Travels to feed and food to breed
Trierweiler, Christiane

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Montagu's Harrier *Circus pygargus*

Christiane Trierweiler  
Ben J. Koks

To talk of Montagu’s Harriers, or Monties as they are known by harrier aficionados, is to conjure up farmland, protection and volunteers; or, in the case of The Netherlands, waving cereals, flowering oilseed rape and butterfly-covered lucerne. ‘Empty’ quarters which are not empty at all, but the remote corners of a small country otherwise packed with human beings. The protection of nests demands unfailing dedication on the part of both farmers and volunteers. Hundreds of people have helped us over the years and are immortalised in our hall of fame, or in the names of those Monties which carry satellite transmitters (www.grauwekiek-endief.nl). A special place in our hearts is reserved for Rudi Drent. After his retirement as an animal ecologist at the Centre for Ecological and Evolutionary Studies (Groningen University), he continued to supervise our Monty research. Rudi was the ideal sparring partner, keeping sight of the larger picture amidst a multitude of details, pointing out promising avenues for further research and honing the data to perfection. His death on 9 September 2008 was a shock to all of us.

Superscript numbers in the text refer to endnotes at the end of this chapter.
Breeding areas

Montagu’s Harriers have a wide but patchy distribution across Europe, extending eastwards to the Caspian lowlands, Kazakhstan and the upper Yenisey at 93°E. The latest estimate of the European population, including Russia, stands at 35,000–65,000 pairs, with stable or slightly increasing numbers in the 1990s (BirdLife International 2004, but see below).

Wintering areas

On the Indian subcontinent, notably NW India, large roosts have been found, containing several thousand individuals (Clarke 1996b, 1998). These birds are most likely to come from the eastern breeding grounds. The latter population may also, at least partly, winter in eastern and southern Africa, given the vast migration of Montagu’s Harriers observed in Georgia during early autumn 2008 (B. Verhelst unpubl.), and the average migration directions attributed to birds recovered along the Dnepr, Don and east of the Volga (Mihelsons & Haraszthy 1985). If this interpretation is correct, the Sahel from Chad/Nigeria eastwards and eastern and southeastern Africa are a melting pot of Montagu’s Harriers breeding from Fennoscandia (10°E) eastwards to at least 55°E. Three birds ringed in spring and autumn at Dzjambul in southern Kazakhstan (45°50’N, 71°25’E) were recovered in western Asia at distances of 674, 1209 and 1594 km to the NE-NNE (Mihelsons & Haraszthy 1985); these birds may have wintered in India, probably circumventing the impressive Tien Shan mountain range on the way.

In Kenya, the species is considered to be a fairly common visitor to the grasslands and other open habitats in the highlands and in the southeast (Lewis & Pomeroy 1989). Many birds venture further south into the semi-deserts, grasslands, savannas, pans and fallow lands of Tanzania and the eastern half of southern Africa, albeit in ever lower numbers the farther south they fly (Brown et al. 1982, Harrison et al. 1997). However, the birds from Europe are confined overwhelmingly to the narrow band of the Sahel in W Africa.

Migration strategies

By 2008, after almost a century of bird ringing, the EURING files contained 46 African recoveries of Montagu’s Harriers ringed in Europe (fig. 8.1). The picture emerging from these recoveries is one of migratory connectivity: birds from The Netherlands, Britain, France and Spain mostly ended up in the western part of the Sahel, birds from northern Germany and Sweden converged in the central Sahel. Notable exceptions occur, however, showing that birds from western Europe may find their way to the central Sahel (fig. 8.1).

From the information derived from satellite telemetry, radar studies and visual observations in the Central Mediterranean, our perception of the migration of
Montagu’s Harriers has changed substantially from that provided by the ring recovery analysis by García & Arroyo (1998).

Autumn

Pre-migratory movements, following brood failure or shortly after the chicks have fledged, may occupy up to 73 days before true migration commences (own data, Limiñana et al. 2008). During pre-migratory movements, unless blocked by large stretches of open water, Spanish birds dispersed on random headings, shorthopping between sites that abound in food. They may also frequent conspecifics’ breeding haunts up to 500-1100 km away (Trierweiler et al. 2007a, Limiñana et al. 2008). The latter behaviour may function as prospecting for next year’s choice of breeding site, it may be due to wind drift or it may simply involve a brief return to the natal site.

Figure 8.1 European ringing locations of Montagu’s Harriers recovered in Africa (n=47) and Malta (n=2), including 15 south of the Sahara. From: EURING and García & Arroyo (1998). The Montagu’s Harrier ringed as a juvenile near Lippstadt, Germany by W. Prünte on 4 July 1970, and shot in the Dassa-Zoumé district in Benin in February 1971 (indicated by the arrow), is one of several reported well south of the wintering grounds in the western Sahel. The letter reporting the bird is a fine example of the many obstacles which have to be assailed in order to get the report onto the ringing centre’s desk; no wonder that many rings from birds taken in Africa are never reported. From: Vogelwarte Helgoland, Wilhemshaven.
In general, autumn migration follows broad parallel bands in an arc between SW and S. Despite some overlap, western birds winter on average in western Africa and eastern birds do so further east (fig. 8.2A,B; Limiñana et al. 2007). The previous idea that in order to cross the Mediterranean Sea, Montagu’s Harriers converge at suitable short sea crossings, such as the Strait of Gibraltar, the numerous central Mediterranean islands, or the Near East (García & Arroyo 1998), is not substantiated by the course of satellite-tracked birds, nor is it apparent from radar studies in southern Spain (Meyer et al. 2003) and visual observations in the central Mediterranean (Panuccio et al. 2005). Radar observations from the southern coast of Spain, 25 km east of Malaga in autumn 1996, showed that 74% of the Montagu’s Harriers continued their southbound flight without hesitation upon reaching the coastline. The Mediterranean Sea here is only 150 km wide, which in autumn would take about 4 hours to cross at an average ground speed of 11.6 m per second, or 42 km/h (Meyer et al. 2003). The extremely low wing loading of 2.05 (body mass in kg/wing area in m² = 0.300/0.1463), the lowest recorded among the 36 raptor species so far measured (Bruderer & Boldt 2001), and the high aspect ratio of the slender wings allow Montagu’s Harriers to alternate between soaring, gliding and flapping-and-

Figure 8.2 (A) Representation of 34 flight paths of 25 satellite-tracked Montagu’s Harriers during autumn migration in 2005-2008, showing birds from The Netherlands (10), Germany (5), Denmark (2), Poland (4) and Belarus (5); blue: males, red: females, green: juveniles; from Dutch Montagu’s Harrier Foundation, Vogelwarte Helgoland, University of Groningen and Deutsche Bundesstiftung Umwelt. (B) Successive migratory routes in autumn 2006-2008 (black) and spring 2007-2008 (red), based on satellite telemetry of Merel, a female Montagu’s Harrier named after 11-year old Merel Schothorst, our youngest Monty helper in The Netherlands. Lines represent the shortest distances between successive recorded positions (small dots) and not necessarily the actual route (Trierweiler et al. 2007a, 2008).
gliding flight and to migrate in less than favourable thermal and wind conditions (Spaar & Bruderer 1997). That Montagu’s Harriers are able to make long sea crossings is proved from our satellite-tracked birds (see fig. 8.2A, birds crossing the Gulf of Biscay and the eastern Mediterranean near Greece and Crete).

During autumn migration, the average daily distance covered by our satellite-tracked birds was 153 km, a very similar distance to those of other long-distance raptor migrants\(^1\). One of our males made a nonstop flight from The Netherlands to northern Spain in 2006, showing that nocturnal flights are possible. Montagu’s Harriers presumably speed up when crossing the Sahara; an adult female tracked in 2005 averaged 623 km in a day when crossing the Sahara (Trierweiler et al. 2007a). The satellite-tracked Spanish Montagu’s Harriers apparently followed a different strategy, as their daily speed dropped considerably after the first stage of desert crossing in Morocco (more than 450 km in a day). These birds took up to two weeks to complete the remaining 1000–1500 km to the wintering grounds, with average daily distances ranging between 93 and 219 km; they did not fly at night (Limiñana et al. 2007). This strategy would imply feeding along the way, but how this could be accomplished in the Sahara is difficult to envisage.

**Spring**

So far, most satellite-tracks have shown clearly that eastern European birds winter to the east of western European birds, with some overlap in Mali and Niger, and little movement along the length of the Sahel during the northern winter, with the possible exception of birds in the central Sahel (see below). Once settled in the Sahel, many birds remain there or reasonably close nearby (a few hundred km) for the rest of the winter. Eurasian Marsh Harriers were found to perform a small clockwise circular loop movement in West Africa, notably so between the latitudes of 20°N and 35°N, with the loop narrowing going northwards until it intercepted the autumn route in northern Spain (Klaassen et al. 2008a). In West Africa, the widest separation between autumn and spring routes was at 20°N, amounting to slightly more than 400 km. None of the Swedish Marsh Harriers showed any inclination to make the spring crossing of the Mediterranean in the central section (Cap Bon-Sicily), which accords with the spring migration of Eurasian Marsh Harriers which have wintered in West Africa following a more westerly flyway than in autumn (Klaassen et al. 2008a). So far, our NW-European Montagu’s Harriers also refrained from using the central Mediterranean corridor on their return migration (www.grauwekiekendief.nl). Instead they retraced their outward route, except in West Africa, where they drifted slightly to the east or west of the autumn track. In spring 2008, eastern European birds, having wintered in the central Sahel, performed a clockwise loop which took them to the central Mediterranean on return migration. This loop was unrelated to locust movements; the Montagu’s Harriers had been more or less sedentary in their wintering quarters where they fed mostly on resident grasshoppers (migratory locusts are prominent in the diet only during outbreaks; see below). Furthermore, any significant movement associated with grasshopper supply occurred along a north-south axis (as displayed by satellite-tracked Montagu’s Harriers; Trierweiler et al. 2008), following the retreating Intertropical Convergence Zone (ITCZ). Whether

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\(^1\) Chapter 8
a clockwise loop migration is consistent across years has yet to be proven. The suggestion by Klaassen et al. (2008a) that the clockwise loop migration of Eurasian Marsh Harriers in West Africa is influenced by the wind patterns in spring (predominantly from eastern sectors, and stronger in spring than in autumn; see also Zwarts et al. 2009), may also hold for Montagu’s Harriers (but see tracks of female ‘Merel’ at fig. 8.2B). In the central Mediterranean, visible migration of Montagu’s Harriers in spring is more conspicuous than in autumn (unlike at Gibraltar, where migration intensity in both periods is about the same; Tables 3 & 4 in Finlayson 1992), but counts here are very small in comparison to the total volume of Montagu’s Harrier migration (Panuccio et al. 2005). If this seasonal pattern indeed exists in the central Mediterranean, it must then involve Montagu’s Harriers from northern and – especially – eastern Europe, which enter Africa via the eastern and central Mediterranean and return via a clockwise loop in spring. Indeed, five birds ringed at Cap Bon, Tunisia, in spring, were recovered in Hungary, Bulgaria (2), Ukraine and the Voronezh region (SW Russia), having taken directions between NNE and ENE (recovered in the same year, or up to six years later; Mihelsons & Haraszthy 1985).

Fidelity to wintering sites

During the northern winter, many European Montagu’s Harriers, presumably the majority, are confined to the Sahel and northern Sudan zone (fig. 8.2A,B), but until recently next to nothing was known about their temporal distribution and movements within the wintering quarters. The predominance of insects in Montagu’s Harrier diets would suggest a dynamic distribution related not only to outbreaks of locusts and grasshoppers but also to seasonality and movements of local grasshopper species triggered by the cyclic position of the ITCZ (Zwarts et al. 2009). In other words, birds may be forced to exploit different sections of the Sahel and northern Sudan zone each year and to perform seasonal movements within years (as suggested by Thiollay 1978).

Between-year movements

Three tagged birds, which were followed for three consecutive seasons, returned to the same spots in Mali and Senegal (see fig. 8.2B for an adult female). This sample is, of course, too small to conclude that fidelity to the wintering site is the norm for this species in Africa. On the population level, the high migratory connectivity demonstrated by ring recoveries and satellite telemetry of birds from western Europe strongly indicates the fidelity of Montagu’s Harriers to restricted parts of the Sahelian and adjoining Sudan zones (García & Arroyo 1998, our data). A similar conclusion was derived from the ringing data of Eurasian Marsh Harriers (Zwarts et al. 2009), a species for which satellite telemetry hinted at a stronger site fidelity to stopover and wintering areas than to breeding grounds (Strandberg et al. 2008).

Within-year movements

The first results from our tagged birds indicate that upon arrival at the wintering

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quarters the birds remain for several weeks or months within a few km of the places
where they first settle. A gradual southward shift begins as the dry season
progresses, over some 200–250 km, a distance that bears testimony to several factors:
the narrowness of the Sahel belt, the increasingly desiccating conditions in the Sahel
that start in September and end with the first rains in May, and the change in abun-
dance of birds and grasshoppers in conjunction with the southward shifting ‘green
belt’ (fig. 8.3A-C, see also Mullié 2009b, Jones 1995). This process would explain the
Montagu’s Harriers’ movements into the adjacent Sudan vegetation zone.

Habitat use

Montagu’s Harriers in Africa are essentially birds of dry ground that is sparsely
covered by trees. During road transect surveys in West Africa from 1967 to 1973,
Thiollay (1977) found clear latitudinal gradients for the presence and density of
Montagu’s Harriers. Examples from his data are: absence of the species in the
forested regions around 6°N in the Ivory Coast; near-absence in the well-wooded
Guinean zone (0.02 birds/100 km); low densities in the wooded savanna of the Sudan
zone (between 9.30°N and 14.30°N: 0.72-1.17 birds/100 km); the highest densities in
the Sahel (which included the inundation zones of the Niger and Senegal: 0.79-3.11
birds/100 km; dry savanna is preferred over wet floodplains – see Zwarts et al. 2009
for niche differentiation between harriers in the Inner Niger Delta); and, lastly, densi-
ties rapidly declined to zero in the northern Sahel close to the Sahara (near 20°N).

Within the Sahel, densities showed large variations, supposedly in relation to
prey abundance (Orthoptera) and habitat. Our road counts in Niger in 2006-2007
revealed that large stretches of land were devoid of Montagu’s Harriers; line tran-
sects often failed to come up with any grasshoppers there. Montagu’s Harriers were
most commonly encountered where grasshoppers were abundant (fig. 8.3C).

In Niger, Mali and Senegal, Montagu’s Harriers avoided severely degraded habi-
tats (few remaining trees or shrubs and overgrazed), and regions with high tree
cover, but favoured slightly degraded shrubland and cropland. The latter habitats,
often having retained elements of more natural habitats, had the highest bird and
grasshopper densities, a finding in concurrence with bird densities in northern
Nigeria (Hulme 2007). In Niger, tiger bush is an important natural habitat for
Montagu’s Harriers, but such a patterned vegetation community, with alternating
bands of trees and shrubs separated by bare ground or low herb cover (resembling
the stripes on a tiger), is rapidly giving way to cultivation. The widespread replace-
ment of natural habitats by a mixture of degraded natural habitats (fewer trees,
more scrubland, and low herb layer) and cultivated land (with some shrubs and
trees) may have favoured Montagu’s Harriers. However, such a modified landscape
is not a steady state. Ongoing cultivation and human population pressure result in
severe and irreversible degradation. Tree and shrub loss and impoverished bird and
insect life are in evidence over much of the Sahel nowadays, a circumstance that has
negatively influenced almost the entire raptor community in Mali, Niger and
Burkina Faso, with Montagu’s Harriers particularly affected (Thiollay 2006a-c).
Roosts as treasure-troves

Daytime roosts
During the hottest part of the day, many Montagu’s Harriers retreat into the shade of trees or shrubs, either singly or in small flocks. One such roost we accidentally encountered in January 2007 near Birni N’Konni in Niger. Around 14:00, we spotted twelve Montagu’s Harriers, each in a different shrub without undergrowth, on the slope leading to a plateau. Underneath some shrubs, we found pellets and faeces, but in such small numbers that we suspected the site was used only during daylight. In February 2008, another typical daytime roost was found near Kaolack in Senegal, close to a salt lake. The day had been very hot, and we were desperately in search of
some shade. Our bias towards shade-bringing bushes revealed an adult female Montagu’s Harrier standing on bare ground in a small patch of shade beneath a shrub. This site produced some 20 prey remains of the grasshopper *Ornithacris cavroisi* and also some freshly plucked Yellow Wagtail feathers. Because the only raptor species we observed here were Montagu’s Harriers, we feel it safe to assume that the prey remains had indeed been left by this raptor.

**Night roosts**

The conventional way to find roosts is to watch for Montagu’s Harriers flying in steady, straight lines before sunrise or just after sunset (fig. 8.4). Usually, more than one bird will display this ‘atypical’ flight behaviour, not at all representative of that of foraging birds. The latter adopt a more roaming flight mode, meandering in low quartering searches across the terrain, switching direction and stalling frequently. Roost flights head clearly to or from a particular spot. However, to find the roosts one needs a number of well-spaced observers, preferably in contact with each other (walkie-talkie), to plot the general directions of the roost flight. Roosts can then be located either by triangulation of the extrapolated flight paths or by following the birds. This approach to finding roosts is most likely to be successful when roosts are large (the more harriers observed, the greater the chances of encountering roost flights).

By tracking our transmitter-carrying Montagu’s Harriers, using the most up-to-date positions received each day, we were able to locate roosts in a completely different way that often pointed us towards areas which we would not otherwise have visited, because the logistic problems would have seemed too daunting. Furthermore, from the telemetry we detected that some birds, like an adult Polish female residing east of Niamey, Niger, daily switched between roost sites, some of which we managed to reach; at one such site we found the remains of a freshly-eaten grasshopper *O. cavroisi*. A tagged juvenile female, from The Netherlands, led us to find, near Niamey, a 700 ha plateau containing a roost of 2 or 3 Montagu’s Harriers. A particularly spectacular discovery near Mopti, Mali, was a roost containing some 30 Montagu’s and 5 Eurasian Marsh Harriers in a well-wooded agricultural area dominated by tall grasses, not exactly the type of habitat where we would have expected to find Montagu’s Harriers. At some telemetry-indicated locations, we found pellets before we had actually seen a single Harrier, but on 24 January 2008, between 18:50 and 19:40, we recorded Montagu’s Harriers heading inwards from every direction. Around 19:30, ‘Franz’, a seventh calendar-year male, came into view, the satellite transmitter clearly visible on his back. To watch this Dutch bird, whose nest in a field of lucerne we had successfully protected in the preceding summer, in a Malinese setting, made us feel we had received an accolade for our fieldwork. As a bonus, at this site we were able to collect 70 pellets, whose contents of small mammals and reptiles, passerine eggs and a few small grasshoppers were not that different from the average pellets in an average year in NW-Europe.

Satellite-generated data revealed the positions of three roosts in Senegal; two contained ‘only’ 100–200 birds, but the third was enormous in comparison. The exis-
ence of this mega-roost was first detected by Wim Mullié in the evening of 25 November 2006. Although its exact location remained hidden, 500-1000 birds were observed near Darou Khoudoss, just before sunset, flying to a roost. The surroundings of this site were revisited in the evening of 2 February 2008, when a pre-roost gathering of 90 birds on bare farmland was noted. Although the light was failing quickly, the actual roost was conservatively estimated as holding about 1000 birds. Between 17:40 and 19:10 on the next day we counted more than 1000 birds (fig. 8.4). At 19:14 it was almost dark, but, as luck would have it, all the birds began to mill around again just before darkness prevented any further observations; at this time we noted 300 more birds on the side of a hill not yet surveyed. Our totals came to 1300 Montagu’s Harriers and a few Marsh Harriers; perhaps 1500 birds might have been present. We could not be any more precise, because birds were still entering the roost moments before complete darkness descended and we had to leave the area for security reasons.

Until recently, in Africa, the largest roosts mentioned have not usually exceeded 70-160 birds for Senegal (Arroyo & King 1995, Rodwell et al. 1996) and well over 200 birds for Kenya (predominantly Montagu’s Harriers; Meinertzhagen 1956). An apparent exception was the count on 8 February 1989 recorded for a roost in the area of M’Bour and Joal (delta of Sine Saloum, Senegal) of 800-1000 Montagu’s Harriers; this large number was associated with an outbreak of Desert Locusts Schistocerca gregaria (Cormier & Baillon 1991). In February 2008, Montagu’s Harriers on the Darou Khoudouss roost profited from an abundant supply of the medium-sized Acorypha clara (highest densities of 3–5 individuals/m²); pellets contained this grasshopper species almost exclusively; in March, the larger O. cravoisi became the predominant item in the diet of Montagu’s Harriers (Mullié 2009b).

Since at least the mid-1980s in the Indian subcontinent, even larger roosts of Montagu’s Harriers have been recorded by Clarke (1996b), who found up to 2000
birds in Bhavnagar District in NW India. This roost was estimated as holding some 3000 harriers on 6 December 1997; 15–25% comprised Pallid Harriers and a few Eurasian Marsh Harriers, but the great majority were Montagu’s Harriers (Clarke et al. 1998).

The role of resident grasshoppers

Both the general literature and the few real data collected in the field suggest that the locusts *Locusta migratoria* and *Schistocerca gregaria* are of crucial importance as food for acridivorous birds, including Montagu’s Harriers (Brown 1970, Thiollay 1978c, Cormier & Baillon 1991, see also Mullié 2009b). These locust species are certainly abundant in some years at some sites, but the available evidence clearly shows that resident grasshopper species are of far greater importance to Montagu’s Harriers, especially because their cumulative availability, usually in high numbers, is more stable within seasons and across years, thus representing a reliable food source for acridivorous species. The infrequent outbreaks of migratory locusts provide a stark contrast in annual availability, for, characteristically, locusts remain in very low numbers or are absent during the extensive periods of recession or remission. Furthermore, the frequency of such outbreaks has been much reduced since 1965 (Zwarts et al. 2009), often occurring outside the window of presence of Palearctic migrants. Indeed the highest frequency of *S. gregaria* in the Sahel occurs from July until December; Mullié 2009b).

In Niger, both in 2006 and 2007, the most frequently consumed prey were Orthoptera, mostly comprising the resident grasshopper species *O. cavroisi*, but, surprisingly, mantids did form a large share of prey numbers (fig. 8.5). Birds and mammals were insignificant in terms of numbers, but, individually weighing much more than a single grasshopper, were obviously more important in terms of biomass. A high frequency of *O. cavroisi* in Montagu’s Harrier pellets was also recorded in 2008 (Niger, Senegal; analyses not yet fully completed), attesting to the importance of medium-sized (3–7 cm) and large (>7 cm) resident grasshopper species for Montagu’s Harriers (and other acridivorous bird species, such as White Storks; Brouwer et al. 2003).

Montagu’s Harriers wintering in the central and western Sahel have proved to be quite versatile in their choice of prey. In February 2008, for example, we found large differences in prey choice between regions, presumably reflecting local variations in food supply. Pellets collected in Niger, Mali and Senegal contained small insects (termites, beetles), small, medium-sized and large Orthoptera, rodents, passerines, eggs and reptiles (see also Mullié 2009b). Our data suggest an interpretation that is a far cry from the notion of a diet predominated by locusts. Just as in NW India (fig. 8.5), the Montagu’s Harriers in the Sahel make do with whatever is available\(^5\). On the breeding grounds in Europe, Montagu’s Harriers also forage on an assortment of prey species, predominantly passerines in Britain (Clarke 2002), voles and passerines in The Netherlands (Koks et al. 2007) and France (Millon et al. 2002) and birds and insects in Spain (Sánchez-Zapata & Calvo 1998). However, between-year differences
are substantial, in Europe as well as in Africa. The predominance of locusts in the
diet of Montagu’s Harriers in Senegal in 1988/1989 perhaps reflected a dietary
exception rather than the rule; even then, despite the abundance of locusts in the
outbreak that year, rodents remained an important food source (fig. 8.5). Clearly, the
story of the importance of locusts to acridivorous bird species in Africa needs
revising to account for the dietary prominence of resident grasshopper species (see
also Mullié 2009b, for an elaboration on this issue) and alternative prey.

Population change

Wintering conditions
That Montagu’s Harriers wintering in the Sahel have been in decline is shown by a
comparison of road counts in Mali, Burkina Faso and Niger in 1969–1973 and
2003–2004 (down by 74% for unprotected areas and National Parks combined;
Thiollay 2006a). The same effect had earlier been suggested for East Africa: “I have
little doubt that some disaster has stricken the population that used to come to East
Africa”, wrote Leslie Brown (1970). Some support for that view for southern Africa
may also be gleaned from observations in the Transvaal’s Nyl River floodplain,
where Tarboton & Allan (1984) recorded eight birds in 1959-1970, but none in
1975–1981. The information collated by Clarke (1996a) seems to suggest that – at
least in East Africa – numbers since then may have recovered to some extent.
However, according to Simon Thomsett (in litt.): “Brown’s large roosts are no more.”
In southern Africa, the species is now relatively rare throughout the region except in
Botswana, where it is fairly common in the north (Harrison et al. 1997). How
numerous Montagu’s Harriers may once have been in East Africa, is apparent from

Figure 8.5 Frequency distribution of prey categories in pellets of Montagu’s Harriers in Gujarat,
NW India (n=134 pellets; Clarke 1993), in Senegal (n=113; Cormier & Baillon 1991), and in Niger
the casual observations of Meinertzhagen (1956) in Kenya. On 17 January 1956, he recorded 17 harriers (predominantly Montagu’s) during a motor journey of 200 miles between Isiolo and Marsabit (5.3 birds/100 km), and another 11 individuals in February on another 140-mile motor journey in the Rift Valley (4.9/ birds/100 km). In the Sahel, such densities have rarely been encountered, and, if so, only in the very best habitats and many decades ago (Thiollay 1977). Our own road counts, for example, in southern Niger in January and February 2006 and 2007, yielded provisional densities of 0.43 (4172 km) and 0.52 birds/100 km (4950 km) respectively. The road counts by Thiollay (2006a) in the western Sahel in 2003-2004 produced between 0.7 and 0.9 Montagu’s Harriers per 100 km.

The trends of European populations wintering in the western Sahel fluctuate independently of rainfall in the Sahel (fig. 8.6), the variable affecting green vegetation and therefore the food supply of Montagu’s Harriers. The trends of the Dutch Montagu’s Harriers suggest an effect of rainfall in the Sahel on numbers, but this is an artefact of conditions on the breeding grounds (see below). Also, we were unable to replicate the significant positive correlation between the number of Montagu’s Harrier nests found in Britain and the West African rainfall anomaly (Clarke 2002), using a longer time series and the relative change in breeding numbers from one year to the next. Despite large-scale habitat degradation in the Sahel (Thiollay 2006a, 2007) and elsewhere in Africa (Fishpool & Evans 2001), we have little evidence that the ups and downs in Europe are, as yet, triggered by such events. This may change with ongoing habitat loss.

**Breeding conditions**

Montagu’s Harriers are among the best-studied raptor species in Europe. Many of these studies started only in the 1970s or even later (examples in fig. 8.6). Statements based on short-term trends (such as an increase in 1970–1990; BirdLife International 2004a, see Zwarts et al. 2009) can be quite misleading when not viewed against the backdrop of historical data. In The Netherlands, for example, the population was estimated at 500–1000 pairs in the first half of the 20th century, but this had declined to a handful of pairs by the late 1980s (Bijlsma 1993); the subsequent increase to more than 40 pairs in the 2000s is a reminder that this recovery – heartening in itself – still represents only a small proportion of a once large population. The all-time dip in the Dutch population accidentally coincided with the Great Drought in the Sahel (1980s). A closer look at the data, however, reveals that the trends in The Netherlands are driven by local conditions. For example, the embankment of Zuidelijk Flevoland in 1968 created good breeding habitat and high food abundance, resulting in peak numbers around 1980, but the cultivation of that area in subsequent years caused loss of habitat, with a consequent steep decline of Montagu’s Harriers to near-extinction in the early 1990s. However, a sudden upsurge in numbers came after fallow land had been introduced as a measure to counter overproduction in agriculture (part of the European Common Agricultural Policy; Pain & Pienkowski 1997). The ensuing increase in The Netherlands was actively assisted by nest protection and agri-environmental schemes in farmland (Koks & Visser 2002, Trierweiler et al. 2008).
Figure 8.6 Population trends of Montagu’s Harriers in parts of Europe in relation to the Sahel rainfall index of the previous year. From: (A) Koks et al. 2007 and Visser et al. 2008. (farmland, The Netherlands), (B) Soutullo et al. 2006 (natural habitat, Castellón, Spain), (C) Clarke 2002 & British Birds 97: 513; 100: 343; 101: 293 (farmland, Britain), (D) Vandekerkhove et al. 2007 (farmland, Lorraine, France), (E) Hölker 2002 and Illner in litt. (farmland, Hellwegbörde, Germany). The graphs show a wide variety of trends, driven largely by local conditions on the breeding grounds. All studies refer to regions where nests are being protected when necessary.
In many regions in Europe, natural breeding habitats have disappeared, forcing Montagu’s Harriers into farmland where, because of their late laying date, the onset of the cereal and lucerne harvests threaten nest survival (Corbacho et al. 1999). Nest protection is imperative to prevent large-scale nest failure, particularly so in western Europe, where the timing of the cereal harvest has much advanced, e.g. by about two weeks in Lorraine, France, between 1988 and 2006 (Vandekerkhove et al. 2007) and by a month in The Netherlands between 1968 and 2008 (Bijlsma 2006, unpubl.). Without nest protection in farmland, reproductive output cannot sustain existing population levels in farmland populations (Koks & Visser 2002, Millon et al. 2002, Vandekerkhove et al. 2007). On average, 60% of the farmland nests would be destroyed in the absence of nest protection; typical estimates range from 41% to 98% in 14 regions in France, Portugal and Spain (Arroyo et al. 2002, Millon et al. 2002).

The human effort involved in nest protection throughout Europe is enormous. In France, for example, 40–50 groups in 60 districts have been active in nest protection each year; the combined effort safeguarded 11,000 nests from destruction, enabling 22 000 nestlings to fledge in 1976–2001 (Pacteau 2003). This massive involvement is estimated to cover between 7.5% and 17% of the French Montagu’s Harrier population annually, but is apparently insufficient to stop the negative population trend in much of France (Pacteau 2003, Thiollay & Bretagnolle 2004).

Even in the tiny Dutch farmland population (16–48 pairs in 1990–2008), whose nests are protected each year when necessary, nest protection and habitat improvement only just sustain a more or less stable population (Koks & Visser 2002). Colour-ringing has shown some exchange between breeding clusters in The Netherlands and northern and eastern Germany (Visser et al. 2008). Pre-migratory dispersal may be one of the mechanisms by which potential breeding habitats over a wide vicinity are being explored and tested (Limiñana et al. 2007, Trierweiler et al. 2007a). Food abundance, in particular of Common Voles Microtus arvalis (in Britain: Field Vole M. agrestis) and small passerines, may then serve as the trigger for settlement (Salamolard et al. 2000, Arroyo et al. 2007, Koks et al. 2007). The scarcity of formerly common prey species in Europe’s industrialized farmland strains the already precarious status of European Montagu’s Harriers. Nest protection should therefore be merged with improvement of harrier habitat in farmland (Millon et al. 2002, Koks et al. 2007), in addition to the preservation of natural breeding habitats, where reproductive output is – at least in Spain – better than in farmland (Limiñana et al. 2006).

**Conclusion**

The increase of Montagu’s Harriers recorded in Europe between 1970 and 1990 represents only a small recovery from losses incurred earlier in the 20th century. Destruction of natural breeding habitats, and a subsequent shift to breeding in farmland, has had an overriding influence on the fortunes of this species in the 20th century. Harvesting often prevents pairs breeding in cropland from successfully raising chicks, unless nests are being protected. Modern farming has also had a devastating impact on prey abundance (notably voles and passerines). Without
habitat improvement, nest protection in farmland cannot reverse negative trends.

Montagu’s Harriers winter mostly in the Sahel, where the eastwest distribution largely mirrors the longitudinal distribution of the breeding grounds. During that period they may be forced southwards by the desiccating conditions of the Sahel into the southern Sahel or northern Sudan zone. Their main food comprises many resident grasshopper species (with different phenologies and occurring in local outbreaks), which remain a reliable food source throughout the dry season, a diet complemented by passerines, mantids and small mammals; outbreaks of migratory locusts are but a rare dryseason opportunistic food source. Large harrier assemblages may occur wherever small mammals, resident grasshoppers or locusts abound. The present habitat degradation in the Sahel is likely to increase in extent, but for the time being may favour resident grasshopper species and hence Montagu’s Harriers. The impact of Sahel rainfall and habitat degradation on Montagu’s Harriers is overridden by the much greater land changes which have occurred in Europe in the 20th century.

Endnotes

1) Many medium-sized and large raptor species have now been tracked by satellite, providing information on migration speeds relative to sex, age and season (see tab. 8.E1). On average, birds attain higher speeds during the return migration (but see Swainson’s Hawk below), adults move faster than juveniles and immatures, and speeds over deserts are higher than over more hospitable land (European Honey Buzzard, Short-toed Eagle, Eurasian Marsh Harrier).

Table 8.E1 Migration distance and speeds of satellite tracked raptors. Body weight is expressed in grammes (averaged for male and female; Dunning 1993). Distance relates to the one-way distance between breeding and wintering grounds in km (based on tracked birds), origin to the breeding site. Daily migration distances (in km) are given for the entire southbound or northbound migration period (including stopovers), with number of tracked birds in brackets. Notice that Wahlberg’s Eagle is the only species which was tagged in the southern hemisphere, and for which the outward migration is to the north.

<table>
<thead>
<tr>
<th>Species</th>
<th>Body weight</th>
<th>Distance</th>
<th>Origin</th>
<th>South</th>
<th>North</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Osprey</td>
<td>1486</td>
<td>6393</td>
<td>Sweden</td>
<td>162 (12)</td>
<td>244 (8)</td>
<td>Alerstam et al. 2006</td>
</tr>
<tr>
<td>Osprey</td>
<td>1486</td>
<td>15260</td>
<td>Scotland</td>
<td>168 (7)</td>
<td>236 (3)</td>
<td>Dennis 2008</td>
</tr>
<tr>
<td>Osprey</td>
<td>1486</td>
<td>4958</td>
<td>USA</td>
<td>241 (52)</td>
<td>-</td>
<td>Martell et al. 2001</td>
</tr>
<tr>
<td>European Honey Buzzard</td>
<td>758</td>
<td>6709</td>
<td>Sweden</td>
<td>146 (8)</td>
<td>-</td>
<td>Hake et al. 2003</td>
</tr>
<tr>
<td>Egyptian Vulture</td>
<td>2120</td>
<td>4160</td>
<td>France, Bulgaria</td>
<td>194 (3)</td>
<td>-</td>
<td>Meyburg et al. 2004a</td>
</tr>
<tr>
<td>Short-toed Eagle</td>
<td>1703</td>
<td>4365</td>
<td>France</td>
<td>234 (1)</td>
<td>-</td>
<td>Meyburg et al. 1996, 1998</td>
</tr>
<tr>
<td>Montagu’s Harrier</td>
<td>316</td>
<td>5000</td>
<td>Europe*</td>
<td>153 (16)</td>
<td>-</td>
<td>C. Trierweiler et al. in prep.</td>
</tr>
<tr>
<td>Eurasian Marsh Harrier</td>
<td>628</td>
<td>4243</td>
<td>Sweden</td>
<td>127 (23)</td>
<td>161 (13)</td>
<td>Strandberg et al. 2008a</td>
</tr>
<tr>
<td>Broad-winged Hawk</td>
<td>455</td>
<td>6998</td>
<td>North America</td>
<td>69 (3)</td>
<td>105 (1)</td>
<td>Haines et al. 2003</td>
</tr>
<tr>
<td>Swainson’s Hawk</td>
<td>989</td>
<td>12 728</td>
<td>North America</td>
<td>188 (27)</td>
<td>150 (19)</td>
<td>Fuller et al. 1998</td>
</tr>
<tr>
<td>Lesser Spotted Eagle</td>
<td>1370</td>
<td>8725</td>
<td>Central Europe</td>
<td>164 (5)</td>
<td>177 (3)</td>
<td>Meyburg et al. 1995a, 2001, 2004b</td>
</tr>
<tr>
<td>Wahlberg’s Eagle</td>
<td>640</td>
<td>3520</td>
<td>Namibia</td>
<td>214 (1)</td>
<td>185 (1)</td>
<td>Meyburg et al. 1995b</td>
</tr>
<tr>
<td>Hobby</td>
<td>240</td>
<td>9635</td>
<td>Sweden</td>
<td>151 (4)</td>
<td>-</td>
<td>Strandberg et al. 2008b</td>
</tr>
<tr>
<td>Eleonora’s Falcon</td>
<td>390</td>
<td>8600</td>
<td>Italy, Sardinia</td>
<td>134 (1)</td>
<td>293 (1)</td>
<td>Gschweng et al. 2008</td>
</tr>
<tr>
<td>Peregrine Falcon</td>
<td>780</td>
<td>3841</td>
<td>Russia, Kola</td>
<td>190 (2)</td>
<td>-</td>
<td>Ganusevich et al. 2004</td>
</tr>
<tr>
<td>Peregrine Falcon</td>
<td>780</td>
<td>8463</td>
<td>North America</td>
<td>172 (22)</td>
<td>198 (7)</td>
<td>Fuller et al. 1998</td>
</tr>
</tbody>
</table>

*Consisting of birds breeding in Germany and The Netherlands (12), Poland (2) and Belarus (2).
2) Inspired by the work of Jean-Marc Thiollay in West Africa, we adopted the method of road transects to detect spatial and temporal variations in abundance of Montagu’s Harriers. Travelling at a maximum of 60 km/h, we counted all raptors systematically along roads, dirt roads and tracks while estimating the distance of each raptor from the road (Trierweiler et al. 2007b). Whenever a Montagu’s Harrier was seen, we stopped to check whether there was more than one bird, but if so, they were not included in the road count itself. Since starting in SW Niger in the northern winter of 2005/2006, we have covered more than 15,000 km of road transects in Niger, Mali and Senegal. We also used the road counts to record habitat types (every 5 km) and habitat degradation (scored thus: no, little or much, the categories related to pre-determined values for the extent of undergrowth, erosion and tree-felling). In addition, we collected data on prey densities by walking line transects at least 30 m long, recording birds (species and numbers, within 20 m on either side), active burrows of small mammals (rodents, burrows <3 and >3 cm diameter, within 1.5 m on either side), reptiles (within 1.5 m on either side) and grasshoppers (lengths <3 cm, 3-7 cm or >7 cm, within 1.5 m on either side). Samples of grasshoppers were collected on the spot, to be identified at a later date and to be used as references. We used these data to calculate relative prey densities. Between 2006 and 2008, we collected data from more than 1100 prey transects (Trierweiler et al. 2007b, unpubl.).

3) ‘Roost’ is used here in the sense of any place where one or more individuals spend time resting or loafing, at night or during daylight.

4) Finding roosts, and by doing so, finding pellets, is essential when investigating the diet of Montagu’s Harriers in the wintering areas. Large roosts (hundreds of birds) are easier to find than small roosts (a few birds, sometimes only one). However, investigating only the large roosts will bias the results, because large roosts indicate areas of high food abundance, where the diet will usually be less diverse than in areas of lower food abundance. In the latter areas, Montagu’s Harriers normally have a more diverse diet. The small body of literature on the food of wintering Montagu’s Harriers is strongly biased towards large roosts in areas subject to outbreaks of Schistocerca gregaria (Cormier & Baillon 1991, Arroyo & King 1995); this bias is often exacerbated by small sample sizes and short sample periods. A second bias in dietary studies relates to the techniques used to study diets: pellet analysis, collection of prey remains, visual observations or video recordings at the nest. Each method in itself under- or over-represents certain prey categories (Schipper 1973, Simmons et al. 1991, Underhill-Day 1993, Sánchez-Zapata & Calvo 1998, Redpath et al. 2001, Koks et al. 2007), and so a combination of methods is usually considered to provide the smallest bias. Our Sahelian dietary studies are largely based on pellets.

5) An eye-witness account of Chris Magin may serve to illustrate that Montagu’s Harriers in Africa also capitalise opportunistically on sudden outbursts of food. Returning to Addis Ababa from Lalibella, Ethiopia, in late January/early February 2008, he took the lowland route from Dese, descending into the Afar plains. “As we headed south to Awash NP we passed through Yangudi Rasa NP, which straddles the main road. The grassy plains were extremely well vegetated (i.e. the rains a few months previously must have been extremely good) and the grass was absolutely swarming with a super-abundance of small rodents. Every step you took seemed to cause one to scuttle for safety. I cannot say with certainty what species they were. The skies were alive with raptors, almost entirely harriers. I was so impressed with the numbers that at one
point I attempted a rudimentary census, scanning a 90 degree arc very slowly with my 10x50 Zeiss Jenoptem binoculars and counting all harriers seen up to the horizon. I counted 125 in this quarter horizon, so estimated that there were around 500 present within the limits of my visibility. I could see quite far – although it was the middle of the day, this was the cool season, so relatively little heat haze – so probably I could pick out harriers up to 3–4 km away. As there were no locusts or large grasshoppers present and most of the harriers were quartering low to the ground, I assumed that they were congregating to feed on the ‘exploded’ rodent population. The harriers would have been between the hamlet of Gewane and the junction with the Dese road. I also assume that they would have been within the Yangudi NP limits, if only because the amount of good grazing would have attracted hordes of nomads and their livestock herds if it had been outside the NP boundaries. The harriers I saw must have been Pallid and Montagu’s Harriers, which are common in the area.”

6) The reputation of Richard Meinertzhagen, ornithologist extraordinaire in his time, as being a reliable source of information has crumbled in recent years (review in Garfield 2007). Painstaking research by Alan Knox, Robert Prys-Jones, Pamela Rasmussen and Nigel Collar has shown that “much that he left us cannot be taken at face value” (Knox 1993). His note on harriers in Kenya, however, has a ring of credibility, since it was published within months of the actual observation. This is also evident from the remark of Simon Thomsett (in litt.), born and raised in Kenya and intimately familiar with the raptors there: “I believe Meinertzhagen in this case.” Garfield (2007) documents that most of the numerous fabrications occurred long after the event, but concedes that, “All the same, his bird writing, even if sometimes factually wrong, usually tends to be much more dependable and certainly more plausible – therefore less irritating – than his military or political memoirs.”
In this study, we model population change in a Palearctic-African migratory raptor species, Montagu’s harrier *Circus pygargus*, and investigate relative influences of several demographic and extrinsic factors during the annual cycle. Montagu’s harrier is red-listed in many European countries. The species is a ground-breeder and prone to nest losses caused by harvesting practices when nesting in farmland. The factors of main interest in this study were the protection of nests in farmland in relation to harvesting practices, improvement of food supply in agricultural breeding areas, and circumstances during the non-breeding season that influence survival and may carry over to the subsequent breeding season. Our model indicates that protection of nests seems to be the most important factor for population growth under the current circumstances in NW-European breeding and W-African wintering grounds. Furthermore, improved food supply in farmland habitats and high adult non-breeding season survival are important to achieve population growth. Food availability in the breeding areas may be increased by using agri-environmental schemes, e.g. fallow field margins. Adult non-breeding season mortality may be reduced by promotion of bio-pesticides that are not harmful to acridivorous birds like Montagu’s harriers and prevention of illegal persecution during the migration and wintering seasons. Adult non-breeding season mortality can furthermore be restrained from an expected future increase by conservation of threatened habitats along the migratory flyways and in the wintering areas.
**Introduction**

Prey availability may have major effects on predator reproduction and population dynamics (Caughley 1980, Dijkstra *et al.* 1982, Meijer *et al.* 1988, Renshaw 1991). Dynamics of prey populations have thus often been used to explain predator population dynamics, for instance in raptors (Hamerstrom 1979, Taylor 1994, Hone & Sibly 2003). Population dynamics of long-distance migrants are influenced by factors acting in the breeding and wintering areas and along the migratory route (Newton 2008). Montagu’s harriers *Circus pygargus* are long-distance migratory raptors that feed mainly on small mammal and bird prey in the northern European breeding grounds and on grasshopper prey in the African wintering grounds (chapter 2, 8). Montagu’s harrier is red-listed in many European countries. The species is a ground-breeder and prone to nest losses caused by harvesting practices when nesting in farmland. Previous models of Montagu’s harriers’ population dynamics focussed mainly on effects during the breeding season (Koks *et al.* 2001, Arroyo *et al.* 2002, Arroyo *et al.* 2007, Millon *et al.* 2008, Millon & Bretagnolle 2008, Vanderkerkhove *et al.* 2007). These models revealed two important findings. First, changes in abundance of common voles *Microtus arvalis* have great explanatory power regarding Montagu’s harrier population changes. Vole abundance influences the harriers’ reproductive success and also their survival. Second, protection of nests in relation to harvesting practices and subsequent predation influences reproductive success and consequently population dynamics.

In this study, changes in a hypothetical Montagu’s harrier population are modelled based on demographic and extrinsic factors acting in the breeding season and in the non-breeding season. For the breeding season, we include effects of nest protection and food abundance, and the potential up-regulation of food abundance by agri-environmental schemes (e.g. fallow field margins: food abundance is higher in fallow land; chapter 3). The model also includes mortality during migrations and the wintering period as well as carry-over effects from the non-breeding season to the breeding season. Carry-over effects of non-breeding season food abundance are thought to act via delayed spring migration phenology (Balbontín *et al* 2009, Gordo & Sanz 2008), a lower probability of a bird entering the breeding population, a lower probability of starting a clutch, a delayed start of laying and consequently a higher risk of nest loss by agricultural practices (own data).

The goal of our population model is identifying the relative impacts of different phases in the annual cycle (breeding season, non-breeding season) and of different conservation actions (nest protection, agri-environmental schemes) on population change.

**Methods**

**Model**

The deterministic model was based on females. Population change \( \lambda \) (where \( \lambda = N_{t+1}/N_t \)) was determined as follows (Burgman *et al.* 1993).
In this model, we took reproduction, survival and recruitment into account to calculate the reproduction that is necessary every year to compensate losses by mortality (including females and males). Values of the finite population growth rate $\lambda$ indicate a population decrease when $\lambda < 1$ and an increase when $\lambda > 1$.

**Parameter estimates**

In our population model, we mainly used parameter estimates from a Dutch study area in the east of the Province Groningen (chapter 2, and unpublished data) and from own satellite telemetry data of Montagu’s harriers tagged in northern European breeding areas (Trierweiler & Exo 2009, chapter 5, 6). If no reliable parameter estimates were available, we used values of other populations from literature, for example survival estimates (Millon & Bretagnolle 2008). In our model, a female had a probability of settling in a certain breeding population ($p_{settle}$), which was high (high was set to 100 %) after a good winter. Satellite telemetry has shown that birds surviving sandstorms during spring migration may arrive late in the breeding areas and may refrain from starting a clutch, or may not even settle in a breeding area at all (own data). We therefore used a low value of $p_{settle}$ after “bad winters” (low was estimated to be 80%, for the frequency of good and bad winters see below). We have indications that, whereas emigration and immigration in our study population may be balanced in average years, settlement (immigration) is higher in years following years with peak food abundance (Koks et al. 2007, chapter 2). We plan to extend the model with such a feedback loop in the future. Based on Arroyo et al. (2007), we modelled the probability of laying a clutch ($p_{breed}$) for a settled female to be high (94%, median of own data) when food abundance is high and low when food abundance is low (low was set to 84%, which is 94% - 1 standard deviation). Median clutch size was set at 3.6 eggs according to own data. In the model, clutch size was higher when laying date was earlier and when food abundance in the breeding area was higher according to Koks et al. (2007, chapter 2), using the regression equation

$$
\lambda = \left(p_{settle} \times p_{breed} \times \frac{1}{2} \times \text{clutch} \times p_{fledge} \times s_{2\text{CY}} \times p_{\text{recruit}_{2\text{CY}}}ight) + \\
\left(p_{settle} \times p_{breed} \times \frac{1}{2} \times \text{clutch} \times p_{fledge} \times s_{3\text{CY}} \times p_{\text{recruit}_{3\text{CY}}}ight) + \\
\left(p_{settle} \times p_{breed} \times \frac{1}{2} \times \text{clutch} \times p_{fledge} \times s_{2\text{CY}} \times p_{\text{recruit}_{3\text{CY}}}ight)
$$

where

- $p_{settle} =$ probability to settle in the breeding population
- $p_{breed} =$ probability to start a breeding attempt (lay a clutch)
- clutch = clutch size
- $p_{settle} =$ probability that a young fledges (clutch * $p_{fledge}$ = number of fledglings)
- s = survival, with indication of age class (second of third calendar year, or adult i.e. >third calendar year)
- $p_{\text{recruit}} =$probability that a bird enters the breeding population for its first breeding attempt, with indication of age class)
clutch size = 4.396 + 0.035 * food abundance – 0.035 * laydate

Laydate (in the formula expressed as day number starting from 1 May) was set (according to own data) at 25 May for median years, 14 May for early years and 14 June for late years. We reasoned that bad winters (low food supply in the wintering areas) would result in females leaving in poor body condition with lower probability of successful spring migration (Zwarts et al. 2009). This and adverse weather conditions during spring migration would result in late arrival in the breeding areas. Therefore, laydate in years with a bad winter was always set to be late, resulting in smaller clutches and higher agricultural nest losses (see below).

Hatching success was not explicitly modelled and assumed to be constant. Fledging success (pfledge) was set to 68% (Butet & Leroux 1993: 68 ±8%). We accounted for differences in reproductive success between monogamic females and α- and β-females of polygamic males by using the clutch size and fledging success values measured in the field, which are values that are averaged over the different pair forms. The only effect of food abundance on reproduction included in the model was the effect on clutch size (see above), as no relationship between food abundance and number of fledglings was measured in the field (own data). Next to nest protection in relation to harvesting practices, fledging success may also be related to other, not modelled factors, e.g. individual quality of the parents, weather conditions in the early nestling phase and predation.

According to estimates from our small mammal censuses, we set food abundance at 5 for median years, 1 for low years and 20 for peak years (values refer to small mammals/100 trap nights measured during vole censuses, for the frequency of each event see below; Koks et al. 2007, chapter 2). To model the role of alternative prey items, especially farmland birds, which are assumed to replace small mammals in poor years, we include only median and peak years in the model scenarios we run here, and therefore refer to “food abundance” instead of “small mammal abundance”. Food abundance was set to be ten times higher in agri-environmental schemes (fallow field margins) than in regular farmland. This decision was based on Koks & Van Scharenburg 1997 and chapter 2, where small mammal abundance was estimated to be 2 – 6 times higher in fallow than in regular farmland. The estimate was increased to 10 times to include the beneficial effect of the margins on the surrounding farmland. Overall food abundance was calculated as a weighed mean of proportions surface area of land with agri-environmental schemes (food abundance in median/peak years was multiplied by 10) and regular farmland (food abundance was multiplied by 1).

Next, fledging probability (pfledge) was corrected for agricultural losses. Nests were distributed over different vegetation types (e.g. winter wheat, lucerne, winter barley, which was varied according to different model scenarios). In each vegetation type, a nest had a certain survival probability related to harvesting practices and lodged vegetation, which may differ between nests started early or late in the season. In “safe” vegetation types, nests have a high survival probability related to harvesting practices and lodged vegetation, in “unsafe” types a low one. A “safe” type
is for instance late harvested winter wheat, where losses were estimated to be 7% when the laying date is median, but 100% when the laying date is late (own data). “Unsafe” types are early mown lucerne, winter barley, wheat/barley hybrid and oilseed rape, where losses are almost always 100% (own data). With nest protection, agricultural losses were set to zero. Only natural habitats had always zero agricultural losses. We did not model losses of incubating females, as no estimate of the number of females killed annually by harvesting activities was available, and the number was likely to be low (own data).

Age-specific survival estimates were based on a study on wing-tagged Montagu’s harriers by Millon & Bretagnolle (2008). Their study showed that first year survival was 31 ±6% (set to 31 % in our model) and adult female survival was between 60% and 80%. In our model, we distributed mortality for adults over the annual cycle according to insights from satellite telemetry (Trierweiler & Exo 2009, Strandberg et al. 2009a): during spring migration 9%, during the breeding season 5%, during autumn migration 8% and during the wintering season 5%. Catastrophic events such as sand storms during spring migrations can dramatically lower adult survival during migrations (Strandberg et al. 2009a, Trierweiler & Exo 2009). For bad winters, mortality estimates for adults were consequently corrected up to 20% during spring migration based on estimates from satellite telemetry (Trierweiler & Exo 2009), resulting (multiplied) in the annual adult survival of 76% in average years and 66% after bad winters (for the frequency of good and bad winters see below). We assumed that most Montagu’s harriers do not head for the breeding areas in their second calendar year but stay in the wintering grounds until their 3rd calendar year (Clarke 1996a). Survival of 3rd calendar year birds was therefore

\[ S_{3CY} = S_{\text{autumn migration}} \times S_{\text{winter}}^2 \times S_{\text{spring migration}} \]

where \( s \) denotes survival and subscripts indicate periods in the manual cycle.

As females start breeding mainly in their third calendar year (CY; Clarke 1996a, own data), we set the proportion of recruitment into the breeding population \((p_{\text{recruit}}, \text{related to the age of first breeding})\) in the 2nd CY to 2%, in the 3rd CY to 80% and in the 4th CY to 18%.

**Frequencies of rich and poor food abundance and of good and bad winters**

Finite population growth rates were calculated for combinations of normal and low probability of entering the breeding population, for early, median and late laying date and median and high food abundance. We assumed that peak food abundance years as well as bad winters occur each twice every 10 years, other years being median / normal years (own data: small mammal census and satellite telemetry). Scenarios were run by randomly drawing values of \( \lambda \) according to the specified frequencies of peak food abundance and bad winters, taking nest protection and different proportions of agri-environmental schemes into account. Average population change was calculated in scenarios run in MS excel over 50 years with 100 randomisations. For the present purpose, no carrying capacity was set and exponential population
growth was possible. We evaluated the average $\lambda$ and the probability that final population size falls below one individual (extinction criterion) within 50 years.

**Scenarios**

Modelling a hypothetical population with a start value of 40 (the size of the study population in Groningen), we run three scenarios differing in the distribution of nests over different vegetation types. In scenario 1, most nests were located in winter wheat (“safe”) but some also in “unsafe” vegetation types, in scenario 2 most nests were located in winter barley (“unsafe”) and in scenario 3, the population was almost entirely located in winter wheat (details see fig. E.1A-C). In scenario 1, the distribution of nests over different vegetation types represents the situation in Groningen, The Netherlands (53°11’N, 7°4’E) in 2005, and in scenario 2, the distribution represents the situation in Rheiderland, Germany, in 2008, which is adjacent to Groningen. Scenario 3 is a hypothetical scenario.

**Results**

In scenario 1 (“Groningen 2005”), finite population growth rate $\lambda$ was always below 1 (population decrease) in the two situations where nest protection was absent (on average 0.89 and 0.95, with and without bad winters, respectively; fig. E.1A). Without nest protection, extinction risk over 50 years was 100%, whereas with protection, it was 0% (no carrying capacity set). The negative effect of bad winters was slightly larger in the unprotected than in the protected situation (decrease in average $\lambda$ when bad winters were introduced: unprotected, 0.95 to 0.89; protected, 1.05 to 1.01). This is the case because late arrival after a bad winter was modelled to result not only in a smaller proportion settling and breeding as well as smaller clutches, but also in additional agricultural losses (harvest/mowing is more likely to be earlier than fledging date in late nests in an otherwise “safe” vegetation type like winter wheat).

In the situation with bad winters and with nest protection (representing the most realistic situation), deterministic population growth was slightly negative without agri-environmental schemes ($\lambda = 0.99$). Growth rate was positive when in more than 6.6% of surface area, agri-environmental schemes (fallow field margins) were realised. Simulating a surface area a little larger than this value (8%), 100 random runs over 50 years produced an average $\lambda$ of 1.004 with an extinction risk of 0% (no carrying capacity set).

In scenario 2 (“Rheiderland 2008”), the situation without nest protection was more critical than in scenario 1 (fig. E.1B): Population growth was even more negative without nest protection than in scenario 1, due to the high percentage of nests in “unsafe” vegetation. The relative effect of bad winters in the unprotected situation was smaller than in scenario 1, as agricultural losses were high any way. Trajectories in the most realistic situation (with bad winters, with nest protection, 10% agri-environmental schemes) resulted in an average $\lambda$ of 1.008 and 0% extinction risk over 50 years.
In scenario 3, positive population growth could be achieved without nest protection, given that no bad winters occurred ($\lambda > 1$ in the situation "-badwinter-protection", fig. E.1C). When no bad winters occurred, the positive effect of nest protection on population change was relatively small, whereas it was larger in case bad winters occurred.

**Figure E.2** (right) Sensitivity of the model on Montagu’s harrier population growth rate used in this study to changes in different parameter estimates. The basis is scenario 1 (“Groningen 2005”, see text), one variable is changed at a time. Outcomes are shown for several example situations, that are termed after the winter (normal or bad), laying date (early or late) and food abundance (low or high), with (NP) or without (blank) nest protection. Not all situations are shown in each graph. (A) The probability of settlement ($p_{settle}$) in good years is set at one. In the graph, outcomes are shown for variations in the probability of settlement after a bad winter (proportions of females settling in the breeding population). (B) The probability of breeding (laying a clutch, $p_{breed}$) in normal years is set to 0.94 (94%). The graph shows the effect of changes in the probability of breeding in bad years (proportions of females laying a clutch). (C) In the model, food abundance in agri-environmental schemes was assumed to be 10 times higher than in regular farmland. The
Graph (D) shows the effects of changes in the estimate of food abundance in agri-environmental schemes when regular farmland is kept at food abundance = 1. Graph (D) shows the effects of variation in fledging probability (pfledge, expressed as proportion of young that fledge). We set fledging probability at 0.69 (69%) in our scenarios. In graphs (E) and (F), respectively, the effects of variations in adult female survival after normal and after bad winters are shown. In (G), four different situations (1–4) are shown for recruitment into the breeding population. The percentage of females’ age of first breeding was varied as follows. Situation 1: 2nd Calendar Year, 2%; 3rd CY, 50%; 4th CY, 40%; 5th CY, 8%; situation 2: 0% / 50% / 50% / 0%; situation 3: 10% / 60% / 30% / 0%; situation 4: 2% / 80% / 18% / 0%, the latter being the situation used in our scenarios.
winters occurred. This was caused by agricultural losses in winter wheat modelled to be small early in the season, but high late in the season (after a bad winter and consequently late arrival).

To evaluate the sensitivity of the model outcomes to changes in parameter estimates, we chose scenario 1 (“Groningen 2005”) and varied several parameters one by one (fig E.2A-G). It showed that the model outcomes were most sensitive to variations in fledging probability and adult survival, especially adult survival after bad winters.

**Conclusions**

Factors acting during the breeding season seemed to be most important for Montagu’s harrier’s population change, under the current conditions in NW-Europe and W-Africa, which we modelled. Protection of Montagu’s harrier nests in relation to harvesting practices and subsequent predation seems to have the largest influence on population change under different scenarios. Scenario 1 (“Groningen 2005”) and 2 (“Rheiderland 2008”) represent both realistic scenarios with, in Groningen, a high proportion of nests located in “safe” vegetation types (winter wheat, mostly harvested after fledging of the young), and in Rheiderland a high proportion in “unsafe” types (mostly winter barley, causing 100% nest loss without protection). In both scenarios, our model predicts that positive deterministic population growth can only be achieved with nest protection. Due to high agricultural losses, deterministic population growth in the unprotected situation was much more negative in scenario 2 than in 1 (33% vs. 9% annual decline).

In the situation with nest protection, our model predicts that adult winter survival as well as food abundance in the breeding areas become the most important factors determining population change. When all nests were protected in the model scenarios 1 and 2, population growth was still slightly negative without agri-environmental schemes, given that bad winters occur. Improvement of food abundance by fallow field margins on a relatively small surface area of the breeding grounds was necessary to make population growth positive. Our model predicted that agricultural losses (without nest protection) cannot be completely compensated by improving food supply by agri-environmental schemes in scenarios 1 and 2. Even in scenario 3, with the major part of nests located in relatively “safe” vegetation (winter wheat), population growth was slightly negative over the whole range of % surface areas with agri-environmental schemes, without nest protection. Only a higher adult survival made population growth in the “safe” scenario 3 positive without nest protection. In practice, this means that in populations nesting for the major part in safe vegetation, we may not need to protect 100% of nests in need of conservation to achieve positive population growth. This implication is especially relevant at a large scale (e.g. countrywide), when lack of manpower and resources is often prohibitive for 100 % nest protection.

In scenarios 1 and 2 with nest protection, reduction of non-breeding season mortality would have an even larger beneficial effect on population growth than
realising agri-environmental schemes. Exclusion of bad winters (with 0% agri-environmental schemes realised) would result in an annual deterministic population growth of 3%, the same that may be achieved with 24% agri-environmental schemes when bad winters were included. In practice, the occurrence of bad winters in the strict sense cannot be influenced, because headwinds, dust storms and consequently energetic bottlenecks during sea and desert crossings cause extra mortality during bad years. In a wider sense, especially in the light of current human- and climate-induced environmental changes in the wintering and stopover areas, conservation may focus on non-breeding season habitats, aiming at the conservation of reliable food sources for harriers. Next to the expected future loss of non-breeding season habitats, harriers may suffer lethal or sub-lethal effects of harmful chemical pesticides used against migratory but also non-migratory grasshoppers (the latter being the staple food during the non-breeding season): bio-pesticides that are not harmful to acridivorous birds should be promoted (Cormier & Baillon 1991, Mullié 2009b). Prevention of illegal persecution in the non-breeding season should be another priority. Such conservation actions should be aimed at halting a potential future increase in adult non-breeding season mortality.

The numerical results from this modelling exercise should not be taken literally but interpreted as indications. Outcomes of our model are robust to changes in most parameter estimates, but sensitive to changes in adult survival, in particular adult survival after bad winters. The latter shows the possible detrimental consequences of catastrophic events during migration. To further evaluate processes relating to adult survival, we recommend to calculate specific survival estimates for NW-Europe. The estimate of survival after bad winters we used was based on relatively few own data from satellite telemetry. Our results must consequently be seen as first indications and we recommend to refine the model when better parameter estimates, especially for non-breeding season mortality, become available.

Our model was furthermore sensitive to changes in fledging probability. This indicates that improvement of fledging success could be a rewarding conservation strategy. We recommend to investigate correlates of fledging probability in a longer time series of data. In the present dataset, we found no significant relationship of fledging success with small mammal abundance in the breeding areas. Other factors such as predation, weather circumstances and individual quality may also play a role. The positive relationship of hunting yield of Montagu’s harrier males with fledging probability of their broods is, however, an indication that food abundance may in general positively influence fledging probability (chapter 3).

Nest protection is no desirable nor realistic long-term conservation strategy. On the long term, strategies have to be investigated how to create enough safe and attractive breeding habitats in Montagu’s harriers’ breeding areas to counter the high proportion of nest losses. A low proportion of nest losses could be compensated for by improvement of food abundance (agri-environmental schemes) and higher adult survival (stable and on average favourable conditions during the non-breeding season).
The world lies in the hands of those who have the courage to dream and who take the risk of living out their dreams - each according to his or her own talent.

- Paulo Coelho -