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Trierweiler, Christiane

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Home range size and habitat selection of the endangered Montagu’s harrier *Circus pygargus* in NW-Europe: implications for conservation

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Abstract

In many European landscapes that are intensively influenced by human utilization, birds increasingly rely on agricultural habitats. Montagu’s harrier *Circus pygargus* is an example for a diurnal raptor species that is since the middle of the 20th century mainly breeding in farmland habitats in West-Europe. The breeding season is thought to strongly affect population change in this long-distance migrant. Next to nest protection from agricultural practices, it is important to understand the functional relationship of the predator with its habitats and base conservation actions on these ecological insights. In a four – year radio telemetry study in the Netherlands, we identified lucerne, fallow habitats and cereals as most preferred habitats at different home range scale levels in two Dutch farmland areas. For hunting, high habitat diversity in general and especially intensive grasslands, lucerne, natural grasslands and fallow habitat types were most preferred. The frequency with which harriers attempted to catch prey (a measure of food availability) as well as the number of prey caught per hour (hunting yield) were highest in fallow habitats, intensive grasslands and lucerne. Individual differences in hunting yield and home range size related to differences in reproductive success. There was a trend of high proportions of lucerne and fallow habitat types in a ca. 8 km² area (1.6 km radius) around the nest contributing to relatively small core home range size, which in turn related to high reproductive success. We recommend to offer higher proportions of these favourable habitat types in West-European intensively farmed landscapes and to optimise management of natural and extensive grasslands as habitats for potential prey populations. Because Montagu’s harrier is a top-predator, an optimised habitat management for the harrier must improve the habitat characteristics for the underlying food web, in particular small mammal and farmland bird communities.
Introduction

In many NW-European landscapes that are intensively influenced by human utilisation, birds lost their natural habitats and increasingly rely on farmland habitats (Tucker 1997). In farmland, bottlenecks may arise due to decreasing food abundance with increasing intensification (Butet & Leroux, 2001; Donald et al. 2001) and nest losses due to agricultural practices (Clarke 1996a). An example of a bird species that, since the last century, mainly uses farmland habitats during the breeding season is the diurnal raptor Montagu’s harrier *Circus pygargus* (Arroyo et al. 2002).

European Montagu’s harriers are long-distance Palearctic-African migrants, traditionally breeding in lowland heaths, dunes, wet meadows and (pseudo-) steppes (Clarke 1996a, Leroux 2004, Trierweiler & Koks 2009, chapter 8). Due to the disappearance or decreasing suitability of natural habitats, about 70 – 90% of western European breeding pairs are nesting in agricultural habitats since the 1990s (Arroyo et al. 2002). Because Montagu’s harriers are nesting on the ground, the advanced onset of the cereal harvest and frequent lucerne harvest threaten nest survival in agricultural areas. Depending on the nesting habitat and harvest timing, 20–70% of nests can be destroyed during harvesting activities (Corbacho et al. 1997, Koks et al. 2001, Millon et al. 2002, Van der Kerkhove et al. 2007). Nest protection in European farmland is thus imperative to prevent large-scale nest failure. Protecting nests has proven successful, but is resource consuming in terms of time, manpower and equipment (Glimm et al. 2001, Arroyo et al. 2002, Koks & Visser 2002b, Koks 2008). In spite of locally successful conservation actions, Montagu’s harrier is included in Annex I of the European Birds Directive (79/409/EEC) being in need of special conservation measures and is red-listed in many West-European countries (e.g. Germany, Netherlands, Denmark, Spain).

Optimally, nest protection should be complemented with improvement of harrier habitat in farmland, in addition to the preservation and regeneration of natural breeding habitats (Millon et al. 2002, Koks et al. 2007, Trierweiler & Koks 2009, chapter 2, 8). In order to improve or increase favourable habitat types within the agricultural landscape, information on habitat use is needed. Extensively used structures (e.g. set-aside farmland with grassy or herbal vegetation, fallow land, fallow field margins) have proven to be important habitat types in the NW-European landscape that may positively influence reproductive effort and population development of Montagu’s harriers (Koks & Van Scharenburg 1997, Koks et al. 2007, Trierweiler et al. 2008, chapter 1, 2). This effect is mainly related to high prey availability in these habitats. Montagu’s harriers in Dutch farmland feed on small mammal prey (especially common vole *Microtus arvalis*; ca. 60% of prey items) and bird prey (mostly yellow wagtail *Motacilla flava*, meadow pipit *Anthus pratensis* and skylark *Alauda arvensis*; birds constituting ca. 20% of prey items) as well as lagomorphs, eggs and invertebrates (Koks et al. 2007, chapter 2). To understand the functional relationship between different habitat types and individuals or populations, information on habitat use and habitat selection of the hunting birds is most important, as well as estimates of food availability in different habitat types. Such ecological knowledge is crucial for the development of conservation strategies required by EU

In this study, we investigate home range size, habitat selection and hunting behaviour of Montagu’s harriers during the breeding season (May – August) using radio telemetry (Kenward 2000). In a four-year study (2003 - 2006), we radio-tagged ten Montagu’s harrier males (two of which twice, in different years) in two agricultural landscapes in the Netherlands, in order to record their spatial and hunting behaviour. Both study sites were large-scale agricultural areas dominated by the cultivation of winter cereals, root crops (potatoes, beetroots, onions) and intensively used grasslands (used for cattle feed).

We investigated (1) habitat selection in general and especially hunting habitat selection compared to habitat and soil types available at different scale levels, (2) the seasonal change in habitat selection and (3) hunting behaviour and hunting success according to different habitat types and breeding phases. The results, also in relation to reproductive output, indicate which habitat types are preferred and profitable in the farmed landscape, potentially supporting successful Montagu’s harriers breeding attempts. This enables us to suggest efficient conservation strategies based on habitat management.

Methods

Study areas and study populations
One study area was in East-Groningen (Province of Groningen, northeastern Netherlands, 53°11’N, 7°4’E, surface area ca. 970 km²), consisting of acclaimed land (polders) from the 16th century to 1924, with a relatively structured and diverse landscape, including agri-environmental schemes (fallow field margins). It hosts a stable to increasing harrier population since the early 1990s (25–30 breeding pairs annually during the study period 2003–2006; Koks et al. 2007, chapter 1, 2). The other study area, located in recently (1959–1968) acclaimed land in the Southern Flevoland polder (Province of Flevoland, western Netherlands, 52°22’N, 5°28’E, surface area ca. 490 km²), was comparatively poorly structured and devoid of agri-environmental schemes during the study period. After thriving of a Montagu’s harrier population in young forest plantations in the 1970s, the population in Flevoland (now located exclusively in farmland) has been on a very low level since the 1980s (5–6 breeding pairs annually in 2003–2006).

Habitat types in the study areas were cereals (mostly winter wheat, also winter barley and others), potatoes, beetroots and onions, grassland and meadows, furthermore lucerne, set-aside, agri-environmental schemes, grassy paths and ditch edges as well as nature reserves in smaller proportions (for details see results, fig. 3.2A,B). Montagu’s harrier breeding pairs in Groningen and Flevoland were monitored by observing territorial and breeding behaviour. Nests were usually visited three times a season (Koks et al. 2007, chapter 2). Farmers, landowners and harvesting companies were informed about the breeding attempt and potentially necessary protection against harvesting practices. Nests were protected against harvesting and against subsequent predation by sparing a small unharvested plot around the nest and
fencing it (chapter 1). Clutch size was either observed directly or taken as being the number of nestlings or fledglings (minimum clutch size). The number of fledglings was recorded after all young had left the nest. Laying date was back-calculated from nestling age determined from wing length (Bijlsma 1998, Koks et al. 2007, chapter 2). Most Montagu’s harriers are supposedly monogamic (Simmons 2000) but a certain part of the population may be bigamic (e.g. 11% in Groningen in 2005, Trierweiler et al. 2006a). Bigamy is only easily identified when the bird is radio-tagged. For all tracked males, the number of nests/females was determined.

Pellets and prey remains were collected weekly in the vicinity of the nests (Koks et al. 2007, chapter 2): on average over all nests, 64% of the number of prey items consisted of voles and mice (38% of total diet were determined as common voles), 19% of birds (18% of total diet were passerines), 9% of insects, 4% of eggs, 2% of lagomorphs and 2% of other small mammals. In terms of estimated biomass (number multiplied with average body mass of prey item, Koks et al. 2007, chapter 2, Box A), diet consisted of 55% voles and mice, 18% lagomorphs, 16% birds, 9% other small mammals, 2% eggs and 0% insects.

Radio telemetry
Montagu’s harrier males need to provide food not only for themselves, but also for their female (or females in case of polygamy) during the pre-breeding (courtship), incubation and nestling phase. Furthermore, they need to provide food for their young in the early fledgling phase. Incubation and nestling phases take each about 30 days, pre-breeding phase and post-fledging care may be of variable length (ca. 1–3 weeks each). Only females incubate and they contribute to the feeding of the young only from the late nestling phase onwards, if at all. We therefore radio-tracked exclusively males (10 males, two of which twice, in different years). They were caught on a perch trap, which is a wooden pole equipped with a nylon maze closing around the bird’s feet when the catching mechanism is triggered by the landing bird. Wing length, wing span, body mass and claw size of the captured males were measured. A 4.7 g tailmount radio transmitter (Advanced Telemetry Systems Inc., Minnesota, US) was tied and glued to one of the central tail feathers. Radio signals were picked up with ATS-100 Fieldmaster receivers and three-element hand-held yaggi antennas. The males were caught in different phases of the breeding cycle (as they could not all easily be captured) and were tracked for periods of different lengths depending on the performance of the tracking equipment. In one case, tracking stopped after nest failure because the male left its breeding home range. For details of study area, biometry, reproduction and tracking period of all males see appendix 3.1.

Tracking sessions usually lasted from 8.00–18.00 h and were conducted two or more times a week. At the start of each session, the signal of the bird’s transmitter was mostly picked up near the nest. Subsequently, the bird was radio-tracked by two observers by car, with the aim to stay as long as possible in visual contact with the bird (possible during ca. 40% of the time). During visual contact, behaviours of the bird were noted every minute using either the bare eye, binoculars or a telescope. Behaviours were categorised as hunting (low quartering flight), flying (in a
straight line), circling, transporting prey, sitting, feeding, nest site defence and aerial display (courtship). Events noted were strikes (attempts to catch prey) with outcome (successful or not, or unknown; type/species of prey), food passes to female or young, copulations and conspecific or interspecific aggressive interactions. Locations of the bird were noted with numbered dots in daily maps. These numbers correspond to the accompanying behaviour records. From the behaviour records, the number of attempts to catch a prey per minute (strike frequency), the success of the attempt (strike success) and the hunting yield per hour (strike frequency * strike success * 60) were calculated (Dijkstra et al. 1995, De Voogd 2004).

Spatial and statistical analyses
Visual fixes (n = 4,426) were digitized in ESRI ArcView 3.2. The fixes were used to calculate different home range contours in ESRI ArcMap 9.3.1 (ESRI Inc.). The smoothing parameter h_ref used to calculate fixed kernel home ranges was taken from program Animal Space Use 1.3 (Horne & Garton 2007). With Hawth’s Analysis Tools 3.27 (www.spatialEcology.com), 50%, 90% and 100% home range contours were generated. Sample size of visual fixes per bird did not significantly affect home range size at different levels (100% kernel home range: r = –0.13, n = 12, p = 0.69; 90%; r = –0.32, p = 0.32; 50%; r = –0.50, p = 0.10).

Habitat preferences were calculated using digital maps showing agricultural land cover types for each year of our study period (2003–2006; copyright Dienst Regelingen, Dutch Ministry of Agriculture, Nature and Food Quality). Agricultural land cover of 2007 was used to calculate habitat diversity within 1 × 1 km squares according to the Shannon-Weaver Index as relative diversity (proportion of the maximum possible diversity): J' = H'/H'_max where H' = – ∑i=1^k p_i log p_i (Zar 1996). Here, k is the number of categories and p_i the proportion of the observations found in category i. Additional information was derived from digital topographical maps (showing houses, roads, parcel boundaries etc.) of Groningen and Flevoland (copyright Topografische Dienst Kadaster) as well as of the German area Rheiderland (copyright Niedersächsischer Landesbetrieb für Wasserwirtschaft, Küsten- und Naturschutz NLWKN) that is adjacent to Groningen and was part of some home ranges as well. Furthermore, a soil type map of Groningen (copyright Province of Groningen) was used.

Analyses of hunting behaviours were conducted using two-level random intercepts regression models in MLwiN 2.02 (Institute of Education), including bird ID as level in order to correct for pseudo-replications of the birds tracked twice. To analyse habitat selection, compositional analyses (Aebischer et al. 1993) were carried out in R (package adehabitat, function compana; method: randomisation test, Calenge 2006). Habitats were grouped as follows. Category 1 (“potatoes/beetroots/onions”): all categories of potatoes, beetroots, onions and flower bulbs; category 2 (“urban”): roads, paths, buildings; category 3 (“fallow”): all types of fallow and set-aside land (except for bare land and set-aside tree plantations) and agri-environmental schemes (fallow field margins); category 4 (“wood”): all woods (also set-aside tree plantations, in the study area > 10 years old); category 5 (“winter cereals”): mainly winter wheat and winter barley; category 6 (“summer cereals”): mainly
results of hunting behaviour, the categories winter and summer cereals were merged. Other statistical tests were run in SPSS version 16.0 (SPSS Inc.). Due to the small sample size of radio-tracked birds in Flevoland, analyses of spatial and hunting behaviour were combined over both study areas. Results were interpreted as significant at the $\alpha = 0.05$ level.

**Results**

**Home range size**

Surface areas of home range contours taken over 1 track (a track comprises all fixes from one breeding season of one male) based on kernel analyses were on average 8.4 ± 1.0 km$^2$ (50% kernel, n = 12), 34.9 ± 3.8 km$^2$ (90% kernel) and 131.1 ± 13.9 km$^2$ (100% kernel, fig. 3.1). In a two level random intercepts regression model (level i: track, level ii: individual) on home range size, individual differences were significant (50% kernel home range: $\chi^2 = 104.4$, df = 9, $p < 0.001$; 90%: $\chi^2 = 662.0$, df = 9, $p < 0.001$; 100%: $\chi^2 = 30.3$, df = 9, $p < 0.001$). The individual effect was then substituted by number of offspring: home range size was significantly smaller when the number of offspring was larger (50%: $\chi^2 = 4.1$, df = 1, $p = 0.04$; 90%: $\chi^2 = 6.6$, df = 1, $p = 0.01$; 100%: $\chi^2 = 4.7$, df = 1, $p = 0.03$, fig. 3.7C).

**Habitat selection: habitat types**

A compositional analysis showed that proportions of habitat types within Montagu’s harriers 100% kernel home ranges differed significantly from the available habitat surface area in both Groningen and Flevoland (fig. 3.2A,B). Lucerne, fallow habitats, winter cereals and summer cereals were ranked as the four most preferred habitat types (pairwise comparisons revealed no significant differences at the $\alpha = 0.05$ level). Habitats that were least preferred were natural grassland (mostly nature reserve Oostvaardersplassen in Flevoland and salt marsh in Groningen), water (mudflats and open water), intensive grasslands, the category “other” habitat types and urban areas. Proportions of habitats within the 90% kernel home ranges were not significantly different from proportions in the 100% kernel home ranges ($\lambda = 0.003$, 11 habitat types, 12 tracks, $p = 0.8$). Proportions of habitats within the 50% kernel home ranges significantly differed from proportions in the 90% home range (fig. 3.2C,D). The four most preferred habitat types in the 50% home ranges were lucerne, winter cereals, fallow habitats and summer cereals (pairwise comparisons revealed no significant differences between these habitat types).

The proportion of habitat types with fixes during active hunt (hunting fixes) differed significantly from the available habitat in the 90% and 100% kernel home ranges.
ranges (90%: $\lambda = 0.003$, 10 habitat types, 12 tracks, $p = 0.006$; 100%: $\lambda = 0.002$, $p = 0.001$). At both levels, most preferred hunting habitats were intensive grasslands, lucerne, natural grasslands and fallow habitat types (pairwise comparisons not significant). Least preferred were urban areas, water, woods and the category potatoes/beetroots/onions.

In a two level linear regression model (level i: track, level ii: individual) on 50% kernel home range size, there was a trend of smaller home range size with higher proportions of lucerne ($\chi^2 = 2.8$, df = 1, $p = 0.09$) and fallow habitat types ($\chi^2 = 3.3$, df = 1, $p = 0.07$), the two most preferred habitat types in the home ranges. The proportion of winter cereals was excluded from this model as its effect was not significant ($\chi^2 = 0.0$, df = 1, $p = 0.9$). In a model on 90% home range size, all effects of proportions of preferred habitat types within the home ranges were not significant (lucerne: $\chi^2 = 2.0$, df = 1, $p = 0.2$; winter cereals: $\chi^2 = 0.9$, df = 1, $p = 0.3$; fallow habitats: $\chi^2 = 1.6$, df = 1, $p = 0.2$).

No significant effects on 90% kernel home range size of proportions of preferred hunting habitat types were found (intensive grasslands: $\chi^2 = 0.6$, df = 1, $p = 0.5$; lucerne: $\chi^2 = 2.5$, df = 1, $p = 0.1$; natural grasslands: $\chi^2 = 0.7$, df = 1, $p = 0.4$).

Figure 3.1 Montagu’s harrier fixed kernel home ranges calculated from visual fixes using ground radio telemetry (10 birds, 12 breeding season tracks, 174 tracking days, 2003–2006). Black dots indicate visual fixes. (A) Study area Flevoland (outlined in black) with two tracks; (B) study area Groningen with 10 tracks. Inset: both study areas (black) in map of the Netherlands. Topographical maps: copyright of Topografische Dienst Kadaster and NLWKN.
for 100% kernel home range size, neither effects of proportions of preferred habitat types within the home range nor of proportions of preferred hunting habitats were significant (all $p > 0.2$).

**Habitat selection: habitat diversity and soil types**

Habitat diversity (based on $1 \times 1$ km squares) did not significantly differ between the 50, 90 and 100% home range levels (Kruskal-Wallis test, $\chi^2 = 3.5$, df = 2, $p = 0.18$).
Habitat diversity averaged over a 1 km radius around each hunting fix was compared to diversity within the home ranges at different levels (fig. 3.3b). Habitat diversity was significantly higher around hunting fixes than in 100% kernel home ranges (Mann-Whitney U test, U = 1708536, n = 4270, p = 0.01) but did not differ significantly from 90% and 50% home ranges (90%: U = 494917, n = 3440, p = 0.4; 50%: U = 130367, n = 3197, p = 1.0).

Variation in habitat diversity may be the result of different underlying soil types. Most diverse habitats are present on peat bog and sandy soils and less diverse on sea clay soils and in coastal habitats (Kruskal-Wallis test of Shannon-Weaver relative diversity index \( J' \) per \( 1 \times 1 \) km square according to soil type in the centre of the square: \( \chi^2 = 103.7 \), \( df = 3 \), \( p < 0.0001 \)). In the Groningen study area, the available soil types were peat bog soils (40%), sea clay soils (31%), sandy soils (20%), tidal zones (4%), salt marsh (1%) as well as several other types (e.g. mixed soils or lakes) that occurred in low percentages (fig. 3.3A).

Habitat use in 100% kernel home ranges in Groningen according to soil types was significantly different from random (compositional analysis, randomisation test: \( \lambda = 0.02 \), \( n = 10 \) animals, 7 soil types, \( p = 0.01 \)). Sea clay, sandy and peat bog soils were
preferred over other soil types; preferences did not differ significantly between these soil types. Mixed soil types, lakes, salt marsh and tidal areas were least preferred.

To calculate preferences within the 100% kernel home ranges, soils were grouped into four main types to avoid very small availability values: sea clay, peat bog and sandy soils as well as coastal habitats (salt marsh, tidal areas). Proportions of soil types in 90% home ranges differed significantly from 100% home ranges ($\lambda = 0.1$, $n = 10$ animals, 4 habitat types, $p = 0.009$). In the 90% kernel home ranges, sea clay soils dominated, occupying 47% of total surface area, and were preferred. Proportions of soil types in the 50% home range were significantly different from the 90% home range ($\lambda = 0.09$, $n = 10$ animals, 4 habitat types, $p = 0.008$). Sea clay soils occupied 66% of these home ranges and were most preferred. Proportions of hunting fixes did not differ significantly from proportions of soil types available at the 90% home range level ($\lambda = 0.3$, $n = 10$ animals, 4 habitat types, $p = 0.4$).

Hunting time spent on different habitat types
The average daily proportion of total time spent hunting differed significantly between habitat types (fig. 3.4). Individual differences were not significant ($\chi^2 = 3.2$, df = 9, $p = 1.0$). The daily proportion of hunting time on lucerne fields significantly differed between breeding phases (tab. 3.1). Lucerne was mostly used in the pre-breeding and incubation phase and least in the nestling and fledgling phase. Proportions of intensive grasslands used for hunting did not differ between breeding phases. There was a trend of natural grasslands being used more often during incubation and least often during the fledgling phase. There was a trend of cereals being used least often during incubation and nestling phase and most often during pre-

![Figure 3.4](image_url)

*Figure 3.4* Daily proportion of hunting time spent on different habitat types ($n = 10$ Montagu’s harrier males, 12 breeding season tracks [2003–2006], 174 tracking days, Groningen and Flevoland). Two level regression model (level i: track, level ii: individual), $\chi^2_{\text{habitat type}} = 1030.7$, df = 9, $p < 0.001$. Asterisks indicate preferred hunting habitat types at all home range levels (compositional analysis, see text).
breeding and fledgling phase. Differences in the use of fallow habitats were not significant, as hunting use during incubation, nestling and fledgling phase were similar, only usage in the pre-breeding phase was low. The use of potatoes/beetroots/onions was significantly highest during incubation and fledgling phase and lowest in the pre-breeding phase.

Table 3.1 Results of two-level regression models (level i: track, level ii: individual) on arcsine-transformed daily proportions of hunting habitats used, n = 10 Montagu’s harrier males, 12 breeding season tracks (2003–2006), 174 tracking days. Slopes of each breeding phase are given (β and s.e.) as well as significance of the main effect of the categorical variable “breeding phases” in each model. For each model, the most positive slope(s) are printed in bold grey, the most negative are printed in bold black.

<table>
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<th>breeding phases</th>
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<th>nestlings</th>
<th>fledglings</th>
<th>$\chi^2$</th>
<th>df</th>
<th>p</th>
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<td>3</td>
<td>&lt;0.001</td>
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<td>-0.30 0.15</td>
<td>-0.26 0.16</td>
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<td>3</td>
<td>0.250</td>
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<tr>
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<td>ref.</td>
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<td>-0.07 0.13</td>
<td>-0.14 0.14</td>
<td>6.45</td>
<td>3</td>
<td>0.090</td>
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<tr>
<td>cereals</td>
<td>ref.</td>
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<td>0.060</td>
</tr>
<tr>
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<td>4.81</td>
<td>3</td>
<td>0.190</td>
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<tr>
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<td>0.19 0.08</td>
<td>20.77</td>
<td>3</td>
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</tbody>
</table>

Hunting behaviours and success
The frequency with which the tracked harriers attempted to catch a prey per minute (strike frequency) differed significantly between habitat types (fig. 3.5A). Strike frequency was significantly higher later in the season ($\chi^2_{\text{daynumber}} = 8.2$, df = 1, p = 0.004). When the effect of daynumber was replaced by breeding phase, differences between breeding phases were significant (fig. 3.6A). Strike frequency did not differ between individuals (all effects tested in the same model, $\chi^2_{\text{individual}} = 0.6$, df = 9, p = 1.00).

Strike success (the proportion of attempts to catch a prey that was successful) was not significantly different between different habitat types (fig. 3.5B). There were no significant seasonal/breeding phase nor individual differences ($\chi^2_{\text{daynumber}} = 0.0$, df = 1, p = 1.00; $\chi^2_{\text{breeding phase}} = 0.0$, df = 3, p = 1.00; $\chi^2_{\text{individual}} = 0.0$, df = 9, p = 1.00).

Hunting yield (the number of prey caught per hour) significantly differed between habitat types and individuals, and increased significantly in the course of the breeding season ($\chi^2_{\text{daynumber}} = 8.7$, df = 1, p = 0.003; $\chi^2_{\text{individual}} = 114.7$, df = 9, p < 0.001; fig. 3.5C). The effect of breeding phases, substituting daynumber in the model, was significant (fig. 3.6B).
Figure 3.5 (A) Frequency of attempts to catch a prey (strike frequency), (B) proportion successful attempts of all attempts to catch a prey (strike success) and (C) number of prey caught per hour (hunting yield) of tracked male Montagu’s harriers in Groningen and Flevoland, The Netherlands (n = 10 birds, 12 tracks, 14,591 hunting minutes, 2003–2006). Statistics were tested in two level (logistic respectively normal) random intercepts regression models with level i = track and level ii = individual. Strike frequency: $\chi^2_{\text{habitat}} = 152.2$, df = 7, $p < 0.001$; strike success: $\chi^2_{\text{habitat}} = 0.0$, df = 7, $p = 1.0$; hunting yield: $\chi^2_{\text{habitat}} = 114.4$, df = 7, $p < 0.001$.

Figure 3.6 (A) Strike frequency and (B) hunting yield of tracked male Montagu’s harriers in Groningen and Flevoland, The Netherlands, according to breeding phases (n = 10 birds, 12 tracks, 14,591 hunting minutes, 2003–2006). Differences between breeding phases were significant (strike frequency: $\chi^2 = 10.83$, df = 3, $p = 0.013$; hunting yield: $\chi^2 = 29.63$, df = 3, $p < 0.001$).
The individual differences in hunting yield were highly correlated with the number of fledged young and the young’s fledging success (fig. 3.7A, B). Hunting yield was not significantly different between monogamic and bigamic males (Spearman correlation, \( R = 0.37, n = 12, p = 0.2 \)).

**Discussion**

**Habitat selection: vegetation, soil type and diversity**

Montagu’s harriers choose habitats in their breeding range at different spatial scales. We compared the 100% kernel home range (ca. 130 km²), representing the entire individual breeding season range, with regionally available habitats (970 km² in Groningen and 490 km² in Flevoland). We also compared the 90% kernel home range (ca. 35 km²), the usual movement range, with 50% kernel home range (ca.
8 km²), representing the core home range. The selection of the core home range probably relates to choice of the nest site (which is always located in the core home range) as well as the core hunting range, whereas the 90% home range may correspond to the usual hunting range, and areas outside the 90% within the 100% home range are used for infrequent excursions. Our 90% kernel home range estimates are ca. twice the size of home range estimates in western French farmland populations (in the regions Deux-Sèvres and Charente-Maritime), which may at least partly result from different radio-telemetry protocols and more conservative home range methods chosen in those studies (Salamolard 1997, Denonfoux 2003, T. de Cornulier & V. Bretagnolle in Thiollay & Bretagnolle 2004). Home range sizes of Montagu’s harriers estimated in German, Dutch and French studies in the 1960s–80s are summarised by Salamolard (1997) and report that home ranges are not larger than 15 km². However, these conclusions are drawn only from visual observations and are not based on telemetry. Maximum hunting distances from the nest of not more than 8 km were observed in these studies, whereas in our study, the maximum distance was 18 km. It is questionable whether the differences described above arise solely from methodology or may be affected by differences in food abundance and thus hunting behaviour between the study areas and time periods. A study in an intensively farmed area in northern Germany (Rheiderland, ca. 40 km², adjacent to Groningen), using the same methods as in the present study, showed that Montagu’s harrier home range size can be considerably smaller than we found and more comparable to above mentioned estimates (50% kernel: 1 km²; 90%: 7 km²; 95%: 11 km²; n = 1; Arisz et al. 2008). This difference in home range size between Rheiderland and Groningen/Flevoland may be attributed to the extensification in Rheiderland by ca. 13% agri-environmental schemes (fallow field margins): abundance of small mammal and especially bird prey was during the study period considerably higher than in Groningen/Flevoland (Arisz et al. 2008).

In our study, proportions of habitats in 100% kernel home ranges differed significantly from proportions present in the entire study areas. At this scale level as well as at the smallest analysed level (core home ranges vs. 90% kernel home ranges), lucerne, fallow habitats and winter and summer cereals were most preferred habitats. This is similar to results of French Montagu’s harriers preferring (next to oilseed rape) cereals, grasslands and lucerne in their home ranges (Denonfoux 2003). In our study areas, lucerne and cereals are potential nesting as well as hunting habitats. In contrast, fallow land is often covered with dead biomass at the start of the breeding season and is thus usually not attractive for nesting, but is especially rich in small mammal prey (Buskirk & Willi 2004, Koks et al. 2007, chapter 2). The general preference of Montagu’s harriers for fallow structures is thus probably based on food availability within these structures, and the potentially positive influence on food availability in the surrounding hunting grounds (voles colonising also surrounding other habitat types).

Whereas intensive grasslands were not preferred habitats at the different home range levels, these were most preferred hunting habitats, together with lucerne, natural grasslands and fallow habitats. Intensive grasslands and lucerne are habitat types that are regularly mown during the breeding season of Montagu’s harriers,
making these habitats especially attractive during several days after the mowing event, when the cover for prey animals (mainly small mammals and lagomorphs) is reduced (Bechard 1982, Simmons 2000, Vulink 2001, chapter 4). A strong preference for lucerne as hunting habitat has also been shown in a farmland population of Montagu’s harriers in Bavaria (southern Germany), where lucerne is an equally scarce habitat as in Groningen and Flevoland (Kracher 2008). Similar to our results, intensive and extensive grassland types were the second most preferred hunting habitats in Bavaria (fallow habitats were absent from the area). In western France, harriers also preferred grasslands and especially lucerne as well as cereals as hunting habitats (Denonfoux 2003).

Reasoning that high prevalence of the most preferred hunting habitat “intensive grasslands” in the home range would reduce far hunting trips, we hypothesise that this prevalence may negatively influence home range size (Newton 1979). We could not show this effect, however, at the 90% and 100% home range levels. The only effect of preferred habitat types on home range size we could show was the trend of high proportions of lucerne and fallow habitats (both preferred in general and as hunting habitats) being related to smaller core home range sizes. A smaller core home range may save the hunting bird energy and time otherwise needed for longer hunting trips. Lucerne as well as fallow habitats are not widely available in the study areas (lucerne: on average 1% in both study areas, fallow habitats: 3% in Groningen, 1% in Flevoland; fig. 3.2A,B), whereas intensive grasslands are more widespread (Groningen: 13%, Flevoland 16%).

Hunting harriers showed a preference for high habitat diversity at a large scale (within the 100% home range). Habitat diversity may be a result of differences in agricultural use between different soil types. Within the Groningen study area, Montagu’s harriers showed a preference for sea clay soils at all investigated home range levels. Habitat diversity on sea clay soils is relatively low. The preference for sea clay soils may thus not be related to diversity but potentially to the high availability of winter cereals and lucerne on these soils, which are widespread nesting and hunting habitats. During hunting, harriers do not have a clear preference for either soil type. The absence of a preference indicates that other than sea clay soils may be more often used for hunting than for nesting. We consequently show that the criterion for harriers to choose their hunting habitat at a large scale seems to be habitat diversity in itself and not diversity linked to differential agricultural use according to underlying soil type. Harriers may choose relatively high diversity in hunting habitats because diversity may result in more diverse prey available at different times of the season, but also other effects may play a role, for instance higher prevalence of extensive edge structures hosting more prey than large-scale intensive monoculture fields.

**Influences of habitat types: hunting time and success**
Different hunting habitat types were used preferentially during different times of the season. In the pre-breeding phase, lucerne and cereals were used to a high extent. Vegetation height in both habitat types is relatively low at that time of the year. Cereals grow quickly during the incubation and nestling phase of Montagu’s
harriers, and the large height probably makes (small mammal) prey less available than in the beginning of the season. During the incubation phase, lucerne was still favoured as well as natural grasslands and potato/beetroot/onion fields. The latter may be due to the availability of passerines (nestlings) as prey in root crop (potato/beetroot/onion); high vole densities are not typical for these habitats (own observations). During the harriers’ nestling phase, no peak use of any hunting habitat was indentified, but intermediate use of root crops, fallow habitats, intensive and natural grasslands. In the fledgling phase, cereals were again frequently used, before or after they are mown. Whereas before mowing, bird prey such as yellow wagtail may be highly available in cereals, after mowing, voles become more available than before. Also root crop fields were frequently used in the harriers’ fledgling phase, possibly because of the availability of recently fledged prey birds. Whereas seasonal peak use occurred in lucerne, root crops and as a trend also in natural grasslands and cereals, both intensive grasslands and fallow land appeared to have an equally important function as hunting habitats throughout all breeding phases.

Strike frequency, the frequency with which the harrier attempts to catch prey, probably relates to food abundance, mediated by vegetation density and height, resulting in food availability. We can thus conclude that habitats with highest food availability are fallow lands, lucerne and intensive grasslands, especially after mowing (fig. 3.5A, chapter 4). That fallow habitats host highest densities and diversity of small mammals, birds and insects is confirmed by field data (Van Buskirk & Willi 2004, Koks et al. 2007, Boatman et al. 2010, chapter 2). Hunting yield, the product of strike frequency and strike success, expressed as number of prey caught per hour, was highest in intensive grassland and fallow habitats, as well as lucerne and natural grasslands. In Bavaria and West-France, lucerne and grasslands (the latter including in France both intensive grasslands and fallow habitats) have also been shown to be habitats with highest strike frequency and hunting yield (Denonfoux 2003, Kracher 2008) and thus appear to be favourable habitat types for Montagu’s harriers on a West-European scale.

Strike frequency and hunting yield were different between the breeding phases, probably related mainly to seasonal differences in prey availability (Dijkstra et al. 1995). Reasons for this may be that small mammal populations increase from very low levels in May to a peak in September (Dijkstra et al. 1995, own unpublished data) and nestling and fledgling prey birds become gradually more available during the season. On the other hand, a higher hunting yield may also be (partly) influenced by a higher motivation of the hunting harrier: hunting yield got higher the more food was required, from the incubation to the nestling and fledgling phase. Moreover, hunting yield was relatively high during the pre-breeding phase, when food availability is supposedly low, and the male has to courtship feed his female partner in order to pair-bond and to get her in a body condition well enough to breed (Simmons 2000).

As hunting yield directly related to reproductive output, this measure should indicate most reliably which habitat types are crucial for Montagu’s harrier individual fitness and population dynamics resulting from reproduction. As the nests in
our study areas were protected from agricultural practices, no agricultural nest losses occurred and next to food availability, only factors such as predation and bad weather during the nestling phase may have contributed to fledging success. Individual quality of the male (for instance inherited, based on prior breeding experience or on physiological body condition) may be another important factor causing differences in reproductive output. We found several indications supporting this hypothesis in our study: home range sizes (presumably resulting in different amounts of energy and time needed for hunting) differed significantly between individuals, and home range size related inversely to reproductive output. Whereas hunting time spent on different habitats, strike frequency and strike success were not significantly different between individuals, hunting yield was, and it correlated strongly with reproductive output. A possible explanation is that slight individual differences in choice of hunting habitats, strike frequency and strike success added up to significant differences in hunting yield.

Conservation implications: contributions to individual fitness

Montagu’s harriers’ population dynamics are influenced during the breeding season but also during the non-breeding season. Based on the current situation in NW-European breeding grounds and West-African wintering grounds, models have shown that breeding season effects are probably most profoundly affecting population dynamics (box E). In a conservation context, a focus on habitat management and cultivation practices in the breeding areas is thus highly relevant. Conservation management of Montagu’s harrier farmland populations is imperative because populations in natural breeding areas have almost completely disappeared in West-Europe. A first prerequisite for population growth in the current farmland situation in many West-European areas is protection of nests against agricultural losses. Nest protection is, however, futile when harrier populations become unsustainable due to decline in suitability of the agricultural landscape by increasing intensification and consequently declining food abundance (Butet & Leroux, 2001; Donald et al. 2001, Arroyo et al. 2002).

Taking results from studies in Bavaria and West-France into account, we suggest that the findings of the present study may be widely applicable in Montagu’s harrier populations in West-European intensively used agricultural landscapes, which is a prerequisite for generic species conservation recommendations (Salamolard 1997, Denonfoux 2003, Whittingham et al. 2003, Kracher 2008). Consequently, we suggest the following strategies to keep or make agricultural areas suitable habitats for Montagu’s harriers.

First, we roughly calculate the total number of prey caught during the breeding season in each habitat type, assuming a three months breeding season with eight hours hunting per day (hunting yield*daily proportion of hunting time per habitat*728 hunting hours): intensive grasslands, 1490 prey items (range based on s.e.: 1050–4470); cereals, 740 (500–2180); natural grasslands, 424 (280–1230); fallow habitats, 380 (240–1090) and lucerne, 160 (88–420). Lucerne and fallow, the most preferred and profitable habitats, do currently only contribute a small part to the total number of prey that male Montagu’s harriers capture to feed themselves, their
female partner and their young during the breeding season. We thus recommend offering a higher percentage of these habitat types in the breeding areas, which may (given the agricultural occurrence of cereals and intensive grasslands), make the Dutch agricultural landscape more attractive to Montagu’s harriers and result in higher breeding success. Proportions of lucerne and fallow habitats available in the core home range showed a trend of negative correlation with core home range size, and small home range sizes correlated with a high number of fledged young. Additionally, harriers hunting on lucerne and fallow habitats achieved a high hunting yield, and high hunting yields correlated with a high reproductive output. A similar strategy is recommended for the conservation of hen harriers Circus cyaneus on Orkney, where an increase in the favoured habitat type (rough grass) in a radius of 2 km around nest sites is thought to contribute to an improved breeding success (Amar et al. 2008, Arroyo et al. 2010). The relevant scale for favoured habitat occurrence identified in the present study is very similar, i.e. at the 50% home range level, an on average 8.4 km² area with a radius of 1.6 km.

Second, our study indicates that natural and extensive grasslands offered less food for Montagu’s harriers than some intensive farmland habitat types. Natural and extensive grasslands comprise diverse kinds of grasslands, managed e.g. as nature reserve only mown after 20 June (just as fallow habitat types), and areas that are grazed year-round. Our results are in line with densities of prey animals (e.g. skylark) being relatively low in the extensive grassland reserve Oostvaardersplassen in Flevoland during the study period (Bijlsma 2008). In the Groningen salt marsh, vole densities are generally low, whereas densities of bird prey may be significant (e.g. meadow pipit, late in summer juvenile starlings Sturnus vulgaris, own observations). Extensive grassland habitat types are often managed by public institutes (such as nature reserves, ditch edges, road verges), making management adjustments relatively easily possible, for instance adjustment of grazing and mowing intensity. Future research should reveal which management adjustments are needed to optimise these habitat types as small mammal, insect and bird habitat. Mowing management is not only likely to make habitat types such as intensive grassland and lucerne attractive due to short term peak food availability after mowing (chapter 4), but could also be used to adjust food availability in natural and extensive grasslands, ditch edges and road verges or fallow field margins, as long as it does not interfere with other conservation goals. Especially relevant may be the increase of food availability during the harriers’ nestling phase, when no habitat type is preferentially used, and the increasing need of food for the nestlings causes an increasing demand for prey delivery at the nest, whereas the peak of food availability occurs only later on.

The recommended conservation actions (offering higher percentages of fallow structures and lucerne in the farmed landscape as well as optimising natural and extensive grasslands as farmland animal habitats) would not only benefit harriers. Next to Montagu’s harrier, originally a steppe or grassland bird, also its grassland prey bird species are nowadays farmland birds (e.g. skylark). Grassland obligate bird populations have been shown to especially benefit from fallow structures in the farmed landscape (Herkert 2009). In general, harriers can act as a flagship species,
indicating benefits for the underlying ecological community that supports the top-predator: fallow habitat types generally enhance farmland small mammal, insect and bird biodiversity (Van Buskirk & Willi 2004). When nesting periods of ground-breeders are taken into account, or by mowing high enough above the ground to spare birds’ nests or young, diverse mowing regimes create small-scale heterogeneity that may next to hunting harriers also benefit other farmland birds. These may profit from the combination of (low vegetation) foraging habitats and (high vegetation) cover, e.g. skylark *Alauda arvensis*, lapwing *Vanellus vanellus* and grey partridge *Perdix perdix*.

Preferences of Montagu’s harriers in our study indicate that habitat diversity of the agricultural landscape should be maintained or increased, as harriers preferred high habitat diversity not only within their large scale home range, but especially during the hunt. The importance of diverse (mosaic) landscapes has earlier been shown for hen harriers and is playing an important role in other farmland bird populations (Arroyo *et al.* 2008, Boatman *et al.* 2010). Realising agri-environmental schemes, for instance fallow field margins, in farmland is a conservation action that also contributes to the target of diversifying the agricultural landscape.

Conservation of farmland habitat diversity and consequently biodiversity is an especially relevant topic in the light of current and future agricultural land use changes: the Common Agricultural Policy of the European Union requests 0% set-aside from 2008 onwards, resulting in smaller proportions of fallow habitats in European farmland than in previous decades and potentially lowering biodiversity (Stoate *et al.* 2009). Additionally, the recent increase in cultivation of energy crops as well as agriculture led by solely commercial interests may result in further intensification and decrease of diversity in European farmland (Henle *et al.* 2008, Boatman *et al.* 2010).

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### Appendix 3.1 Study area, biometry, tracking periods (start to end date), reproduction, observation sample sizes and kernel home range sizes of ten radio-tracked Montagu’s harrier males (12 tracks, 2003–2006).

<table>
<thead>
<tr>
<th>bird (colour ring code)</th>
<th>bird name</th>
<th>year</th>
<th>location</th>
<th>nesting habitat female 1</th>
<th>nesting habitat female 2</th>
<th>age (calendar year)</th>
<th>wing length (mm)</th>
<th>wingspan (cm)</th>
<th>body mass (g)</th>
<th>claw with nail (mm)</th>
<th>claw without nail (mm)</th>
<th>start date</th>
<th>end date</th>
</tr>
</thead>
<tbody>
<tr>
<td>Y22 Bliepo</td>
<td>2003</td>
<td>Groningen</td>
<td>winter wheat</td>
<td>winter wheat</td>
<td>11</td>
<td>365</td>
<td>108.5</td>
<td>250</td>
<td>65</td>
<td>53</td>
<td>17-jun-03</td>
<td>22-jul-03</td>
<td></td>
</tr>
<tr>
<td>Y27 Leo</td>
<td>2003</td>
<td>Groningen</td>
<td>lucerne</td>
<td>winter wheat</td>
<td>6</td>
<td>389</td>
<td>114.2</td>
<td>272</td>
<td>63</td>
<td>48</td>
<td>24-jun-03</td>
<td>29-jul-03</td>
<td></td>
</tr>
<tr>
<td>Y97 Jan</td>
<td>2004</td>
<td>Groningen</td>
<td>wheat-barley hybrid</td>
<td>winter wheat</td>
<td>ad</td>
<td>370</td>
<td>110.0</td>
<td>275</td>
<td>66</td>
<td>49</td>
<td>19-jun-04</td>
<td>31-aug-04</td>
<td></td>
</tr>
<tr>
<td>Y95 Cors</td>
<td>2004</td>
<td>Groningen</td>
<td>winter barley</td>
<td>winter wheat</td>
<td>ad</td>
<td>373</td>
<td>110.3</td>
<td>284</td>
<td>68</td>
<td>52</td>
<td>23-jun-04</td>
<td>05-aug-04</td>
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<tr>
<td>Y72 Hans</td>
<td>2005</td>
<td>Groningen</td>
<td>wheat-barley hybrid</td>
<td>3</td>
<td>389</td>
<td>111.5</td>
<td>278</td>
<td>66</td>
<td>51</td>
<td>14-mei-05</td>
<td>13-jun-05</td>
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</tr>
<tr>
<td>YNL Harrie</td>
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<td>383</td>
<td>112.2</td>
<td>333</td>
<td>19-mei-05</td>
<td>06-jul-05</td>
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<tr>
<td>Y97 Jan</td>
<td>2005</td>
<td>Groningen</td>
<td>winter wheat</td>
<td>369</td>
<td>110.8</td>
<td>280</td>
<td>71</td>
<td>52</td>
<td>17-jun-05</td>
<td>13-aug-05</td>
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<tr>
<td>Y99 Kees</td>
<td>2005</td>
<td>Groningen</td>
<td>winter wheat</td>
<td>393</td>
<td>115.3</td>
<td>250</td>
<td>67</td>
<td>50</td>
<td>01-jul-05</td>
<td>16-jul-05</td>
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</tr>
<tr>
<td>Y27 Leo</td>
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<td>winter wheat</td>
<td>370</td>
<td>107.8</td>
<td>305</td>
<td>66</td>
<td>50</td>
<td>23-jun-06</td>
<td>24-jun-06</td>
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<tr>
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<td>Flevoland</td>
<td>winter wheat</td>
<td>377</td>
<td>111.2</td>
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<td>30-jun-06</td>
<td>11-jul-06</td>
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<tr>
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<td>Flevoland</td>
<td>wheat-barley hybrid</td>
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<td>17-aug-06</td>
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<td></td>
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</tbody>
</table>

| bird (colour ring code) | bird name | number of females | clutch size (total) | laying date nest 1 | laying date nest 2 | number of successful nests | number of fledglings (total) | number of all visual fixes | number of hunting fixes | number of all tracking minutes, also without visual or radio contact | number of hunting observation minutes | number of all tracking observations | 100 % kernel home range size (km²) | 90 % kernel home range size (km²) | 50 % kernel home range size (km²) |
|------------------------|-----------|-------------------|---------------------|-------------------|-------------------|---------------------------|-----------------------------|--------------------------|------------------------|-------------------------------------|-------------------------------------|---------------------------------|---------------------------------|---------------------------------|
| Y22 Bliepo             | 2         | 7                 | 16-mei-03           | 25-mei-03         | 2                 | 4                          | 101                          | 69                       | 2.740                  | 92                                 | 88.1                                 | 28.7                           | 9.7                             |
| Y27 Leo                | 1         | 5                 | 25-mei-03           |                   | 1                 | 3                          | 246                          | 177                      | 7.637                  | 255                                 | 94.7                                 | 21.7                           | 3.6                             |
| Y97 Jan                | 2         | 8                 | 17-mei-04           | 20-mei-04         | 2                 | 6                          | 850                          | 625                      | 15.305                 | 1977                                | 117.9                                | 26.4                           | 6.4                             |
| Y95 Cors               | 2         | 9                 | 18-mei-04           | 24-mei-04         | 2                 | 6                          | 399                          | 250                      | 9.890                  | 836                                 | 147.0                                | 39.3                           | 9.5                             |
| Y72 Hans               | 1         | 4                 | 20-mei-05           |                   | 1                 | 3                          | 381                          | 336                      | 6.102                  | 1680                                | 92.0                                 | 22.7                           | 4.8                             |
| YNL Harrie             | 1         | 4                 | 03-jun-05           |                   | 0                 | 0                          | 582                          | 513                      | 10.580                 | 2390                                | 230.0                                | 57.3                           | 10.9                           |
| Y97 Jan                | 1         | 4                 | 15-mei-05           |                   | 1                 | 4                          | 999                          | 829                      | 13.543                 | 3050                                | 80.8                                 | 19.6                           | 4.2                             |
| Y99 Kees               | 1         | 5                 | 26-mei-05           |                   | 0                 | 0                          | 100                          | 76                       | 2.503                  | 343                                 | 162.6                                | 48.7                           | 11.3                           |
| Y27 Leo                | 2         | 4                 | 27-mei-05           |                   | 1                 | 4                          | 255                          | 191                      | 3.183                  | 742                                 | 75.8                                 | 23.1                           | 5.8                             |
| GT3 Helmut             | 1         | 4                 | 19-mei-06           |                   | 1                 | 4                          | 220                          | 154                      | 3.288                  | 575                                 | 141.1                                | 35.7                           | 8.4                             |
| YTS Elzo               | 1         | 2                 |                   |                   | 0                 | 0                          | 73                           | 49                       | 2.717                  | 238                                 | 154.0                                | 45.3                           | 14.7                           |
| YTV Harold             | 2         | 1                 | 17-jun-06           |                   | 1                 | 1                          | 220                          | 141                      | 4.444                  | 701                                 | 188.8                                | 50.6                           | 12.1                           |
It is not explanations that carry us forward; it is our will to proceed.

- Paulo Coelho -