study 49 Montagu's harrier pairs were breeding in the area. Nests were located and protected against predation and harvesting by fencing. Young received rings and were measured as described in Bijlsma 1998 (weight, wing length, claw with and without nail, eye colour, number of fault bars).

Harrier diet and vole abundance

During the breeding season, perch posts, field margins and paths along ditches near nesting-sites were checked regularly for pellets. Pellets at nest sites were also collected after chicks had fledged. Pellets were stored (dry) and processed at the end of the season (a detailed description of pellet analysis can be found in Koks et al. 2007). Five main categories of prey were distinguished: 'voles', 'birds', 'hare/rabbit', 'insects' and 'other'. The first three categories were identified to species level if possible (for 1992-2005 see Koks et al. 2007)

For estimating the abundance of small mammals, two different approaches were used. (1) In Eastern-Groningen and in Flevoland, small mammals were trapped during the first week of August according to a standard protocol (Koks et al., 2007): five snap-traps were baited with carrots and arranged in a circle with a 4 m diameter, forming one station. One transect comprised of 10 stations spaced 10 m apart. This protocol has been used from 1992-2011. In 2011, 19 transects were checked on three consecutive days. Transects were located in different habitats grouped in non-fallow vegetation types and fallow vegetation types (for a detailed description of all habitat types included see Koks et al. 2007). Almost all small mammals trapped were identified to species level. As most of the trapped small mammals were voles, 'small mammals' is hereafter referred to as 'voles'.

(2) Vole abundance in the breeding area in Eastern-Groningen was also measured by conducting transect counts. While walking a straight line of 100 m, each vole burrow was counted within one meter to both sides. Most transect counts were executed on recently mown fields of different habitats (barley, grass, lucerne, winter wheat and set aside). Depending on the size of a field, 2-6 transects were conducted per field, half of which was located in the middle and half at the edge of the field. For each transect, a GPS waypoint was taken at the beginning and at the end of thetransect. In total, 310 prey transect counts were conducted during the breeding season, dispersed over 76 fields (3 barley, 44 grassland, 5 lucerne, 12 winter wheat, 12 set-aside).

The vole trap method is used for 20 years in a row and the transect counts for the first time in 2011. The two approaches were calibrated by counting all vole holes (as described above) along vole trap transects. Due to locations with high and dense vegetation it was impossible to obtain reliable counts for every vole-trap transect. Only transects with low or recently mown vegetation were included in the comparison (8 out of 19).

Habitat availability and habitat use

In 2009 and 2010 8 adult Montagu's harriers (2 females and 6 males) were fitted with 14 g solar powered UvA-BiTS GPS logger (http://www.uva-bits.nl/). Four of these birds (one female and three males) returned in 2011 to the study area. However, one male disappeared before the incubation phase. For another bird, the GPS logger was broken, and new data could only be collected after the GPS logger was replaced.

In 2011 five more adult male Montagu's harriers were captured and fitted with GPS loggers. No females were captured as they contribute to feeding of the young only from the late nestling phase onwards while males need to provide food for themselves, their female and their young during the whole breeding season.

The birds were caught near their nest. Wing length, wing span, body mass and claw size were measured. GPS loggers were attached using a Teflon ribbon harness (Trierweiler et al. 2007) and the birds were released within ca. 30 min of catching. Subsequent monitoring revealed no abnormal behaviour or nest desertion. The males were caught in different phases of the breeding cycle resulting in tracking periods of variable length.

The birds were tracked using the UvA-BiTS, consisting of one base-station and several relay stations (for a detailed description of the UvA-BiTS system see http://www.uva-bits.nl/system/). A network of 5 relay antennas secured communication with each GPS logger bird. Data was downloaded regularly and new measurement schemes could be uploaded when desired. In the breeding season, the fix interval was set to one fix every 5 minutes during the day (7:00-21:00), and one fix every hour during the night. On days with high solar radiation, the time interval was increased to one fix every 3-6 seconds.

Hunting on mown and unmown grassland and distance from the nest

Grasslands, meadows and ditch and road edges were typically mown two to three times (interval: four-five weeks) and lucerne was mown once or twice (interval: seven-eight weeks) during the breeding season. Parts of most set-aside fields and strips were also mown once after 15 July. Mowing dates of most grassland in the breeding area were recorded on a daily basis or estimated in case the actual mowing date was not observed. About three days after mowing, farmers fertilise grasslands by use of liquid (artificial) manure. After a field is fertilised, Montagu's harriers (and other raptors) do not seem to use these fields for hunting anymore (own observation).

Spatial analysis and statistics

The number of vole holes counted with the vole hole transects were compared to the number of dead voles found with the snap-trap transects using a general linear model (glm) (lme4 package) in R (version 2.14.0). The same test was used for analysing the effect of habitat type, presence of fallow habitat, and whether the transect was laying at the edge or in the middle of a field. When necessary a glht test (multicomp package) was used as posthoc test. Because vole holes were counted on only three barley fields, barley and wheat were emerged in the category 'cereals'. The distance from the middle of each 100m transect till the edge of the field was measured in ArcMap 9.3 and its relation with the number of vole holes was tested with a glm (lme4 package) and a class interval test (classIntervals, classInt package).

A compositional analysis was carried out in R (package adehabitat, function compana, method: randomisation test, Calenge 2006) which compares use of habitat categories relative to their proportional availability. With Hawth's Analysis Tools 3.27 (www.spatialecology.com) the 95% kernel home ranges were generated for all six Montagu's harrier males. Proportions of different habitat types within home ranges were calculated using digital maps showing agricultural land cover types for the year 2011 (copyright *Dienst Regelingen*, Dutch Ministery of Agriculture, Nature and Food Quality). Habitats were grouped depending on availability in the breeding area. The category 'wheat' includes both summer and winter wheat although the proportion of summer wheat is very small (ca 8%). 'Fallow habitats' include all types of fallow and set-aside land (except for bare land and set-aside

tree plantations) and agri-environmental schemes (fallow field margins). The category 'grassland' consists of intensive grasslands (grassland intensively used for grazing or for production of cattle food or grass-seed) and includes both temporary and permanent grasslands. All other agricultural vegetation types e.g. onions, vegetables, rapeseed, woods, beetroots etc. are joined in the category 'other'. Habitat use is the proportion of 5 minute hunting fixes in each category. Fixes were considered 'hunting fixes' when at least two fixes in a row were made in the same agricultural field during the day (7.00-21.00). Fixes made within fields used as nesting fields or fixes made in fields with frequently used sitting spots (often next to a nesting field, own observations) were excluded from the analysis. While hunting, birds regularly sat on the ground to handle prey or to rest between strikes, which was still considered hunting behaviour.
A log likelihood ratio test (G-test, rJava and Deducer package) was used to investigate whether hunting habitat selection was random with respect to presence of fallow habitat. Only the most preferred habitat types were included in the analysis. Fields that were within 100m distance from fallow habitat were categorised as being adjacent to fallow habitat. No unambiguous dispersal distance is reported for voles but within fallow habitat (wildflower strips) voles maintain home ranges of about 125 m^2 (Boyce and Boyce, 1988, Jacob and Hempel, 2003, Briner et al. 2005).

Hunting by Montagu's harriers on mown and unmown grasslands and the effect of distance from the nest on the use of these fields were analysed using a glm in Statistica. Some mowing events were recorded after the actual mowing activities were completed. In the analysis each mowing event therefore consists of 6 days in a row: the day a field was recorded as mown field, two days before this date because the actual mowing event may have been earlier (not three days because liquid manure would have been visible on the field), and three days after the recorded date in which the birds use the fields for hunting (more than three would show liquid manure on the field). Depending on the number of days birds gathered GPS data, for each grass field either one or two mowing events were recorded during the breeding season, resulting in 6 or 12 days the fields were available as mown fields.
A theoretical model of the energetic cost of foraging was made to investigate the trade-off between distance from the nest and availability of prey. The model calculates the energy gain in joule per second for foraging areas with variable prey availabilities and at different distances from the nest. Prey availability is represented by the strike frequency in strikes per minute, which is positively correlated to prey capture rate (Trierweiler et al. 2010). The model only applies to short hunting trips: the bird leaves the nest and directly returns to it after it catches a prey. The energy gain is calculated by dividing the energy gain of a foraging trip by the total time it takes the bird to fly from the nest to the foraging area, hunt for a prey, and return to the nest. Because this study focusses on voles as the most important prey, the energy gain is a result of the energetic value of an average sized vole minus the energetic costs of flying to and from the foraging area and the energetic costs of hunting. No difference was made between directional flight and flight speed during hunting (Masman and Klaassen, 1987). Avian flight costs (e_f) are predicted from an equation based on published data on flight costs in 14 species (Masman and Klaassen, 1987).

$$e_f = 17.360M^{1.013}b_w^{-4.236}s_w^{1.926} \quad \text{Watts}$$

where M is body mass (g), b_w is wing span (cm), and s_w is wing area (cm^2).

This theoretical model is evaluated by plotting the change in energy gain for hunting birds with varying strike frequencies (0.1-1 strikes/min), for distances from the nest ranging from 500 m up to 6000 m (figure 4B). All variable of the energetic model are summarized in table 1.

Table 1: All variables used in the theoretical model of energetic costs of foraging

Variables	Value	Source
Body mass voles	24.5 g	Mean weight voles captured in this study
Metabolic energy voles	4.6 kJ/g	Masman et al. 1986
Body mass Montagu's harrier	300 g	Bruderer and Boldt, 2001
Wing span Montagu's harrier	112.5 cm	Bruderer and Boldt, 2001
Wing area Montagu's harrier	1463 cm2	Bruderer and Boldt, 2001
Flight speed Montagu's harrier	6 m/s	This study
Distance	500-6000 m	This study
Strike frequency	0.1-1 strikes/m	Szentirmai et al. 2010 and this study

We used 'high-resolution data' (fixes every 3-6 sec) to study the relationship between prey availability and prey capture rate. Earlier work with radio telemetry data showed that prey capture rate is a fixed proportion of the strike frequency (Trierweiler et al. 2010 and Szentirmai et al. 2010). In this study we used vole holes as measure for prey availability and strike frequency, determined using GPS high resolution data, as measure for prey capture rate. While hunting on mown grassland, Montagu's harrier males were assumed to strike when the horizontal speed dropped below 0.1. We tested for the relation between prey availability and strike frequency using a general linear model in R (lme4 package).

Results

Harrier diet and vole abundance

In 2011, pellets collected in Eastern-Groningen contained 41 different prey species divided in 5 prey groups: 67% voles, 17% birds, 1% hare/rabbit, 13.5% insects, and 1.5 % others.

The number of vole holes counted along the vole trap transects did not correlate with the number of voles that were trapped (n=8, df=23, z=1.396, P=0.1628). The number of vole holes counted on recently mown/harvested fields did not differ between crop types (n=76, df=313, t= -4.890, p>0.05 deduced from posthoc test). Independent of crop type, fields within 100 m of fallow habitat have a higher number of vole holes compared to fields further than 100 m from fallow habitat (n=62, df=61, t=3.293, P=0.00167) (figure 1C).
Within fields, a significantly higher amount of vole holes were counted at the edges of the fields compared to the middle (n=62, df=313, t=4.051, P<0.001) (figure 1A). There is no gradual decrease in the number of vole holes towards the middle, but there seems to be a break point at about 27 meter from the edge till where the number of vole holes is higher than at further distances (class interval test: number of classes=4, first break at [0.18,26.905], n=62) (figure 1B).

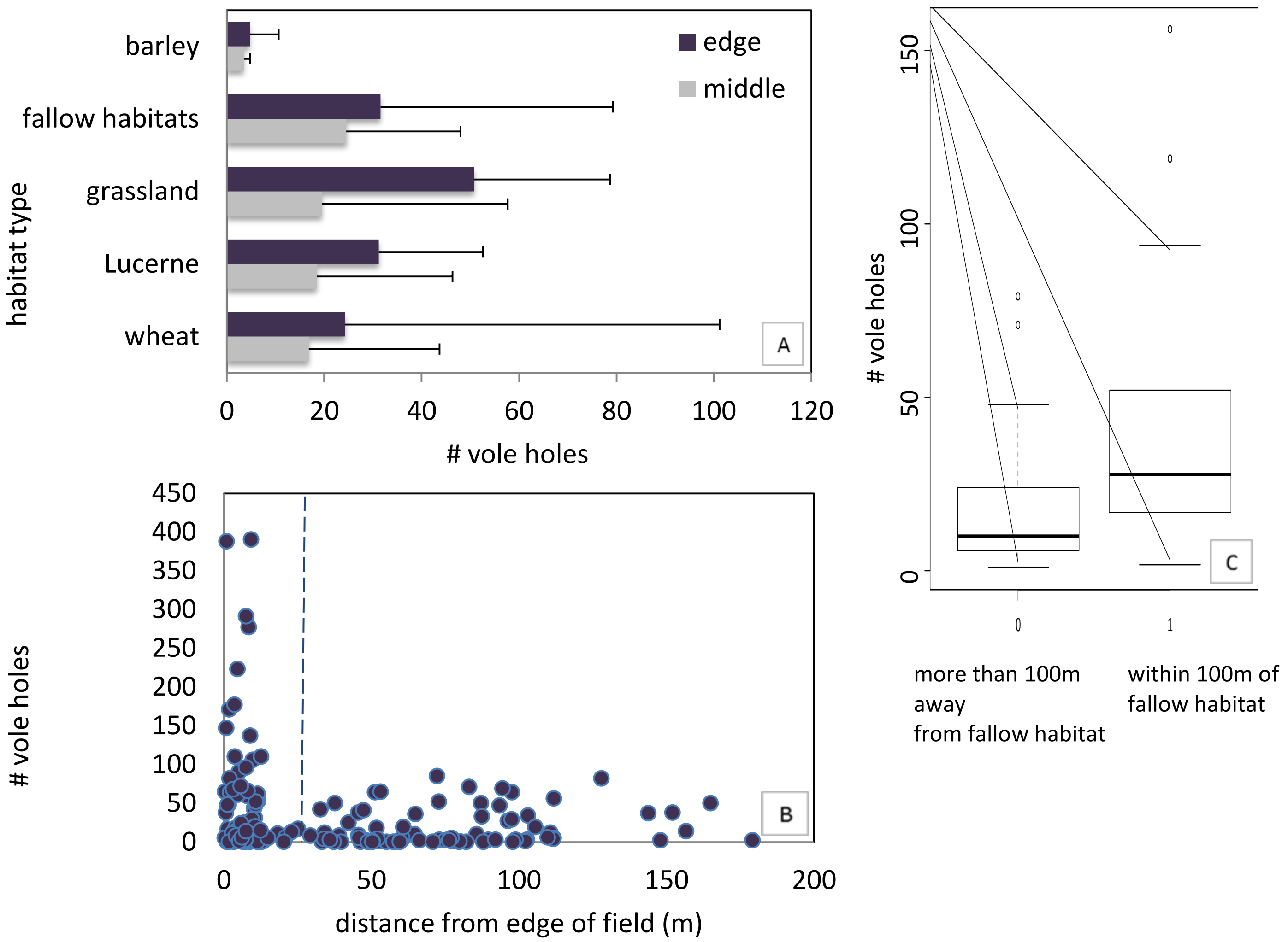

Figure 1. (A) Comparison of the number of vole burrows at the edge of fields and in the middle of fields for five different habitat types. Error bars represent standard errors. (B) Number of vole burrows in relation to distance from the edge of the field. The dotted line indicates the distance till where vole burrow numbers are higher than at further distances (class intervals test, 26.9m). (C) Comparison of the number of vole holes in fields adjacent to fallow habitat and fields that are not within close distance of fallow habitat (boxplot range 'more than 100m away from fallow habitat'= 17-52, median=28, boxplot range 'within 100 m of fallow habitat'= 6-29, median = 10, stdev. 0.257).

Habitat availability and habitat use

Compositional analysis demonstrated that proportions of habitat types used for hunting differed significantly from the available habitat in the 95% kernel home ranges of the Montagu's harriers (6 animals and 8 habitat types, λ = 0.00636, P=0.04) (figure 2 A,B). Grassland, wheat and barley were ranked as the three most preferred hunting habitat types. The preference for barley is based on two birds and one field of barley which was next to their nesting field. Most of the hunting fixes recorded in the barley are assumed to be fixes of when the birds were sitting (own observation). Barley is therefore not considered to be either a preferred or non-preferred habitat type. Corn, fallow habitats, lucerne, potatoes and the category 'other', were not preferred as hunting habitats.

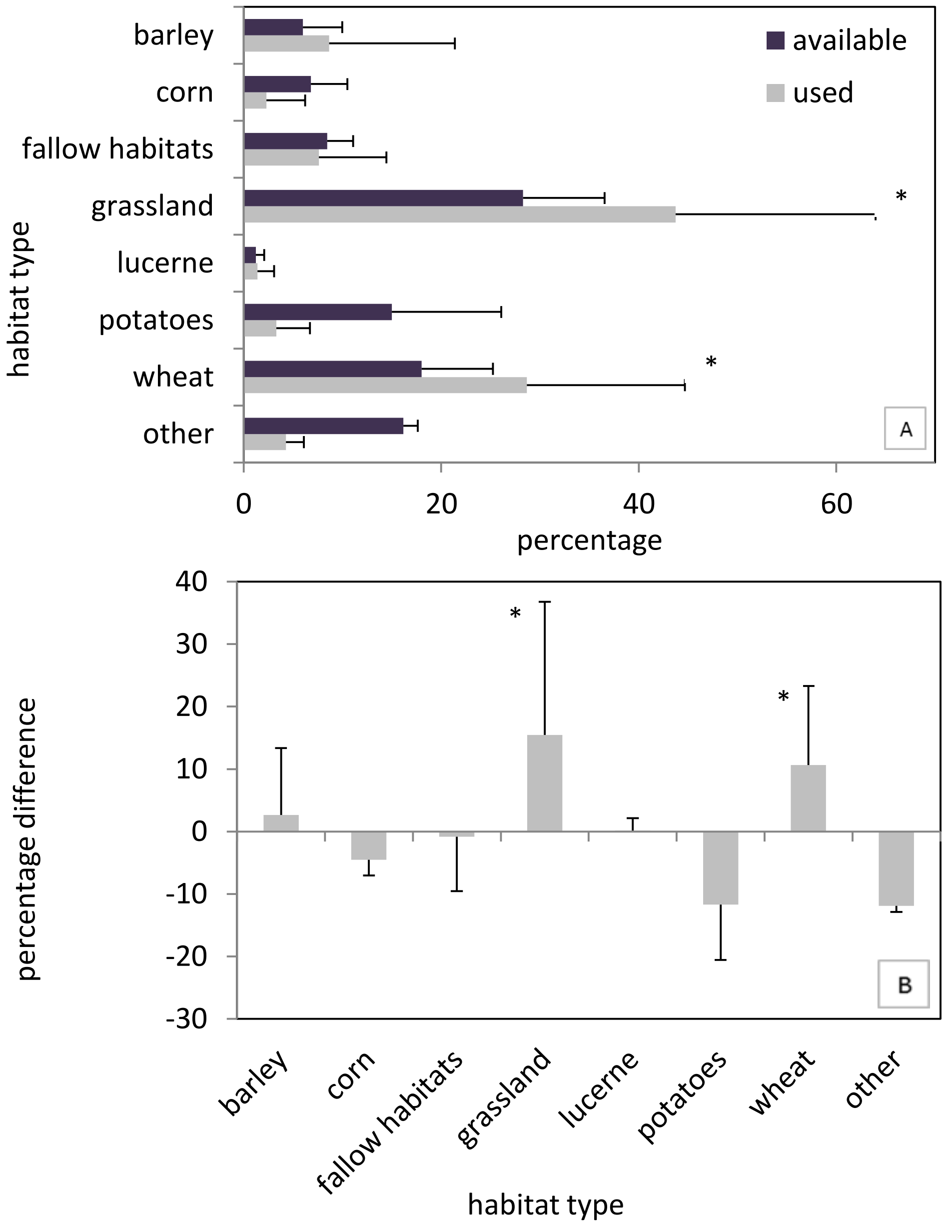

Figure 2. (A) Comparison of percentage available habitat (percentage of total number of fields) in the 95% home ranges of the GPS-tracked Montagu's harriers and the percentage habitat used for hunting (percentage of 5 min hunting fixes within each habitat type), averaged across the 6 birds. (B) The difference between percentage available habitat and percentage habitat used for hunting for 8 different habitat types. A positive value indicates that a habitat type was selected as hunting area more relative to its availability. Asterisks indicate preferred hunting habitat types (compositional analysis). Error bars represent standard error.

For all six birds, the 5 minute hunting points within the two preferred habitat types were non-randomly distributed with respect to fields that are adjacent to fallow habitat and fields that are not (Log likelihood ratio test (G-test) of independence: n=6, G = 20.799, X-squared df = 1, P<0.001). On grassland and wheat fields adjacent to fallow habitat more 5 minute hunting fixes were made during the breeding season than on grassland and wheat not within close distance to fallow habitat (figure 3). This would not be expected from the proportion of fields that are adjacent to fallow habitat.

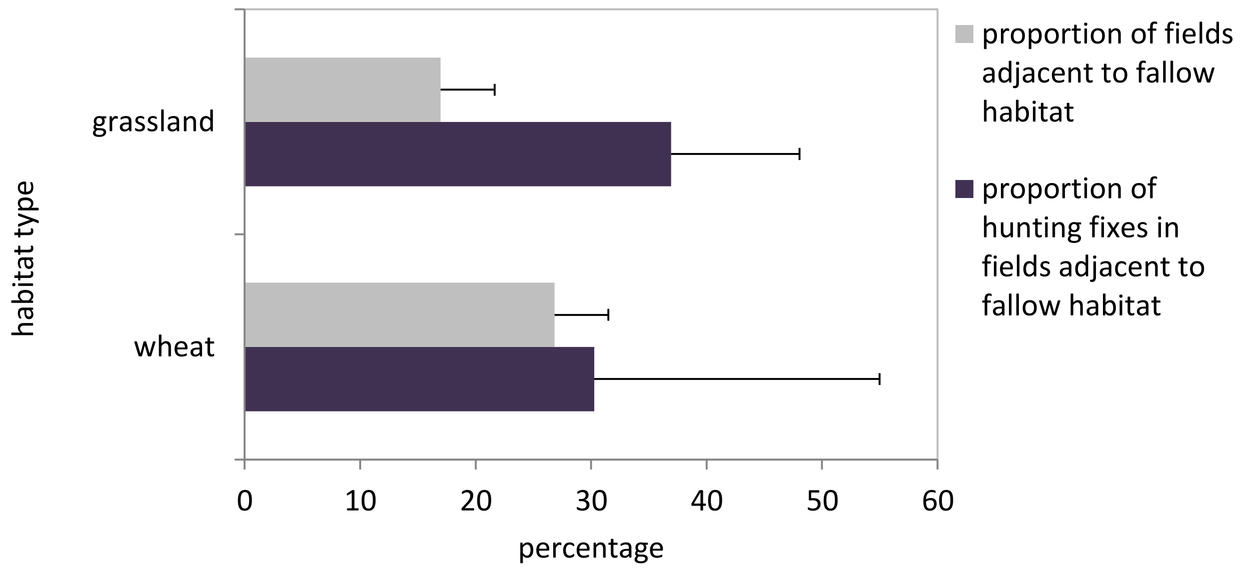

Figure 3. Comparison of the proportion of fields adjacent to fallow habitats and the proportion of 5 min hunting fixes in fields adjacent to fallow habitats, for the two preferred hunting habitats. Error bars represent standard error values. For example, on average across the six birds, 37% of all hunting fixes on grassland were on fields adjacent to fallow habitat while only 16% of all available grassland fields are close to fallow habitat. Grassland adjacent to fallow habitat is selected as hunting habitat more relative to its availability.

Hunting on mown and unmown grassland and distance from the nest

For all grassland where mowing dates were recorded, the number of 5 minute hunting fixes per day decreased with increasing distance from the nest (glm: n=33, df=1, F=11.17, P=0.0017). Grassland was visited significantly more during days grasslands were mown (dark dots in figure 4A) than during days grasslands were unmown (grey dots in figure 4A; glm: n=33, df=1, F=11.33, P=0.0016). Grasslands in the study area were recorded as mown either 6 or 12 days during the breeding season (see materials and methods) and grass fields were recorded as unmown for on average 63 days. At days grasslands were mown, birds did not go further away from the nest than on days the fields were not mown (glm, mowing*distance: n=33, df=1, F=3.02, P=0.09).

The theoretical model shows the change in energy gain for hunting birds with varying strike frequencies (strikes per minute), for distances from the nest ranging from 500 m to 6000 m (figure 4B). For each strike frequency the energy gain is higher when hunting at a closer distance. Close to the nest the increase in energy gain with increasing strike frequency is high whereas at great distance from the nest the energy gain at low strike frequency is almost equal to the energy gain at high strike frequencies. Hunting at a distance of more than 3500 m away from the nest with a high strike frequency is less rewarding than hunting close to the nest with a low strike frequency (dotted line in figure 4B). The Montagu's harrier males with GPS logger did not seem to hunt at distances further than 3500 m from the nest (dark dots in figure 4B), when excluding longer foraging trips with visits to multiple fields before returning to the nest (see materials and methods).

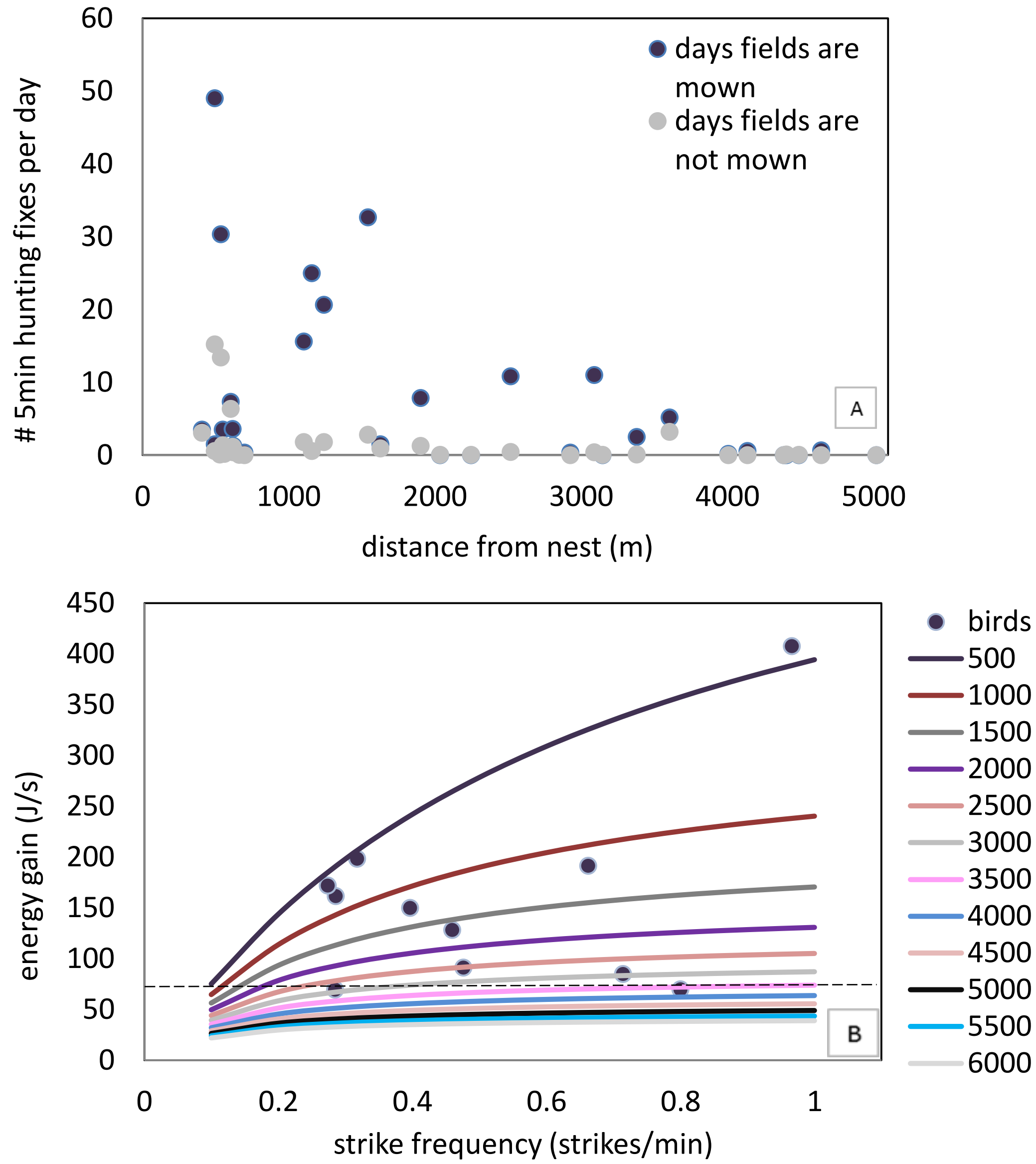

Figure 4. (A) Number of 5 minute hunting fixes for varying distances from the nest for both fields that are mown and fields that are not mown. For each field there is a mean of 5 minute hunting fixes for days that field is mown and days that field is not mown resulting in paired mown-unmown points in the graph.
(B) Theoretical model showing changes in energy gain for hunting birds with varying strike frequencies, for distances from the nest ranging from 500 m up to 6000 m (B). It is more rewarding to hunt at 500 m from the nest with a low strike frequency than at any distance further than 3500 m with high strike frequencies (dotted line). Male Montagu's harriers equipped with GPS loggers did not hunt on fields further than 3500 m from the nest during short foraging trips (dark dots).

Hunting behaviour on mown grasslands

High resolution data (gps fix every 3-6 seconds) of male Montagu's harriers hunting on mown grassland showed an increase in strike frequency with increasing numbers of vole holes (glm, quasipoison: n=11, df=10, t=2.69, p= 0.02) (figure 5).

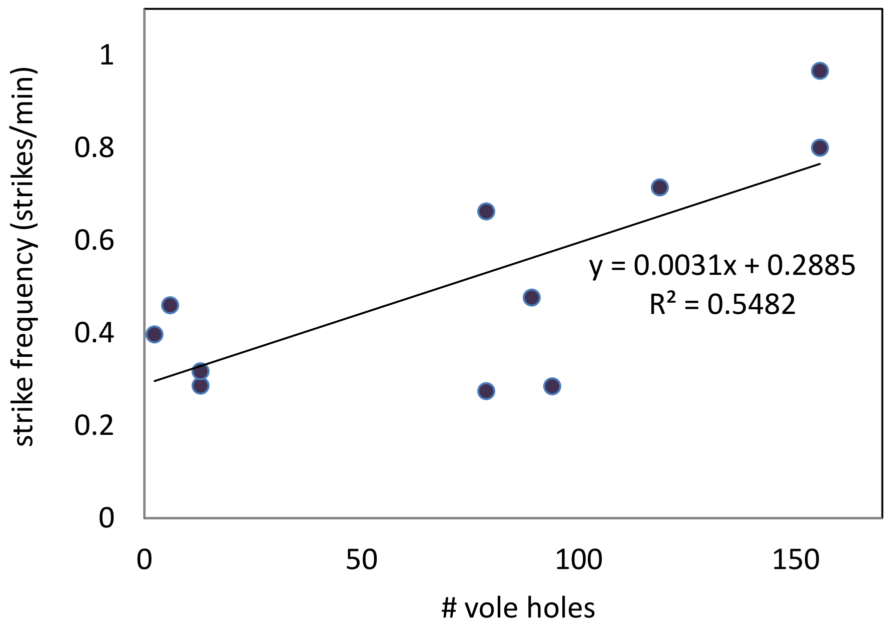

Figure 5. Number of vole holes against strike frequency (strikes/minute) on mown grasslands.

Discussion

The Montagu's harrier population in the Netherlands dependents on conservation measures for its sustainability in the long term. Insight in prey abundance and availability and how this affects Montagu's harriers hunting site selection, may improve current conservation schemes.

Vole abundance in Eastern Groningen

Pellet analysis confirmed the importance of voles during this study (67%) and, as in previous years, the dominant species found in pellets was the common vole (*Microtus arvalis*). In Western France, where voles also represent the greatest part of harrier diet, vole abundance influences breeding density, clutch size, breeding success and age structure (Salamolard et al. 2000, Butet and Leroux 2001, Arroyo and Garcia 2006). Additionally, Montagu's harriers breed more frequently in areas where food abundance is high, and where the number of fledglings produced in the previous breeding attempt was high (Arroyo et al. 2002). Koks and Trierweiler (2007) found that vole abundance can affect timing (laying date) and effort (clutch size) of Montagu's harriers breeding in the Netherlands, and perhaps influence local settlement in the following year.

Vole hole transects and snap-trap transects were not comparable. Voles search for food around their holes at distances up to 30 meters (Boyce and Boyce 1988) which means that voles lured to traps with food do not necessarily have holes within two meter of the trap. Differences between the two vole abundance measurements can also derive from variation in vegetation height. Vole hole transects were done on mown fields while vole snap-trap transects were often in non-mown habitats where vole holes are more difficult to count. More vole abundance measurements of both methods on mown habitats may lead to other results. To measure vole abundance in the breeding area in Eastern-Groningen vole hole transects seem to be the best method to cover a large area within reasonable time.

Since vole hole transects on non-mown fields were highly time consuming, all measurements were done on mown fields (except for some fallow habitat fields). Barley and lucerne were both scarce in the study area compared to grassland and wheat, and also only few fallow habitat fields were sampled. Small sample sizes for these habitats could explain why we found no difference in vole abundance between habitat types (figure 1A) whereas in other studies they did (Butet and Leroux

2001, Koks and Visser 2002, Koks and Trierweiler 2007, Arlettaz et al. 2010). In all studies, small mammal abundance and biodiversity tended to be higher in fallow habitat such as wild-flower and herbaceous strips. Positive effects of set-aside land on vole abundance and biodiversity can be reinforced by increasing the area set aside and the length of time for which it is left fallow (Buskirk and Willi 2004, Koks et al., 2007, Macdonald et al. 2007). Relatively new fallow habitat in the breeding area was also included in the habitat comparison which may have resulted in total lower vole abundance in fallow habitat as new areas have to be recolonized first. Fallow habitat left unattended for too long will be dominated by grass species and probably loose bird and vole diversity, indicating the importance of set-aside habitat management (personal communication).

Snap-trap data of vole abundance collected during earlier studies in Eastern-Groningen showed higher vole numbers in fallow habitat (Koks et al. 2007). Even though vole abundance in fallow habitat appeared similar to other habitat types in this study, fields within 100 meter of fallow habitat did have higher vole abundances than fields not within close distance of fallow habitat (figure 1C). During favourable conditions high vole reproductive rates in fallow habitat can induce density-dependent dispersal of voles towards less favourable habitats (Butet and Leroux 2001, Aschwanden et al. 2005). Wildflower and herbaceous strips may thus act as source habitats and enhance vole numbers in their direct surroundings (Arlettaz et al. 2010). Although Briner et al. (2005) concluded that voles in wildflower strips did not expand their home ranges into the surrounding crops, local resource competition as a consequence of population growth results in vole dispersal and should mostly translate into colonization of empty patches through new colony foundation (Gauffre et al. 2009).

Besides colonization of adjacent crops, in agricultural landscapes, non-cropped habitat such as field margins, linear scrub along field boundaries, woodland, ponds, ditches and fallow land can act as dispersal corridors for voles (Benton et al. 2003, Renwick and Lambin 2011). Grassy field margins in the UK harboured a higher small mammal biomass than conventional arable field edges (Shore et al. 2005) and Renwick and Lambin (2011) found that within intensively farmed landscapes wider margins provided suitable habitat for field voles and narrow conventional strips between crops were important links between areas of more suitable habitat in Scotland. In the Netherlands ditches have been shown to function as habitat corridors for root voles because ditches are often connected to root vole habitat patches and ditch habitat is qualitatively similar to root vole habitat patches (Mauritzen et al. 1999). In unfamiliar areas, root voles even preferred to stay in ditches. Vole species common in agricultural areas in the Netherlands may also use similar non-cropped structures in the landscape for dispersal. Moreover, as high numbers of vole holes were observed regularly in ditch and field edges (own observations), these habitat corridors seem to function as permanent habitat in a landscape dominated by annual crop fields. Ploughing in annual crops has great impact on presence of common voles and repopulation of the fields depends solely on immigration from refuge habitats (Jacob 2003, Jug et al. 2008). In concordant with this, common voles in the Netherlands have earlier been found to use ditch margins intensively (Van der Reest 1989, Ellenbroek et al. 1998).
If larger suitable habitat patches and annual crops are invaded from the non-cropped structures surrounding it, this can explain the higher numbers of vole holes at the edges of fields. The subterranean area of common vole burrow systems ranges from 0.5-28.8 m^2 (Brügger et al 2010) and young females born to grouped breeding mothers have a mean dispersal distance of 20-27 m (Boyce and Boyce 1988). This can explain why vole hole counting on fields showed a breakpoint of 26.9 m from the edge of the field under which the number of vole holes was significantly higher (figure 1B).

Hunting habitat preferences and hunting on mown and unmown grassland
Habitat choice analysis showed that male Montagu's harriers preferred grassland and wheat as hunting habitat (figure 2AB). Grassland seems quite similar to grassy field margins and ditch edges, which harbour high vole densities as described above. As field margins and ditch edges, grassland can be considered perennial habitat but measured vole abundance in this and several other studies did

not reveal higher number of voles living in grassland compared to other habitats (Aschwanden et al. 2007, Jacob 2008, Arlettaz et al. 2010, Szentirmai et al. 2010, Bretagnolle et al. 2011). Grasslands in Eastern-Groningen are mainly high-intensity grasslands and, in contrast with low-intensity grasslands, are intensively managed. Voles living in intensively managed grassland face periodic changes in habitat conditions due to frequent mowing and fertilisation (Jacob and Hempel 2003, Szentirmai et al. 2010). In contrast to ploughing in annual crops (Jacob 2003, Jug et al. 2008), mowing itself does not destroy nest sites (subterraneous burrows) but potentially eliminate a substantial proportion of the local population by direct killing (Bretagnolle et al. 2011) and reduced vegetation height leads to increased risk of predation (Jacob and Hempel 2003, MacDonald et al. 2007, Bretagnolle et al. 2011). Injection of liquid manure after mowing may ruin burrows close to the surface and voles may die in their burrows after being trapped due to soil compressed by machines (Jacob and Hempel). The regular mowing (first cut in April and afterwards about every five weeks until October) and subsequent application of liquid manure therefore appears to prevent the establishment of high vole densities (Aschwanden et al. 2007).
Still, in this study, high-intensity grassland (together with wheat) was the most preferred hunting habitat of Montagu's harrier males. Similar, Barn Owls preferred to forage in grassland and cereal fields even though small mammal abundance in wildflower areas was much higher (Arlettaz et al. 2010). Grassland and cereal fields are more open and probably easier to exploit compared to wildflower areas with their dense vegetation structure (Arlettaz et al. 2010). A closer look at habitat choice reveals that this is not the complete story for Montagu's harriers as they mainly use grassland when freshly mown (figure 4A). In a comparable study by Aschwanden et al. (2005) kestrels and long-eared owls hunted on freshly mown low-intensity meadows and artificial grasslands, despite low densities of small mammals. Wildflower and herbaceous strips had 8-times higher small mammal abundance than grasslands but were not preferred as hunting habitat. This study and several others conclude that detectability and accessibility (i.e. availability) is more important than prey abundance (Aschwanden et al 2005, Ontiveros et al. 2005, Arlettaz et al. 2010, Szentirmai et al. 2010, Mirski 2010, Garratt et al. 2011, Peggie et al. 2011). Mowing of grasslands improves detectability of prey by reducing vegetation cover and machinery used for mowing and removing hay can injure or kill voles, leaving easily accessible prey (Jacob and Hempel 2003, Aschwanden et al. 2005, Szentirmai et al. 2010, Mirski 2010).
The same principle of accessibility may explain the preference of Montagu's harrier males for wheat. Aschwanden et al. (2007) found that small mammal densities in autumn-sown wheat were very low in March and May, and increased only from May to July. Small mammals seem to exploit the huge food resource shortly before harvest (Aschwanden et al. 2007, Renwick and Lambin 2011). Harvesting itself, similar to mowing, increases detectability of voles and may injure or kill voles (Jacob and Hempel 2003). Increased vole abundance and accessibility may result in sudden extensive exploitation of wheat by Montagu's harriers late in the breeding season, after harvesting. On rape and maize crops in Germany, hunting by Lesser Spotted Eagles was firstly noted after the harvest (Mirski 2010). Vole abundance in wheat in this study was measured after harvesting. Vole hole counting early in the season together with exact harvesting dates and Montagu's harrier crop use before and after harvesting can confirm when during the breeding season wheat fields are preferred.

The apparently profound effect on prey availability after mowing and harvesting only lasts for a few days (this study, Szentirmai et al. 2010). High prey availability on mown fields attracts several predator species, and thus the prey source can be quickly depleted (Szentirmai et al. 2010). Furthermore, reduced vegetation cover exposes voles to increased predation risk which affects patch choice and feeding behaviour of these mammals (Jacob and Brown 2000, Jacob 2008). Voles adapt to the new conditions with restricted spatial activity and reduced home ranges making them less susceptible to predation (Jacob 2003, Jacob and Hempel 2003, Aschwanden et al. 2007, Peggie et al. 2011). Because of this short hunting profitability of fields after mowing and harvesting, wheat seems less important for Montagu's harriers than grassland as wheat can only be used as hunting habitat from the end of July (start of harvest) while grassland is mown about four to five times in a season.

However, Montagu's harrier young require an increasing amount of food approaching the end of July and the large number of wheat fields harvested over a period of several weeks may also represent a valuable food source at this point.

Grassland and wheat appear important hunting habitat in Montagu's harrier breeding areas because of high prey availability after vegetation reduction (mowing and harvesting). Montagu's harriers did not prefer wildflower and herbaceous strips as hunting area even though fallow habitat is assumed to contain higher prey densities than both grassland and wheat. Yet, fallow habitat still had an influence on hunting as males did hunt more often on grasslands and wheat fields adjacent to fallow habitat (figure 3). Density-dependent dispersal of voles from fallow habitat to surrounding fields is reflected by Montagu's harriers hunting habitat choice.

Distance from the nest

For birds foraging from a central place (e.g. a nest) the choice of using a resource patch within a heterogeneous environment will be a function of quality and availability of food resource and distance from the nest (for the theory of central place foraging see Houston and McNamara 1985) (Arroyo et al. 2009). For Kestrels as single prey loaders (Houston and McNamara 1985) it was found that birds select foraging habitat non-randomly, and travelled to areas where access to 'higher value' prey is enhanced (Rudolph 1982, Garratt et al. 2011). Also for Montagu's harriers we wanted to study foraging decisions in terms of energetics. Charnov (1976) predicted that a foraging animal should leave a patch when it could do better by travelling to another patch. Translated to this study, Montagu's harrier males have to consider both prey availability of hunting fields and the distance from the nest when choosing where to forage. Since voles form the main part of Montagu's harrier's diet, prey value is not assumed to vary much between hunting areas and a mean value of vole weight is used in the model. We expected males to go further away from the nest for mown fields compared to unmown fields because of significantly higher vole availability. Although there is a tendency that Montagu's harriers travel larger distances for mown fields (figure 4a), this relation is not significant. The theoretical model (figure 4b) shows a quick decrease in energy gain with increasing distance, especially for higher strike frequencies (higher vole availability, see below). Hunting on fields with low vole availability at close distance (500 m) is energetically more rewarding than hunting on fields with high prey availability at distances over 3500 m from the nest (dotted line in figure 4b). There seems to be a trade-off between energy gain and distance travelled as is found in some other central place foragers (Rudolph 1982, Staniland et al. 2007, Burke and Montevecchi 2009, Rayner et al. 2010, Garratt et al. 2011). The tracked Montagu's harrier males in this study do not seem to go on short hunting trips (the bird leaves the nest and directly returns to it after it catches a prey) at distances over 3500 m from the nest (dark blue spots in figure 4b). The costs of flying over large distances seems to be of much greater value in the trade-off than the capture rate at a field and therefore the number of preferred habitat fields within relatively close distance of a bird's nest appear important for an adequate food supply to the nest.

Hunting behaviour on mown grasslands

Trierweiler et al. (2010) described the positive relation between strike frequency and strike success. Strike frequency, the frequency with which a harrier attempts to catch a prey, probably relates to food abundance, mediated by vegetation density and height, resulting in food availability (Masman et al. 1988, Trierweiler et al. 2010). Using high resolution data of one GPS point every 3-6 seconds in this study shows that there is indeed a positive relation between vole abundance and strike frequency. The range of strike frequencies found with GPS loggers for Montagu's harriers hunting on mown grassland is this study is similar to the strike frequencies reported in Trierweiler et al. (2010), as established by direct observation of hunting radio-tracked birds. High resolution GPS data gathered by individual birds may reveal valuable information on prey availability in different hunting areas. Time consuming vole hole counting could be omitted and true vole availability could be determined in habitat types where high or dense vegetation restricts vole hole counting.

Further research and management implications

The use of UvA-BiTS GPS loggers in this study has led to new valuable insights in the ecology of the study species. One bird can collect a large amount of data in a relatively short period of time and only a small fraction of the possible analyses with this data is shown in this research. Nonetheless, it is important to combine GPS technology with spatial and temporal scale information about the resources and behaviours that were present at the actual GPS locations of the animal (Hebblewhite and Haydon 2010).

In this study GPS data was combined with vole abundance measurements in the Montagu's harrier breeding area in Eastern-Groningen. The process of agricultural intensification and land-use changes has led to impoverished vole abundances (Butet and Leroux 2001, Arroyo et al. 2002, Millon et al. 2002, Arlettaz et al. 2010). This could have detrimental effects on the Montagu's harrier population sustainability as their population dynamics are driven by the abundance of their prey (Butet and Leroux 2001, Arroyo et al. 2002, Millon et al. 2002, Redpath et al. 2002, Arroyo and Garcia 2006, Koks et al. 2007, Bretagnolle et al. 2011). We suggest that vole abundance in agricultural areas can be improved by creating a network of set-asides, which can constitute very high-quality habitat for voles, connected by dispersal corridors. Positive effects of set-aside land should be reinforced by increasing the area set aside and their management (Koks et al. 2007, Macdonald et al. 2007). This way, fallow fields also increase biodiversity and abundance of several other taxa (Koks and Visser 2002, Koks et al. 2007). As opportunistic predators, Montagu's harriers can switch to other prey when the preferred resources are scares (Redpath et al. 2002, Arroyo and Garcia 2006). Voles form the main part of the diet of Montagu's harriers but in years when vole abundance is low diet diversity increases (Koks et al. 2001). Meadow Pipit *Anthus pratensis*, Skylark *Alauda arvensis*, Yellow wagtail *Moticilla flava* and Starling *Sturnus vulgaris* are common farmland birds and, together with juvenile lagomorphs (especially hares) form part of the Montagu's harrier's diet in certain times of the breeding season. These prey species may affect habitat preferences and their precise role should be investigated in future research. Even though Arroyo and Garcia (2006) found that years when diet was less diverse (with one prey species dominant in the diet) were associated with a higher productivity, creating favourable conditions for both voles and other prey species forms an important part of Montagu's harrier conservation.

Increasing the number of prey in the breeding area is not enough to compile higher food availability for Montagu's harriers. This study shows that it is not the absolute density of voles, but their accessibility that determines were to hunt. Montagu's harrier males prefer freshly mown grassland and harvested wheat especially those bordering set-aside habitat. The construction of new set-aside habitats next to grassland not bordering any fallow habitat can increase the number of grasslands with high prey availability and thus the overall food availability in the breeding area. At times when none of the preferred habitats are available (weeks of rain) high prey abundance in fallow habitat can compensate for low prey accessibility (Mirski 2010) and males start to use set-aside habitats (Dutch Montagu´s Harrier Foundation, unpublished data). It will be interesting to find out exactly how often Montagu's harrier males use set-aside land, grassland and annual crops as hunting area in the absence of optimal foraging grounds. Following, because of sex difference in parental role, habitat selection may differ between the sexes and information on habitat selection of females may improve management recommendations.

In conclusion, to provide high prey availability in the breeding area of Montagu's harriers, a combination of refuge areas with high vole abundances and adjacent a mosaic of freshly mown grasslands would be optimal. Because of the high energetic costs of flying, high quality hunting area is necessary on a relatively small scale, as close as possible to Montagu's harrier nesting habitat. High food availability and good nesting habitat positively influence Montagu's harrier reproduction but without nest protection many nests would be destroyed by farming practices each year and the population would nevertheless decline. By creating well considered high quality habitat, Montagu's harrier pairs can be attracted to the most productive and stable colonies in the agricultural areas.

These core areas can be protected more efficiently both logistically and economically and it may be easier to apply agri-environmental measures on relatively small scales.

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