Chapter 1

General introduction

Christiane Trierweiler
Conservation status of long-distance migratory birds

The ecology and population dynamics of migratory animals are influenced by events that occur in different, often widely separated places and during different seasons (Greenberg & Marra 2005, Newton 2008). Reproductive success is not only directly influenced by effects operating during the breeding season, but also by pre-breeding conditions and carry-over effects from previous seasons. For example, delays during spring migration may result in late arrival in the breeding areas, resulting in turn in acquisition of poorer quality breeding territories and lower reproductive success (Newton 2008). Consequently, processes that have an impact during the non-breeding season can ultimately influence reproductive success, additionally to their potential influence on survival (Marra et al. 1998).

Populations of long-distance migratory birds have declined during the last decades, whereas populations of short-distance migrants or residents generally did not show such a decline (Sanderson et al. 2006). Hence, long-distance migratory populations are of particular conservation concern. Next to factors during the breeding season, the decline points towards the importance of factors acting during the non-breeding season and outside the breeding range, affecting survival and subsequent reproduction (Webster et al. 2002, Bairlein 2003, Newton 2008). Consequently, additionally to understanding ecology and conservation concerns in the breeding areas, identification of migration routes, of en-route stopover sites and of population specific wintering areas is of prime importance for effective conservation measures (Moore et al. 1995, Newton 2006, Norris & Marra 2007).

This thesis is investigating the year-round ecology of a Palearctic-African long-distance migratory raptor. The study species is Montagu’s harrier Circus pygargus, a model species for migratory raptors and at the same time as a top – predator also a key species for other birds that share similar ecological niches in the different year-round habitats (e.g. farmland or steppe bird species in the breeding areas). Montagu’s harrier travels between the worlds, breeding in NW-European farmland areas, but wintering in farmland areas of the West-African Sahel and crossing a whole range of landscapes during migration. Because of population declines or small population sizes, Montagu’s harrier is red-listed in many European countries. It is therefore relevant to investigate whether conservation actions can be taken in breeding areas, stopover sites and wintering areas to enhance reproduction and survival and thus population growth. However, the bottlenecks in the annual cycle that determine population growth rates are still one of the most important open questions in the population ecology of Montagu’s harrier.

Study species: Montagu’s harrier

Montagu’s harrier is strictly migratory with a Southwest-Palearctic breeding and Afrotropical/Indomalayan wintering distribution (Del Hoyo et al. 1992, Glutz von Blotzheim 1989, Ferguson-Lees & Christie 2001, fig. 1.1). Breeding grounds include Europe as well as West- and central-Asia (East to Kazakhstan and the upper river
Yenisey). Wintering areas comprise sub-Saharan Africa, the Indian subcontinent and adjacent South-Asia South to Sri Lanka (Del Hoyo et al. 1992). Montagu’s harrier is currently categorized as a species of least conservation concern with a global population estimate of up to 100,000 breeding pairs (BirdLife 2009). These estimates, however, are liable to considerable uncertainty (chapter 8, 9). Montagu’s harriers in Europe represent more than half of the global population and therefore have a special protection status (Annex I of the European Birds’ Directive, 79/409/EEC; Burfield & Van Bommel 2004, Arroyo et al. 2004).

Montagu’s harriers are ground breeders and consequently especially vulnerable during the breeding season. Problems arise since the harriers shifted - because of habitat loss and degradation - from natural breeding habitats like dunes and moors to mainly (70–90% in W-Europe) agricultural breeding habitats since the late 20th century (Koks & Visser 2002b). In modern agricultural landscapes and depending on weather and vegetation circumstances, 20–70% of nests (and sometimes even

Figure 1.1 Global distribution of Montagu’s harriers (light grey: breeding areas, dark grey: wintering areas, after Leroux 2004). Star indicates the presumed migratory divide between populations wintering in Africa (to the West) and in India (to the East), after Moreau (1972). Numbered dots: study sites of the Dutch Montagu’s Harrier Foundation and co-operation partners that are referred to in this thesis. Netherlands: Flevoland (1), northern Fryslân and Northwest - and East - Groningen (2); Germany: Northwest Lower Saxony (3), Soester Börde in Northrhine-Westphalia (4); Denmark: Ballum (5); Poland: Siedlce (6); Belarus: Hrodna (7); Georgia: Batumi (8); Niger: Lake Chad (9), Niamey (10); Burkina Faso: Oursi (11); Mali: San (12); Senegal: Khelcom (13).
breeding females) need protection of harvest and subsequent predation (Corbacho et al. 1997, Koks et al. 2001, Millon et al. 2004, Vanderkerkhove et al. 2007). The second important hazard to Montagu’s harrier populations in agricultural habitat is the declining food availability in today’s intensively used farmed landscapes (Butet & Leroux 2001; Donald et al. 2001). In many well-studied farmland Montagu’s harrier populations, declining population trends are reported during the last decades (Millon et al. 2004).

Montagu’s harriers’ breeding season lasts four to five months a year (fig. 1.2). The largest part of the year is spent outside the breeding areas: on migrations and in the wintering grounds. Complete moult takes place during parts of the breeding and wintering season and is probably suspended during autumn migration (Forsman 1999, fig. 1.2). In contrast to the reasonable profound understanding of Montagu’s harrier ecology during the breeding season, knowledge on ecology and hazards during migrations and during the wintering season has been limited.

**Background of current Montagu’s harrier conservation and research in NW-Europe**

The Dutch Montagu’s Harrier Foundation monitors and conserves populations of Montagu’s harriers in the Netherlands (E-Groningen, NW-Groningen, Flevoland, Fryslân) and in parts of adjacent Lower Saxony (Rheiderland) in Germany by professional as well as volunteer work since the 1990s (fig. 1.1). Conservation and research are closely interwoven, in co-operations with the University of Groningen, the
Netherlands, and the Institute of Avian Research “Vogelwarte Helgoland” in Wilhelmshaven, Germany. The Dutch Montagu’s Harrier Foundation strives to realise a two-component model of Montagu’s harrier conservation in the breeding areas; component one is nest protection, component two is hunting habitat improvement by extensification of the farmed landscape using agri-environmental schemes (fallow field margins).

The beneficial effect of fallow structures on Montagu’ harrier populations became clear already when in 1988, farmland was set aside on a large scale by a European law meant to decrease the grain over-production. In East-Groningen, the Netherlands, around 20% of farmland was turned into fallow land. Soon after, the Montagu’s harrier population increased in that region from occasional nesting attempts (zero in 1989) to 29 breeding pairs in 1993 (Koks & Van Scharenburg 1997, Koks et al. 2007, chapter 2). Concluding from population models, this increase cannot have been achieved by reproduction alone but must have been at least partly due to immigration (C.W.M. van Scharenburg pers. comm.). After the percentage of set-aside was brought back to ca. 2% in 1993, the breeding population declined to 20 pairs in 1998.

In 1997, agri-environmental schemes (fallow field margins) were introduced in East-Groningen. In an area of ca. 40,000 ha, the Montagu’s harrier population increased from 19 breeding pairs in 1997 to 38 in 2009 (fig. 1.3). The same happened in the German Rheiderland (ca. 5,000 ha), where enthusiastic farmers, organised in the Agricultural Nature Association “Rheiderländer Marsch”, introduced fallow field margins. There, the number of breeding pairs increased from zero in 2003 to 11 in 2007 (fig. 1.3). Also in NW-Groningen (ca. 10,000 ha), fallow field margins were introduced in 2005, initiated by the Agricultural Nature Association “Wierde en

**Figure 1.3** Number of breeding pairs of Montagu’s harriers in different study areas in The Netherlands and in Rheiderland (Germany). Open symbols represent the situation before/after the introduction of agri-environmental schemes (fallow field margins), closed symbols correspond to years with effective schemes.
After the last nesting attempt had been recorded there in 1999, a first (successful) attempt was recorded in 2006 and subsequently the number of pairs increased to 15 in 2009, representing now a substantial part of Montagu’s harriers in the Netherlands (fig. 1.3). Evidence that a decline in fallow structures in agricultural landscapes results in a decline in breeding numbers comes from the German Hellwegbörde, where the population declined concurrently with the decreasing surface of fallow structures since 1993 (Illner 2007). The clear positive effects of fallow habitats on Montagu’s harriers’ population trends resulted in a pilot project with fallow field margins since autumn 2007 in the Dutch province of Flevoland (Visser et al. 2007). It will show whether the number of breeding pairs (four in 2009) will increase when these measures will be scaled up. This experiment on a landscape scale will show whether agri-environmental schemes are indeed effective to manipulate carrying capacity of intensively used agricultural landscapes for farmland birds.

Since not only the situation during the breeding season, but also all other events in the annual cycle are crucial for individuals and thus for population trends, our current research does not only focus on the breeding areas but also tracks the harriers during their migrations and investigates their ecology in the West-African wintering areas. By studying the harriers year-round, we strive to identify bottlenecks in their annual cycle (Drent et al. 2007, Buehler & Piersma 2008) and investigate potential carry-over effects. We are interested in connectivity between European breeding populations (Koks & Visser 2002a), as well as migratory connectivity between breeding and wintering populations. Two important elements of migratory connectivity are whether populations use specific migratory routes and wintering areas, and whether individuals stick to chosen routes and areas (site fidelity).

Thesis outline

Part I: Processes during the breeding season
Montagu’s harriers arrive in the Dutch and German breeding areas from the end of April onwards (figure 1.2). Courtship behaviour by males includes courtship feeding of females. Montagu’s harriers do not establish hunting territories, but both members of a breeding pair defend a small breeding territory in the immediate vicinity of the nest against conspecific and other intruders. Semi-coloniality occurs when the food situation is favourable with several nests built at close distances (Arroyo et al. 2004). Montagu’s harriers are often monogamic but a significant proportion of males may be bigamic, having nests with two females that are mostly as far as 1 km apart (Dutch Montagu’s Harrier Foundation, unpublished data). On average three to four eggs are laid in a flat nest on the ground built of grass; mean laying date is in the end of May. The females incubate the eggs during one month, meanwhile being fed by the male. During the first two weeks of the nestling phase, both female and young are fed by the male. When the young are at an age of about two weeks and able to thermoregulate their bodies independently, females may set
out hunting for themselves and contribute to prey deliveries at the nest for the remaining nestling phase. After fledging, especially the males are observed feeding the young for up to several weeks, before the start of autumn migration (Clarke 1996a).

To study breeding biology, we usually visit nests three times during the breeding season, while taking precautions that disturbance is at the lowest possible level. Clutch size, brood size and number of fledglings are recorded when possible. We distinguish breeding pairs starting a clutch and territorial pairs not starting a clutch. Farmers, land owners and harvesting companies are informed about necessary nest protection measures. They participate on a voluntary basis in the protection activities. In lucerne (alfalfa), a square of $10 \times 10$ m around the clutch is spared and protected by an electric fence against ground predators. Lucerne is harvested several times during the breeding season, starting early in the season, which is also a hazard to the incubating female. For nests in winter barley, where the young fledge shortly after the harvest, a strong metal fence with a diameter of 2 m is sufficient to protect the young from being trapped under lodged grain and against ground predators during the remaining time in the nest. This method has been invented in France (J.-L. Bourrioux pers. comm.). In years with an early harvest, nests in winter wheat need to be protected from harvesting and subsequent predation in the same way. Protection fences are placed shortly before (cereals) or immediately after harvest (lucerne) of the surrounding field.

To investigate prey choice, we need methods to study the diet of free-living Montagu’s harriers. Raptor diet studies mostly make use of three methods: direct observations of prey brought to the nest, which is assumed to be the least biased record of diet, the collection of pellets, and the collection of prey remains. Using a feeding experiment with a captive Montagu’s harrier, we investigate in box A (“pellet analyses”) whether pellet analyses employing a numerical or a gravimetrical method are more suitable for diet studies.

In our Dutch study areas, diet of breeding pairs is monitored by weekly collection of pellets (regurgitated indigestible prey parts) and prey remains (pluckings) in the vicinity of the nest, e.g. close to an especially placed wooden pole used as perch by both members of the breeding pair. Pellets of young are collected during nest visits. These studies and videography at the nest revealed the diet of Montagu’s harriers in Dutch farmland, consisting for the major part of small mammals, similar to elsewhere in agricultural habitat (chapter 2: “Do voles make agricultural habitat attractive?”). Main and alternative prey species are documented in chapter 2.

To get a more complete picture, diet studies need to be complemented by accounts of prey abundance. We quantified prey abundance in the breeding areas using a small mammal census each year in the first week of August (since 1992). We show how the East-Groningen Montagu’s harrier population responded to changes in small mammal abundance in chapter 2. Availability of small mammals may influence reproductive parameters because small mammals often represent readily available staple food for the harriers. We seek to answer the question whether small mammal abundance is the most important factor making agricultural habitat attractive to Montagu’s harriers.
To investigate which habitat types in the agricultural landscape are used and preferred by Montagu’s harriers, we tracked a number of Montagu’s harrier males in Dutch farmland during several breeding seasons (2003 - 2006) by radio telemetry. The males were followed by car during their hunting trips, by tracking signals of a 4.7 g light tailmount radio transmitter attached to a tail feather. The enthusiasm of a large number of volunteers, students and professionals made it possible to track the males for 10 hours a day and for several days a week. Each minute that the bird was in sight, its activity and location was reported. Using these spatial and behavioural data, we investigate home range size, habitat use, habitat preferences and hunting success on different vegetations, as well as consequences of these factors for reproductive success (chapter 3: “habitat selection using radio telemetry”). Ecological insights from these analyses enable us to formulate recommendations for conservation actions in the breeding areas.

In chapter 4 (“mowing enhances hunting yield”), we investigate whether not only vegetation type, but also vegetation management, for instance mowing management, is important to warrant good hunting success for Montagu’s harriers. Mowing may make habitats more suitable for hunting harriers by reducing the cover for small mammal and bird prey (Bechard 1982, Simmons 2000, Vulink 2001).

Part II: Processes during migrations
It is relevant to investigate processes during the migration seasons, as these may cause the highest proportion of annual mortality in long-distance migrants (Sillett & Holmes 2002). Natural causes of mortality such as barrier crossings but also human impacts such as illegal shooting at migratory bottlenecks may contribute to this mortality (Strandberg et al. 2009a, own observations). Species conservation strategies should take such mortality into account and migratory routes needs to be documented, so that important bottlenecks and en-route staging sites can be identified.

Wintering areas of western European Montagu’s harriers are located in different West-African countries (Fransson & Petterson 2001, Arroyo et al. 2004). It has been hypothesised that harriers leave Europe via Gibraltar and return in a loop via Italy (Agostini & Logozzo 1997, Garcia & Arroyo 1998). The exact migration routes and wintering areas were unknown. Satellite tracking has proven to be a useful technique to document migratory routes of large bird species, such as white storks (Ciconia ciconia; Berthold et al. 1992, 2004), peregrine falcons (Falco peregrinus; Fuller et al. 1998), ospreys (Pandion haliaetus; Hake et al. 2001; Alerstam et al. 2006) and different eagle species (Meyburg et al. 1995, 2003). In 2005, the first satellite transmitters became available that were light enough to attach on Montagu’s harriers and we deployed satellite transmitters on two Dutch Montagu’s harrier females (Trierweiler et al. 2007a, chapter 5: “dual migration pathways”). Subsequently, we chose to use this technique in several NW- and NE-European Montagu’s harrier populations to investigate the migratory system of the Palearctic-African populations. In total, the migrations of 20 NW-European (Dutch, German, Danish) and 10 NE-European (Polish, Belarusian; figure 1.1) Montagu’s harriers were tracked by analysing satellite telemetry data (box B: “standardisation of ARGOS..."
data”) between 2005 and 2009. We retrieved 36 autumn tracks of 26 individuals and 16 spring tracks of 13 individuals. Important migration routes were documented, correcting and supplementing earlier suppositions (Trierweiler et al. 2007a, chapter 5, chapter 6). We also investigated daily travel distances and compared these to other satellite tracked raptor species (Trierweiler et al. 2007a, Trierweiler & Koks 2009, chapter 5, 8). Daily travel distances were used to identify potentially important staging sites during migration and wintering (chapter 6, 7). Furthermore, we investigated connectivity between breeding and wintering areas as well as site fidelity in the breeding and non-breeding season and explored potential conservation implications (chapter 6: “migratory connectivity”). Recently started systematic raptor autumn migration counts at the Georgian Black Sea coast have revealed unprecedented concentrations of harriers funneling through this migration corridor in the W-Palearctic (Trierweiler et al. in prep.). Results from satellite telemetry (Trierweiler et al. 2007a, chapter 6, 7), ring recoveries (García & Arroyo 1998, Trierweiler & Koks 2009, chapter 8) and count data led to insights in the global migratory system of Montagu’s harrier and the relative importance of different pathways (box C: “global migratory system”).

Part III: Processes during the wintering season
Environmental conditions in Montagu’s harriers wintering areas in the West-African Sahel have changed during the last decades. Intensification of agriculture, cultivation of natural habitats, overgrazing, excessive woodcutting and climatic causes resulted generally in lowered food availability for birds (Thiollay 2006a, Zwarts et al. 2009). Birds may cope with environmental changes in the Sahel to some extent (Wilson & Cresswell 2006), but many raptor species in the Sahel have declined dramatically during the last decades (Thiollay 2006a). Additionally to man-made changes in the landscape, hazards in the wintering areas arise when pesticide treatment of large insects confronts harriers, which mainly feed on grasshoppers during the wintering season, with poisoned food sources. Harmful pesticides are not only used against nowadays seldom occurring migratory locust swarms, but also against mainly non-migratory grasshoppers that are pests to agriculture (Mullié 2009a, b). Consequences for acridivorous birds may be direct mortality (Cormier & Baillon 1991) or long-term negative impacts on fitness and reproduction (Mullié 2009b). Montagu’s harrier mortality is furthermore caused by illegal persecution in the wintering areas, by which we lost one satellite tracked bird (Thiollay 2006a, Trierweiler et al. 2007a, chapter 5).

Since 2006, the Dutch Montagu’s Harrier Foundation investigates Montagu’s harrier ecology and conservation in the wintering grounds, mainly in Niger and Senegal (figure 1.1). Distribution and habitat preferences are determined during transects counted along roads by car (Thiollay 2006a, Trierweiler & Koks 2009, chapter 7, 8). Prey abundance per habitat type is determined during transects by foot, when birds, small mammal holes and grasshoppers are counted. Diet is studied by analyses of pellets from night and day roosts. We strive to refine the idea that Montagu’s harriers’ main preys in the wintering areas are migratory locusts (Cormier & Baillon 1991, Arroyo & King 1995, Trierweiler & Koks 2009, chapter 7, 8).
In the West-African Sahel, the rainy season falls in the period of the northern hemisphere summer. More rain falls at latitudes closer to the equator, and the rainy season is shortest just south of the Sahara (the northernmost region of Montagu’s harriers’ wintering grounds). When the rains cease and the vegetation gradually desiccates during the dry season (the northern winter), this gives rise to a gradient of vegetation greenness, with highest greenness remaining at latitudes furthest south of the Sahara (closest to the equator). Large-scale vegetation greenness patterns in the Sahel are thus caused by patterns of previous rainfall and ultimately the shifting Intertropical Convergence Zone (ITCZ). Forbivorous grasshoppers need green vegetation to survive, indicating that food supplies for Montagu’s harriers may shift southward with the seasonal shift in vegetation greenness (Thiollay 1989, Mullié 2009b). For harriers, sparse vegetation may be profitable, as cover for prey is relatively low and prey availability thus relatively high. When green vegetation gets sparser throughout the dry season, optimal harrier hunting habitats may also for this reason shift southwards (P. Jones pers. comm.). We test the hypothesis whether Montagu’s harrier movements (changes between different home ranges, box D: “satellite telemetry home ranges”) during the wintering season relate to the southward shift of what presumably is a gradient of food abundance and food availability, represented by vegetation greenness, in chapter 7 (“following the green belt”). Our hypothesis describes a phenomenon similar to the patterns termed in Barnacle geese Branta leucopsis “following the green wave” of starting vegetation growth along the migratory route in spring (Van der Graaf et al. 2006). Parallel to this hypothesis, we termed the phenomenon in Montagu’s harriers “following the green belt” of optimal vegetation greenness, representing high prey abundance and availability, during the wintering season. The patterns we investigated in Montagu’s harriers may change dramatically in years with migratory locust outbreaks, which may then dominate harrier diet (Cormier & Baillon 1991, Arroyo & King 1995) and lead to different movement patterns.

Synthesis
In chapter 8 (“Montagu’s harrier”), we sum up current knowledge on Montagu’s harriers in their year-round habitats. We provide results from additional studies on ring recoveries and new insights from recent and ongoing fieldwork in the Sahelian wintering areas. Furthermore, factors influencing population change are investigated, such as rainfall in the Sahel. In box E (“population model”), we feed data and insights from our studies into a population model determining the relative importance of different seasonal effects on reproduction and survival, i.e. on population change. In chapter 9 (“general discussion”), we strive to identify which periods in the annual cycle are crucial for the change in Montagu’s harrier numbers, and recommend conservation priorities. We furthermore identify gaps in current knowledge and recommend future research that is needed to gain an even more complete understanding of Montagu’s harrier ecology, enabling us to formulate efficient year-round conservation strategies.
Part I

Processes during the breeding season
Food intake in a diurnal raptor revealed by two methods of pellet analysis - a feeding experiment

Christiane Trierweiler & Arne Hegemann

Abstract Dietary studies reveal important information on the ecology of bird populations. In raptors, out of several different methods, pellet analysis is the most frequently used tool to investigate diet. Food intake is usually estimated by multiplying prey numbers found in pellets with mean prey weights from literature or local data (numerical method). However, the reliability of this method has been rarely tested in harriers *Circus* spp. In this study, we perform a feeding experiment with a captive Montagu’s harrier (*Circus pygargus*) to test whether pellet weight is a reliable indicator of food intake and if this approach should be favoured above the numerical method. We show that a dietary shift was accurately reflected in pellet composition with a delay of 1–2 days. Pellet weight represented 3.1% of the previous day’s food intake. Our estimates of food intake, using the numerical method, closely resembled actual food intake, even in the absence of clues as to the number of individuals in pellets. We found no evidence that this method performs poorer than predictions from pellet weight taken from the literature.
Introduction

Dietary studies reveal important information on the ecology of raptor populations (Newton 1979). Field studies of raptor diets use direct and indirect methods (Marti 1987, Rosenberg & Cooper 1990). Observations and videography at the nest are used as direct methods (Rutz 2003, Lewis et al. 2004), but are fraught with several drawbacks. Prey consumed away from the observer/camera is not recorded (Lewis et al. 2004), and many prey items cannot be identified to species level (Lewis et al. 2004, Huang et al. 2006, Tornberg & Reif 2007, Redpath et al. 2001). The large investment in time and resources is often prohibitive to generating representative samples using direct methods (Lewis et al. 2004, Huang et al. 2006).

Indirect techniques infer diets from evidence collected at or near nest sites and perches. Analyses of regurgitated pellets and pluckings are most widespread (Marti 1987). Falconiformes often pluck their prey before consumption and only a proportion of indigestible prey parts is ingested (Rosenberg & Cooper 1990, Lewis et al. 2004). Furthermore, the strong gastric acids of falconiformes leave relatively few clues to identify prey species from pellets (Duke et al. 1975). Identification of prey species from pellets alone is thus biased (Rosenberg & Cooper 1990) and should be backed up with results from remains. Prey remains, however, are biased towards large and conspicuous prey items (Redpath et al. 2001, Lewis et al. 2004, Tornberg and Reif 2007, Bielefeldt et al. 1992, Simmons et al. 1991, Seguin et al. 1998, Marchesi et al. 2002 and references therein, Selás et al. 2007, Schipper 1973, Oro & Tella 1995). Combining analyses of pellets and prey remains is thus recommended and appears to yield good results in some raptor species (Simmons et al. 1991, Lewis 2004). Still, indirect methods usually underestimate the daily prey capture rate of raptors and should preferably be calibrated with direct observations (Rosenberg & Cooper 1990). No matter the provisos, indirect methods are widely used because they are cost-effective and provide large samples with little disturbance to the birds (Lewis 2004, Marti et al. 2007).

Montagu’s harriers Circus pygargus have a diverse diet, including small mammals, birds, reptiles and insects (Schipper 1973, Koks et al. 2001, Arroyo & García 2006, Millon et al. 2002, Höller & Wagner 2006), leading to the characterisation of being an “opportunistic specialist” (Arroyo 1998). Prey choice between different populations within Europe differs considerably (Leroux 2004) and has locally changed over time with changing environmental circumstances (Schipper 1973, Koks et al. 2007, chapter 2).

Observations and videography (Maurel & Poustomis 2001, Koks et al. 2007, chapter 2), as well as analyses of pellets and prey remains, have been used to study Montagu’s harriers’ diet (Schipper 1973, Sánchez-Zapata & Calvo 1998, Arroyo & García 2006, Underhill-Day 1993, Koks et al. 2001). Food intake has been estimated on the basis of pellet analyses (Arroyo 1998, Salamolard et al. 2000, Underhill-Day 1993, Trierweiler et al. 2006a, Koks et al. 2007, chapter 2), calculated by multiplying prey numbers found in pellets with mean prey weights from literature or local data, a numerical method (Hartley 1947). However, the reliability of this method has been rarely tested in harriers Circus spp. (see Newgrain et al. 1993 for Swamp harrier
In this study, we test whether pellet weight is a reliable indicator of food intake in Montagu’s harriers, by performing a feeding experiment with a captive bird. We investigate whether this method should be favoured above the numerical method.

**Methods**

An eight months old captive male Montagu’s harrier was experimentally fed during 21–27 February 2008 at a room temperature of 15°C. Its body weight of 260 g was below-average compared to free-living Montagu’s Harrier males during the breeding season (on average 285 g; unpublished data). The bird was born in farmland in Northrhine-Westphalia (Germany) and kept in a rehabilitation centre because of heavy wing damage that occurred shortly after fledging in mid-July 2007.

The harrier was kept on a diet of dead day-old chickens. During the experiment, the bird was fed with known quantities of dead laboratory House mice (*Mus musculus*), a substitute for common voles *Microtus arvalis*, the latter being the main prey in Germany and The Netherlands (Hölker & Wagner 2006, Koks *et al.* 2007, chapter 2). The regime of a diet based on house mice was switched again to day-old chickens after seven days.

Whereas the harrier was kept in a large aviary (3.5 × 3.5 × 3 m) for its recovery, the bird was kept in a small cage (55 × 70 × 85 cm) under veterinary supervision during the experiment. Dead mice with known weights were daily offered *ad libitum*. Excess food and pellets were collected once every day, and discarded mice were weighed. By subtracting the mass of uneaten from offered prey, ingested prey mass was calculated.

Pellets were dried in paper envelopes. Pellets were weighed digitally to the nearest 0.05 g after having kept the pellets at room temperature for one month. The dry pellets were dissected and prey species identified. The bone content of the pellets was negligible, and no clues as to the number of individuals were obtained, so the number was set to one per pellet (Clarke *et al.* 1993, Arroyo 1998). To simulate field conditions, food intake was estimated from pellets by multiplying average body weight of eaten mice (23.7 g) and literature estimates of mouse weight with the estimated number ingested (set to one per pellet).

We used Microsoft Office Excel 2003 and paired-samples t-tests in SPSS 16 (SPSS Inc.) for calculations and tests. Averages are presented ± 1 s.e.

**Results**

During the 7 days of the experiment the harrier ate 195 g of 831 g (24%) of food offered (28 ± 3 g per day). The bird produced 18 pellets (in total 7.95 g), ranging from
0.2–1.5 g weight per pellet (tab. A.1). One day after having been on a mouse diet, the Montagu’s harrier produced the first pellet containing hair exclusively (tab. A.1). After the diet was switched back to chickens on day eight, it took two days before any pellet was produced, which contained chicken remains. We concluded that, on average, pellets best represent the previous day’s food intake. Pellet weight represented 3.1 ± 0.2% (n = 7) of the previous day’s food intake. Taken over the whole period of seven days, pellet weight represented 3.4% of total food intake.

Using a linear relationship (food intake = [pellet weight of following day + 1,1131] / 0.0735; fig. A.1), we estimated food intake from pellet weight. Predicted food intake (tab. A.1) did not differ significantly from actual food intake on the previous day (paired samples t-test, t = –0.543, df = 6, p = 0.607).

An estimate of food intake was also derived from the number of individuals found in pellets (which by the absence of other clues was set to one), multiplied by

Table A.1 Mouse diet of a captive Montagu’s harrier during day 1–7 reflected in pellet contents and pellet weight. The prediction of food intake from pellet weight is based on the regression equation from fig. A.1. The estimate of food intake is based on the number of individuals identified in pellets (in this study all set to 1) times the average weight of mice fed during the experiment (23.7 g).

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<th>pellet weight (g)</th>
<th>pellet content</th>
<th>number of individuals identified in pellet</th>
<th>number of individuals actually ingested the day before</th>
<th>food intake: prediction from pellet weight (g)</th>
<th>food intake: estimate (number of individuals in pellets from day before * average mouse weight, g)</th>
<th>actual food intake the day before (g)</th>
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average 16.5 30.5 27.9
the average weight of mice offered as food (23.7 g; tab. A.1). These estimates did not differ significantly from actual food intake the previous day (t = 0.5, df = 6, p = 0.7). Differences between these estimates and the prediction from pellet weight were not significant (t = –1.9, df = 6, p = 0.1).

In the field, collecting data on prey weights is often difficult, the reason why data from the literature are taken instead. We simulated this approach by using 25 g as the average mass of a laboratory mouse (www.wikipedia.org), and 22 g for free-living house mice (Macdonald & Barrett 1993). The resulting estimates of food intake did not differ significantly from actual food intake (laboratory mouse: t = –0.7, df = 6, p = 0.5, house mouse: t = –0.1, df = 6, p = 0.9).

**Discussion**

During the experiment, our Montagu’s harrier had a low food intake, presumably explained by the fact that it was a relatively small individual, restricted in its movements and having low thermoregulatory costs. The production of small light-weight pellets was in accordance with the low food intake. Montagu’s harriers’ pellets found in the field are usually much larger than the pellets we collected in captivity, as recorded in Long-eared owls (Wijnandts 1984).

We show that a dietary shift was accurately reflected in pellet composition with a delay of 1–2 days, as found for Common kestrels by Yalden & Yalden (1985). In Barn owls *Tyto alba*, it has been shown that the interval between food intake and pellet production is not fixed, but depends on food quantity, time of feeding, and availability of a subsequent meal (Smith & Richmond 1972).

The relationship we found between pellet weight and food intake is based on small mammal prey. Yalden & Yalden (1985) showed for Common kestrels that various prey species were represented in pellets with different proportions of their fresh weight, from 1.0% in Wood mice *Apodemus sylvaticus*, 1.4% in House sparrows
Passer domesticus to 1.6% in Brown rats Rattus norvegicus. The proportion of house mice retrieved from pellets of our Montagu’s harrier was 3.1 % on a daily basis (3.4 % over 7 days), i.e. more in line with the 3.3% found in American kestrels Falco sparverius and 6.9% in Rough-legged buzzards Buteo lagopus (Duke et al. 1975). As digestive rates are known to show seasonal variations (Wijnandts 1984), feeding experiments with larger-sized mammals, birds and insect prey should be undertaken to account for seasonal variations and to refine the regression line we determined in our study.

In many dietary studies of raptors and owls, quantifying prey found in pellets is difficult because more than one prey item can contribute to a single pellet when the interval between two successive meals is short (Lewis 2004, Wijnandts 1984), and also because a single prey item can be distributed across more than one pellet (Lewis 2004, Rosenberg & Cooper 1990). The number of prey individuals contained in one pellet is usually estimated by counting jaws, skulls or feet (Arroyo 1997, 1998, Bijlsma 1997, Schipper 1973). If only hair (mammals) or feathers (birds) from one species are found in a pellet, the number of individuals for that species is usually set at one (Clarke et al. 1993, Arroyo 1998).

Our estimates of food intake, using the numerical method, closely resembled actual food intake, even in the absence of clues as to the number of individuals in pellets. Equating the number of individuals per pellet to one yielded satisfactory results in the setting of our experiment. For Common kestrels, it has been suggested to set the number of individuals in small pellets to 1 and in large pellets to 2 (Kochanek 1990). This may also be a useful approach in harriers, because the average number of prey per pellet in hen harrier was almost 2 (Redpath et al. 2001) and only 69 % of rodents fed to a captive Northern harrier was retrieved from pellets (Craighead & Craighead 1956). To use estimates from the numerical method reliably, it is important that estimated prey weight accurately reflects real prey weight. This prompts data to be collected locally rather than using average prey weights from published sources (Steenhof 1983). We found no evidence that this method performs poorer than predictions from pellet weight (contra Wijnandts 1984), although results should be corrected for biases inherent in pellet analyses when used in the field, for instance by including correction factors based on prey remains and calibrations by using direct observations or videography.

Acknowledgements
We are very grateful to Dr. Dieter Hegemann who carried out the daily feedings in February 2008. Rob Bijlsma significantly improved earlier drafts of this manuscript.
Look at the birds in the sky.
They don’t plant or harvest or gather food into barns,
and yet your heavenly Father feeds them.

- Matthew 6:26 -