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Trierweiler, Christiane

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Raptor foraging efficiency and agricultural management: mowing enhances hunting yield of the endangered Montagu’s harrier

István Szentirmai
Cor Dijkstra
Christiane Trierweiler
Ben J. Koks
Andrea Harnos
Jan Komdeur
Abstract

Due to the massive loss of natural habitats, increasing numbers of animals are compelled to exploit human-dominated habitats such as farmland. For their conservation, it is important to understand how they adapt to these environments and how agricultural management affects their demography. We investigated hunting behaviour of an endangered farmland raptor, Montagu’s harrier *Circus pygargus*, and quantified the effects of mowing on foraging returns. Hunting harriers spent half of their time and caught more than half of their prey in improved grasslands, and almost all prey they caught in these vegetations were voles. In the short-term (2 days), mowing of both improved grasslands as well as set-asides resulted in a 1.6-3.1-fold increase in harrier hunting yield (prey caught per hour hunting). Harriers also increased time spent hunting on freshly mown habitats. These factors combined resulted in a 37-fold increase in the number of prey captured on freshly mown fields compared to the unmown situation. The higher the proportion of time harriers spent hunting on freshly mown habitats, the less time they hunted in total and the more prey they ate. Improved grasslands are important sources of prey for Montagu’s harriers in rural areas in Western Europe. The importance is due to the fact that some fields support relatively high vole numbers, which are easy to catch during the first few days after mowing. Future conservation efforts should consider improved grasslands as potentially profitable hunting habitats for Montagu’s harrier and their appropriate management could complement set-asides.
Introduction

Due to massive loss of natural habitats, an increasing number of animals are compelled to use human-dominated habitats like farmland (Krebs et al. 1999). Therefore, the importance of agricultural habitats for conserving endangered species has increased during the last decades (Donald et al. 2002). The appropriate management of cultivated lands may be a key for the persistence of nearly 120 European bird species. Therefore, it is a major challenge for conservation biology to unravel the influence of farmland management on the birds’ demography (Tucker 1997).

Montagu’s harrier Circus pygargus L. is nowadays more common in agricultural areas than in its original (moor, heather and dune) habitats (Arroyo et al. 2002). Its European population underwent a severe decline during the last century and its current conservation status is vulnerable (Tucker & Heath 1994). The main cause of the species’ recent decline seems to be impoverished food supply due to intensification of agriculture (Arroyo 1998, Arroyo et al. 2002, Millon et al. 2002; Koks et al. 2007, chapter 2). Its main prey species in Western Europe is the common vole Microtus arvalis L. (Koks et al. 2005), and vole abundance is positively correlated with breeding performance of Montagu’s harrier (Butet & Leroux 1993, 2001; Salamolard et al. 2000; Koks et al. 2007; Millon et al. 2008; Millon & Bretagnolle 2008, chapter 2). The causal relationship between food availability and reproductive performance was experimentally shown in another vole-eating raptor, the European kestrel Falco tinnunculus L. (Dijkstra et al. 1982; Meijer et al. 1988).

On the landscape level, prey abundance depends on the distribution of different agricultural habitats. For example, uncultivated field margins and extensively managed set-asides are often richer in food than arable fields, and therefore high proportions of these habitats in the farmed landscape are preferable from a conservation perspective (Buskirk & Willi 2004; Koks et al. 2007, chapter 2). Accordingly, the main emphasis in conserving Montagu’s harrier has been on optimising existing and creation of new grass sown set-asides (Koks et al. 2007, chapter 2). Meanwhile, other habitats have been somewhat neglected, although improved grasslands for example may also support large vole populations (Delattre et al. 1992).

On the level of agricultural fields, prey abundance is mainly determined by farming management, i.e. pesticide and fertiliser use, use of machinery and timing of agricultural activities (Robinson & Sutherland 2002). For predators, however, prey availability also influenced by its detectability and accessibility (Ontiveros et al. 2005). In intensively managed grasslands and alfalfa Medicago sativa L., prey detectability and accessibility are low, since these vegetations produce large amounts of biomass and are homogenously tall and dense (Janes 1985; Widen 1994). The detectability and accessibility of voles are expected to substantially increase after mowing, since both vegetation height and cover decrease (Bechard 1982; Yosef & Grubb 1993; Wittingham & Devereux 2008). Thus, agricultural habitats may become favourable hunting habitats, especially after mowing.

This study has two objectives. First, we investigated the exploitation of improved grasslands and set-asides by Montagu’s harriers during their breeding season. Second, we investigated how mowing of grasslands, alfalfa and set-asides influenced
hunting yield. We expected that harriers detect more voles and strike more often in mown habitats, and their strikes will be more often successful. Consequently they will catch more prey per hour hunting on mown compared to unmown habitats. If so, we expected that harriers prefer mown over unmown habitats and capture more prey per day from mown than from unmown habitats. Harriers will profit from hunting on mown fields through enhanced prey delivery rates and reduced total hunting effort. To test these hypotheses, we carried out two studies. First, we followed radio-tagged males and related their individual hunting behaviour to the mowing status (unmown or mown) of their hunting habitats, and we related prey delivery rates and daily hunting effort to the proportion they hunted in mown habitats. Second, we observed variation in hunting parameters of harriers on experimental fields in relation to mowing date, i.e. immediately before, and during the days after mowing of these fields.

Methods

Study area

Field work was carried out from 2003-2005 during the Montagu’s harriers’ breeding season (April-August) in East Groningen, north-eastern Netherlands, in an area (ca. 650 km²) characterised by a mosaic of agricultural lands, i.e. crop fields, improved grasslands, alfalfa fields and set-asides. Grassy ditch and road edges were also typical habitats. Improved grasslands and edges were typically mown two to three times (interval: four-five weeks) and alfalfa once to twice (interval: seven-eight weeks) during the breeding season. Most set-asides were also mown once after 15 July. The local Montagu’s harrier population was ca. 30 breeding pairs each year (Trierweiler et al. 2006a; Koks et al. 2007, chapter 2). Additional field work in 2001–2002 was carried out in the Lauwersmeer area (ca. 100 km²) in the northern Netherlands, which is a freshwater lake surrounded by marsh vegetation, unimproved grasslands and small woods. Unimproved grasslands were managed by gradually mowing the whole area once, from mid-June until mid-August.

Hunting of individual males on mown and unmown habitats

To obtain information on individual behaviour, breeding males were fitted with radio transmitters and observed in East Groningen in 2003 (n = 2), 2004 (n = 2) and 2005 (n = 5, see appendix 4.1). In addition, one breeding male without radio transmitter was followed by a team of four observers at the Lauwersmeer in 2001 (see appendix 4.1). This male was individually recognizable by a broken primary feather. Males were caught by using a pole-trap placed at the edge of the field where they nested, and individually ringed. Radio transmitters (ATS Inc, type 4570, weight 4.7 g, ca. 1.5–2% of adult male body weight) were glued and tied on the base of one of the middle tail feathers (Kenward 2000). Radio-tagged males were tracked using three-element Yagi antennas connected to a receiver (ATS, FM100), receiving signals from within 1.5–2 km. After release, males were tracked for six to eight hours a day for 15.7 ±3.3 days between 14 May and 31 Augustus (see appendix 4.1).
During tracking, we noted whether the male was in sight (42.6 ±1.8% per male of total observation time, n = 141 tracking days), and if so, we recorded his behaviour during each full minute. We distinguished between hunting, flying, sitting and eating, noted each strike and added whether it was successful or not. For each minute of hunting we noted the type of habitat where the male was hunting. Habitats were assigned to three types based on vegetation and management: (1) improved grasslands (grasslands for grazing, silage or seed, grassy edges and alfalfa); (2) crops (cereals, sugar beet, oil-seed rape, potatoes, corn); and (3) set-asides (fallows: entire fields set aside for at least five years; fauna edges: grassy stripes between fields with extensive management; semi-natural grasslands). Improved grasslands and crops were intensively managed with fertilisers and other chemicals and frequent mowing, whereas set-asides were either uncultivated for longer time period or managed extensively by annual mowing. During observations we established whether the field was unmown or mown recently (within approximately 10 days from the day of mowing) based on known mowing dates or the height of vegetation (“mowing status” = mown/unmown). For each minute of hunting we noted the presence or absence of strikes made (attempts to catch prey), and whether the strike was successful in terms of catching prey. For each successful strike, we recorded prey type (vole, passerine or insect) and followed the male to the nest to establish prey delivery to its mate or young. Hunting behaviour was described by three variables. First, strike frequency as the proportion of hunting minutes in which a strike was observed. Second, strike success as the proportion of successful strikes out of all strikes. Finally, hunting yield as the proportion of hunting minutes with a successful strike. For each tracked male we recorded laying and hatching date of his clutch, and observations were assigned to one of three breeding stages (Cramp & Simmons 1980): courtship (length: 6–10 days), incubation (27–40 days) and nestling provisioning (35–40 days).

To investigate time allocation and the amount of prey caught in different habitats, we calculated the proportion of time spent hunting, the number of prey caught, and the proportion of voles, birds and insects among prey for (1) improved grasslands, (2) agricultural crops and (3) set-asides in the East Groningen agricultural study area, where all three habitat types were present within the home ranges of all tracked males. To investigate the effect of mowing on time allocation, we calculated the proportion of time spent either hunting or resting, and the proportion of hunting time allocated to unmown or mown habitats.

**Hunting on experimental fields in relation to mowing date**

To compare hunting behaviour of harriers between different mowing stages, we observed their hunting behaviour on the same grass (5–40 ha) and alfalfa fields (5-30 ha) both before and after mowing. Fields were located in the Lauwersmeer in 2002 (one grass field, 5 June–11 July) and in East Groningen in 2004 (two improved grass and 14 alfalfa fields; 19 May–29 July) and 2005 (six improved grass and 17 alfalfa fields; 30 May–4 August). Each field was chosen such that it fell within the home ranges of several breeding pairs (2–5). Observations were conducted before mowing (10.6 ±0.9 days [mean ±SE] before mowing, n = 63/35 [observations/fields]), on
mown fields on the day of mowing (day 0, n = 12/12), one day (day 1, n = 21/21),
two (day 2, n = 17/17) and more than two days after mowing (day >2, 7.5 ±0.7 days
after mowing, n = 13/11). Note that not each field was observed in all stages after
mowing. Each observation was carried out by one observer, using binoculars and
telescope, and observations lasted for 156 ±9 minutes. For each minute, we
recorded the presence or absence of hunting harriers, whether they made a strike
and whether the strike was successful. Strike frequency, strike success and hunting
yield were also calculated. In addition, we calculated hunting activity as percentage
of observation time (minutes) for which hunting individuals were present at the
field. To estimate the amount of prey caught per field in different mowing stages
over a whole day, we calculated “daily exploitation rate” as hunting yield * 60 (nr of
prey captured per hr hunting) * hunting activity (proportion of observed minutes
spent hunting) * 16.8 (average day length in hours in June-July, when most data
were collected; Meeus 1991). Then, the relative daily exploitation rate per field was
calculated for all mowing stages, relative to the unmown situation, by dividing the
values per mowing stage by the value of the unmown stage. This estimate integrates
effects of mowing on the combination of hunting yield as well as hunting activity on
a daily basis. Harriers observed on experimental fields were not marked, and there-
fore individual identification was impossible. However, each field was situated
within the home range of several breeding pairs, and we potentially observed the
majority of local pairs.

To quantify the effect of mowing on vegetation structure, we measured height
and cover of vegetation both 10.8 ±1.2 days before and immediately (0–2 days) after
mowing at three grass and 16 alfalfa fields. Height was measured by a ruler placed
vertically on the ground. Cover was defined as percentage of surface covered by
vegetation and was estimated visually within a 50×50 cm frame. Both height and
cover were measured at every tenth meter along a 100 m transect across the field
and averaged for the analyses.

Statistical analyses
We analysed hunting behaviour in relation to mowing by Generalised Linear Mixed
Models (GLMM) with binomial error distribution and logit link function including
either the identity (ID) of the observed field (experimental fields observations) or the
ID of the male and the day it was observed (individual males’ observations) as
nested random factors (Venables & Ripley 2002). Hunting activity was analysed as
the probability that a hunting harrier was present at each full minute during the
observations. Strike frequency and hunting yield were analysed as the probability
that a strike was made and that a prey was caught in a hunting minute, respectively.
Strike success was analysed as the probability that a strike was successful. The
explanatory variables in the GLMMs of field observations were mowing stage
(unmown, day 0, day 1, day 2, and day >2), habitat type (grass, alfalfa) and year
males, mowing status (unmown, mown), habitat type (improved grassland, set-
aside), breeding stage (egg-laying, incubation, nestling feeding) and year (2001, 2003,
2004, 2005) were the fixed factors.
Time allocation of individual males in relation to mowing status (mown-unmown comparison) was investigated by Linear Mixed-Effects Models (LM, Venables & Ripley 2002). We related time spent hunting and resting per hour, number of prey caught per hour, the proportion of voles among prey, prey delivered to female and young, and eaten by the male per hour (response variables) to the proportion of hunting time spent on mown grasslands (explanatory variable). Models also included breeding stage and year as fixed factors. All variables except total time spent hunting were normalised by arcsine ($\arcsin(x/0.5)$) transformation.

All statistical analyses were performed by R 2.2.0 Project for Statistical Computing software (R Development Core Team 2005; Ihaka & Gentleman 1996). To estimate parameters, penalised quasi likelihood method (PQL) was used in GLMMs and restricted maximum likelihood method (REML) in LMEs. All tests were two-sided and we rejected the null hypothesis at $P<0.05$. Non-significant terms were removed from the models by step-wise elimination and the results of final models for each factor (the last in which it was included) are presented throughout the paper. Results are reported as means ± SE.

Results

Use of different hunting habitats
In our main study area, the agricultural area of East Groningen, radio-tracked males spent on average 46% of their time hunting. They allocated about half of their hunting time to improved grasslands, around 20% to set-asides and 30% to agricultural crops. Similarly, more than half of their prey was caught on improved grasslands (tab. 4.1). In addition, nearly all prey caught were voles on both improved grasslands and set-asides, although insects and birds were also numerous in crop fields (tab. 4.1).

Table 4.1 Mean ±SE percentage of time spent hunting (120 days), prey caught (803 prey items) and voles, birds and insects among the prey (195 prey items) of seven radio-tracked male Montagu’s harriers on three different habitat types in the agricultural study area of East Groningen.

<table>
<thead>
<tr>
<th></th>
<th>Improved grasslands</th>
<th>Set-asides</th>
<th>Crop fields</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hunting (%)</td>
<td>48.4 ±2.7</td>
<td>19.2 ±2.1</td>
<td>32.4 ±2.4</td>
</tr>
<tr>
<td>Prey (%)</td>
<td>56.2 ±4.0</td>
<td>21.6 ±3.1</td>
<td>22.2 ±3.2</td>
</tr>
<tr>
<td>Voles (%)</td>
<td>96.1 ±2.6</td>
<td>100.0 ±0.0</td>
<td>56.1 ±10.3</td>
</tr>
<tr>
<td>Birds (%)</td>
<td>0.4 ±0.4</td>
<td>0</td>
<td>5.0 ±4.6</td>
</tr>
<tr>
<td>Insects (%)</td>
<td>3.5 ±2.6</td>
<td>0</td>
<td>38.9 ±10.0</td>
</tr>
</tbody>
</table>
Hunting of individual males on mown and unmown habitats

Hunting yield of individual males was 1.6 times higher on mown than unmown fields (tab. 4.2, fig. 4.1A). This increase in hunting yield was caused by a 1.3 fold rise in strike frequency as well as in strike success (tab. 4.2, fig. 4.1B,C).

Strike frequency was higher on set-asides than on improved grasslands ($\beta = 0.23 \pm 0.09, z = 2.447, P = 0.014$), and both strike frequency and hunting yield was higher in 2004 than in the other years (Helmert-contrasts: $t_{7} = 7.328, P < 0.001$).

Hunting on experimental fields in relation to mowing date

By mowing of grasslands, vegetation height decreased from 19.8 ±1.5 cm to 7.5 ±0.6 cm and cover from 78.1 ± 4.5% to 57.4 ±4.1% (n = 3 fields). By mowing of alfalfa fields, vegetation height decreased from 72.7 ±2.3 cm to 7.0 ±0.3 cm and cover from 76.6 ±2.3% to 11.1 ±1.6% (n = 16 fields).

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**Table 4.2** The effect of mowing status (mown/unmown), breeding stage (courtship, incubation, nestling stage) and year (2001, ’03, ’04,’05) on hunting yield, strike frequency, and strike success of eight tracked male Montagu’s harriers (see also fig. 4.1). The results of final GLMMs are presented for each explanatory variable.

<table>
<thead>
<tr>
<th></th>
<th>Hunting yield</th>
<th>Strike frequency</th>
<th>Strike success</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$\chi^2$</td>
<td>df</td>
<td>P</td>
</tr>
<tr>
<td>Mowing status</td>
<td>27.408</td>
<td>1</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Vegetation category</td>
<td>0.054</td>
<td>1</td>
<td>0.816</td>
</tr>
<tr>
<td>Breeding stage</td>
<td>3.928</td>
<td>2</td>
<td>0.140</td>
</tr>
<tr>
<td>Year</td>
<td>10.301</td>
<td>3</td>
<td>0.016</td>
</tr>
</tbody>
</table>

**Figure 4.1** Difference in (A) hunting yield, (B) strike frequency and (C) strikes success between mown and unmown vegetations based on eight radio-tracked male Montagu’s harriers in East Groningen. Markers represent predictions of GLMMs for each mowing status, and error bars represent their confidence intervals (see also tab. 4.4). Numbers in brackets indicate number of hunting hours in (A) and (B), and number of strikes in (C).
Hunting activity, strike frequency, strike success and hunting yield were higher after mowing than before mowing. Hunting activity was 11.8 times higher on day 0 than before mowing and steeply declined after that, although it remained still significantly higher than it was before mowing (fig. 4.2A, tab. 4.3). Strike frequency was 2.6 times higher on day 0 and 1.6 times higher on day 1 than before mowing, whereas it was not significantly different from before mowing from day 2 onwards (fig. 4.2B, tab. 4.3). Similarly, strike success was 1.8 times higher on day 0 and 1.6 times higher on day 1 than before mowing (fig. 4.2C, tab. 4.3). Consequently, the hunting yield (= strike frequency * strike success) was 3.1 times higher on day 0 and 2.4 times higher on day 1 than before mowing (fig. 4.2D, tab. 4.3). As a result of the simultaneous increase of hunting yield as well as hunting activity the prey exploitation rate of fields (see Methods) by hunting harriers was 36.9 times higher at the first day after mowing compared to the unmown situation (fig. 4.3). However, this dramatic effect of mowing was already diminished three days later (fig. 4.3).

Figure 4.2 Changes in (A) hunting activity, (B) strike frequency, (C) strike success and (D) hunting yield of Montagu's harriers with mowing stage (number of days after mowing) for grass and alfalfa fields combined. Dots represent predictions of GLMMs for each mowing stage and error bars represent their confidence intervals. Numbers in brackets indicate the number of fields observed in each mowing stage (for statistics see tab. 4.5).
Table 4.3 The effect of mowing stage (days after mowing) on hunting activity (22,246 minutes), strike frequency (1,259 minutes), strike success (212 minutes) and hunting yield (1,259 minutes) of Montagu’s harriers based on repeated observations of grass and alfalfa fields (see also fig. 4.2). The results of final GLMMs are given and \( \beta \) values indicate differences in the effect sizes compared to the unmown stage (as a reference).

<table>
<thead>
<tr>
<th>Mowing stage</th>
<th>Hunting yield</th>
<th>Strike frequency</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>( \beta \pm SE )</td>
<td>( t ) or ( \chi^2 )</td>
</tr>
<tr>
<td>day 0</td>
<td>1.27 ±0.39</td>
<td>3.242†</td>
</tr>
<tr>
<td>day 1</td>
<td>0.96 ±0.39</td>
<td>2.477†</td>
</tr>
<tr>
<td>day 2</td>
<td>0.12 ±0.38</td>
<td>0.321†</td>
</tr>
<tr>
<td>day &gt;2</td>
<td>-0.13 ±0.37</td>
<td>0.356†</td>
</tr>
<tr>
<td>Vegetation</td>
<td>5.543†</td>
<td>0.063</td>
</tr>
<tr>
<td>Year</td>
<td>6.007‡</td>
<td>0.05</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Mowing stage</th>
<th>Strike success</th>
<th>Hunting activity</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>( \beta \pm SE )</td>
<td>( t ) or ( \chi^2 )</td>
</tr>
<tr>
<td>day 0</td>
<td>1.13 ±0.55</td>
<td>2.048†</td>
</tr>
<tr>
<td>day 1</td>
<td>1.05 ±0.52</td>
<td>2.014†</td>
</tr>
<tr>
<td>day 2</td>
<td>0.86 ±0.57</td>
<td>1.523†</td>
</tr>
<tr>
<td>day &gt;2</td>
<td>-0.08 ±0.51</td>
<td>0.155†</td>
</tr>
<tr>
<td>Vegetation</td>
<td>5.668‡</td>
<td>0.059</td>
</tr>
<tr>
<td>Year</td>
<td>4.390‡</td>
<td>0.111</td>
</tr>
</tbody>
</table>

† \( t \) statistics for the comparison of mowing stages to unmown stage,
‡ \( \chi^2 \) statistics for the overall effect of vegetation and year

Figure 4.3 Relative daily exploitation rates of fields (grass and alfalfa fields combined, mean values) by Montagu’s harriers in relation to mowing stage. Daily exploitation rate equals to hunting yield (= prey captured per hour hunting) * daily hunting activity (= proportion hunting per hour observation * 16.8 daylight hours, see Methods). Bars represent increase in exploitation rate of fields relative to the unmown stage (dashed line = 1).
Time allocation and prey consumption in relation to mowing

The higher proportion of time harriers spent hunting on mown grasslands, the less they hunted in total over a day (fig. 4.4A, tab. 4.4), and the more they tended to spend resting (tab. 4.4). Furthermore, the amount of prey caught and the proportion of voles among prey tended to increase with the proportion of time spent hunting on

\[ \text{Prey eaten by male (h}^{-1} \text{)} = 0.57 + 0.002 \times \text{hunting on mown grasslands, } t = 2.160, P = 0.03 \]

by eight tracked male Montagu’s Harriers.

<table>
<thead>
<tr>
<th>Predictor: Proportion hunting on mown grassland</th>
<th>F</th>
<th>df. error</th>
<th>df</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total hrs. hunting</td>
<td>15.010</td>
<td>1, 117</td>
<td>&lt; 0.001</td>
<td></td>
</tr>
<tr>
<td>Total hrs. resting</td>
<td>3.483</td>
<td>1, 117</td>
<td>0.065</td>
<td></td>
</tr>
<tr>
<td>Total prey captured</td>
<td>3.509</td>
<td>1, 114</td>
<td>0.064</td>
<td></td>
</tr>
<tr>
<td>Voles captured</td>
<td>2.855</td>
<td>1, 590</td>
<td>0.096</td>
<td></td>
</tr>
<tr>
<td>Nr. prey delivered</td>
<td>0.408</td>
<td>1, 107</td>
<td>0.524</td>
<td></td>
</tr>
<tr>
<td>Prey eaten by male</td>
<td>4.666</td>
<td>1, 880</td>
<td>0.034</td>
<td></td>
</tr>
</tbody>
</table>

Figure 4.4 Relationships between the proportion of time spent hunting on mown grasslands and (A) total time spent hunting \( (= 55 - 0.23 \times \text{hunting on mown grasslands, } t = 3.874, P < 0.001) \) and (B) amount of prey eaten \( (= 0.57 + 0.002 \times \text{hunting on mown grasslands, } t = 2.160, P = 0.03) \) by eight tracked male Montagu’s Harriers.

Table 4.4 The influence of proportion of hunting on mown grassland on total time spent hunting and resting (126 days), total number of prey caught (869 prey items) and proportion of voles among prey (205 prey items), prey delivered to female and young (653 prey items) and prey eaten (290 prey items) by eight male Montagu’s harriers per hour. The results of final LMEs are shown for each explanatory variable. The initial models also included breeding stage and year as covariates, but these results, being non-significant are not presented here.
mown grasslands (tab. 4.4). Similarly, the amount of prey eaten by the males increased with the proportion of time they spent hunting on mown grasslands (fig. 4.4B, tab. 4.4). However, the amount of prey delivered to females and young was unrelated to the proportion of time spent hunting on mown grasslands (tab. 4.4).

Discussion

The importance of improved grasslands
Our results show that in the Dutch agricultural landscape, improved grasslands are important hunting habitats for Montagu’s harriers, since they allocated about half of their hunting time and caught more than half of their prey on these habitats (tab. 4.1). In the first place, this high representation of improved grasslands is due to the large proportion of surface area occupied by these habitats. Additionally, our results suggest that prey is readily available in improved grasslands and especially becomes accessible due to mowing. However, these results do not mean that improved grasslands are high quality habitats for raptors, since most of them accommodate very low vole populations compared for example to set-asides or natural grasslands (Koks et al. 2007, chapter 2). The relatively low prey abundance of improved grasslands is mainly due to their intensive management. Regular fertilisation and frequent mowing reduces food availability for raptors in the long run and by destroying the soil directly harms voles (Jacob & Halle 2001; Jacob & Hempel 2003). Our results indicate frequent hunting and regular prey captures of Montagu’s harriers on improved grasslands, but we emphasize that more extensive management is necessary to further improve the foraging possibilities of Montagu’s harriers (Vickery et al. 2001; Verhulst et al. 2004).

Mowing and hunting yield
Our data from both repeated observations of experimental grass and alfalfa fields and tracking of individual males revealed that mowing results in a substantial increase in hunting yield. When hunting on freshly mown fields (day 0), or one day after mowing (day 1) harrier hunting yield was respectively 3.1 and 2.4 times higher than before mowing. This strong effect was only short-term, because hunting yield 2 days after mowing or later did not differ from the unmown situation. Consequently, freshly mown fields attracted more harriers and their hunting activity on the experimental fields showed a 12-fold increase immediately after mowing. This is in line with studies on kestrels and long-eared owls Asio otus L., showing that these species preferred to hunt on freshly mown grasslands (Sheffield et al. 2001; Aschwanden et al. 2005). Furthermore, our data support other studies on avian predators indicating preference for lower vegetation cover and height (Wakeley 1978; Leyhe & Ritchison 2004; Amar & Redpath 2005; Whittingham & Devereux 2008). The combined effect of increased hunting activity and hunting yield resulted in a vast, 37-fold increase in the daily amount of prey exploited from freshly mown fields compared to the unmown situation. This very strong effect is still an under-estimation of the total predation rate on freshly mown fields since we did not quantify additional depletion...
of vole numbers by other predator species (Pers. Obs.). This clearly underlines that mowing of grasslands is a key factor determining hunting efficiency of Montagu’s harriers in agricultural areas. Hunting yield in turn is a crucial life history parameter since it limits the number of nestlings that can be raised, and mowing is thereby linked to the harrier’s evolutionary fitness (see below).

The change in hunting yield was caused by a 1.3-fold increase in both strike frequency and strike success. The increase in strike frequency is most likely explained by two factors. First, by reducing vegetation cover and height, mowing apparently improves the detectability of prey, in our case mainly common voles (Butet & Leroux 2001; Millon et al. 2002; Koks et al. 2007, chapter 2). This effect of mowing was found in other predator species as well and we assume that it is a general phenomenon in most visually searching predators (Bechard 1982; Yosef & Grubb 1993). More generally, it was also found that hunting success of raptors increases with decreasing vegetation cover (Jenkins 2000; Aschwanden et al. 2005).

Second, the machinery used for mowing and removing hay can potentially injure and kill voles and hares, creating easily accessible prey for raptors. This latter effect has not been quantified up to now, but the presence of several dead voles on an alfalfa field immediately after mowing has been confirmed in our study (Pers. obs.). The reason for increased strike success is probably the reduction of hiding cover for voles where they can escape from the attacks of harriers, and the increase of dead or injured prey in the field.

Although mowing had a profound effect on the availability of prey and its exploitation by Montagu’s harriers, this lasted only for a few days. Just two days after mowing there was no significant difference in strike frequency, strike success and hunting yield between mown and unmown fields. A potential reason for the observed pattern is that mown fields attract many Montagu’s harriers and other predator species, and thus the prey source can be quickly depleted. Furthermore, voles can adapt to the new conditions by spending less time above ground, travelling shorter distances from their holes or migrating out of the mown field (Jacob & Hempel 2003).

In contrast to its short-term positive effects, too frequent mowing has a negative effect on vole populations in the long term (Jacob & Halle 2001; Jacob & Hempel 2003). Therefore improved grasslands are highly unstable habitats for voles and other prey species of Montagu’s harriers, and set-asides are necessary to maintain a stable vole population at the landscape level (Briner et al. 2005). Set-asides may also serve as refuges from where voles can re-colonise improved grasslands after local extinctions or emigrations. Furthermore set-asides also provide stable prey availability for raptors all over the year (Koks et al. 2007, chapter 2).

**Mowing and time allocation**

The more time males spent hunting on mown habitats the less they hunted in total. This suggests that the availability of mown hunting habitat enhanced hunting efficiency, and thus decreased the time needed to catch the daily amount of prey needed. Consequently, when harriers could hunt more on mown habitats, they had more time left for resting. The availability of mown hunting habitat seems to reduce
hunting effort and thus may reduce the costs of hunting. There is strong evidence from brood manipulation experiments that high hunting effort results in increased energetic demands and may eventually lead to reduced adult survival prospects in avian predators (Dijkstra et al. 1990; Deerenberg et al. 1995; Daan et al. 1996). The total number of prey caught also tended to increase and the prey eaten by the male significantly increased with the time that males spent hunting on mown fields. Taken together, the availability of mown habitats may have a positive influence on the energy budget and ultimately the annual survival of adult male Montagu’s harriers by reducing the necessary hunting effort.

**Synthesis and applications**

This study reveals two important facts for Montagu’s harrier conservation. First, improved grasslands are important hunting habitats in agricultural areas. Second, mowing of both improved grasslands and set-asides enhances prey availability, and the availability of freshly mown habitats thus may improve the survival probabilities and thereby fitness of harriers.

There are two main limitations of the positive impact of mowing. First, although vegetation cover and height remains largely unchanged for many days after mowing, hunting yield declines steeply from just one day after mowing, probably due to rapid depletion of vole numbers by high predation pressure. Therefore, the amount of available high quality hunting habitat (freshly mown grasslands and set-asides) within a harrier home range may be low on most days of the breeding season. Second, as indicated by large proportion of variance in hunting yield explained by field identity, only some of the fields support large numbers of voles and provide good hunting opportunities for harriers after mowing.

Based on these results, we suggest that future conservation efforts should take into consideration that improved grasslands can be profitable hunting habitats for Montagu’s harrier and their appropriate management could complement set-asides. By reducing fertiliser use and the frequency of mowing and leaving somewhat taller stubble, grasslands could be transformed into much better vole habitats than they currently are (Vickery et al. 2001; Verhulst et al. 2004). It is important to note however, that set-asides are more stable hunting habitats for harriers and may serve as refuges for voles to re-colonise and subsequently vole-depleted grasslands (Koks et al. 2007, chapter 2). In general, the positive but short-term impact of mowing of grass habitats on harrier hunting yield could be enhanced by introducing mowing regimes that may benefit both voles and their predators. Employing temporally and spatially staggered mowing regimes, i.e. mowing different (parts of) fields at different times, may provide freshly mown habitats in the home ranges of harriers more or less continuously over the breeding season, without serious depletion or even local extinction of the voles, and avoiding possible depensation effects on the vole population. The idea of temporally staggered mowing regimes actually reflects a more general theory about the role of spatial and temporal diversity of cultivated lands in maintaining farmland biodiversity (Benton et al. 2003). Leaving uncut stripes within or between grass fields may further improve prey availability for harriers, which may serve as refuges for voles and allow vole population to
recover faster after mowing and to re-colonise mown parts (Aschwanden et al. 2007; Koks et al. 2007, chapter 2).

Optimisation of mowing management facilitating optimal foraging conditions for harriers can only be achieved by investigating the effects of different experimental mowing regimes on vole populations and their predators. Furthermore, feasibility studies are necessary to investigate economic consequences of different mowing regimes.

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Appendix 4.1 Information on the eight tracked male Montagu’s harriers. Seven were followed using radio telemetry in East Groningen, and one was individually recognizable and followed without radio telemetry in the Lauwersmeer (LM).

<table>
<thead>
<tr>
<th>Male identity</th>
<th>Year</th>
<th>Observation period</th>
<th>No. days observed</th>
<th>No. minutes Observed</th>
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<tr>
<td>LM</td>
<td>2001</td>
<td>17 July</td>
<td>1</td>
<td>493</td>
</tr>
<tr>
<td>Y22</td>
<td>2003</td>
<td>17 Jun–22 Jul</td>
<td>8</td>
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<tr>
<td>Y27</td>
<td>2003</td>
<td>24 Jun–4 Aug</td>
<td>18</td>
<td>3013</td>
</tr>
<tr>
<td>Y27</td>
<td>2005</td>
<td>20 Jul–12 Aug</td>
<td>7</td>
<td>1753</td>
</tr>
<tr>
<td>Y72</td>
<td>2005</td>
<td>14 May–16 Jun</td>
<td>15</td>
<td>3034</td>
</tr>
<tr>
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<td>22</td>
<td>5424</td>
</tr>
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</table>

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Part II

Processes during migrations
Im Traum und auf Reisen gibt es keine Unmöglichkeiten.

- János Arany -