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British Montagu's Harriers – what governs their numbers?

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Zusammenfassung

Britische Wiesenweihen – was bestimmt ihre Zahl?

In Großbritannien blieb der Status der Wiesenweihe als Brutvogel äußerst prekär über die letzten Dekaden, während die Rohrweihenpopulation beträchtlich zunahm. Wird der Bruterfolg britischer Wiesenweihen von Faktoren der Brut- oder Überwinterungsplätze kontrolliert? Brutversuche in bestelltem Farmland können unbemerkt bleiben, wo die Ernte eine Bedrohung darstellt und die zunehmende Auswahl von Silage-Grassland als Brutplatz die Art zur frühen Mahd verwundbar gemacht hat. Trotz aller Schutzbemühungen während der Ernteoperationen und einer durchschnittlichen Rate des Flüggewerdens in dem Kerngebiet von Norfolk von 2,19 pro angefangenem Nest, die derjenigen auf dem Festland Europas vergleichbar ist, zeigen die Wiesenweihenzahlen keine Anzeichen einer Besserung. Beute in Britannien sind meist Vögel, allen voran die Feldlerche. Dies steht im Gegensatz zur wühlmausreichen Nahrung z.B. in den Niederlanden, wo der Schutz eine nachhaltige Erholung der Bestände zeitigte. Die häufigste Wühlmaus in Britannien, *Microtus agrestis,* ist ein Oberflächenbewohner und deshalb den Praktiken der Landwirtschaft stärker ausgesetzt als die kontinentale, tiefer grabende *M. arvalis.* In ihren Überwinterungsgebieten in Indien und Afrika spezialisiert sich die Wiesenweihe auf große Heuschrecken. Eine einzelne Weihe braucht ca. 25 Heuschrecken pro Tag. Im Überwinterungsgebiet wird die Häufigkeit der Heuschrecken durch Regen und Pflanzenwachstum geregelt. Über einen Zeitraum von 29 Jahren zeigte die jährliche Regenmenge in der West-Sahelzone und die Zahl der Wiesenweihennester in Britannien im Sommer darauf stets eine positive Korrelation ($r_s = 0{,}38$, $n = 29$, $P < 0{,}025$), was einen starken Indizienbeweis für den Zusammenhang zwischen Dürre und schwachem Brutstatus der Wiesenweihe in Britannien nahelegt. Werden jüngste Fortschritte in der Heuschreckenbekämpfung incl. neu auf dem Markt erscheinender biologischer Methoden eine weitere Bedrohung der Winternahrung darstellen?

Introduction

Over the two hundred years that have passed since the English naturalist George Montagu was the first to realise the difference between his 'Ash-coloured Falcon' (now called Montagu's Harrier *Circus pygargus*) and the Hen Harrier *Circus cyaneus,* Montagu's Harrier has bred widely over the British Isles, in wetland, lowland and upland heathland, and chalk downland habitats. The literature abounds with nostalgic accounts of this harrier breeding not only in the east and south of England where it occurs today, but also in the West Country and Wales, and even as far west as Ireland. Maps for this species in the *New Atlas* (GIBBONS et al. 1993) show contraction of its breeding range in Britain towards the south and east. Today in Britain, breeding Montagu's Harriers are virtually confined to two weak population centres, centred on chalk downland in the south and reclaimed coastal land around the

Wash. Despite strict protection in core breeding areas, annual numbers of nests in Britain now are typically in single figures. So, is breeding effort of Montagu's Harrier in Britain governed by factors in the breeding or winter ranges?

The winter range of Montagu's Harrier is virtually confined to Africa and the Indian subcontinent. In Africa, the species is a trans- or sub-Saharan migrant, and West Africa, where its distribution is centred on the steppe grasslands and acacia savanna of the Sahel and Sudan zones, is probably the most important wintering area for West European breeding populations (CLARKE 1996a). The first recovery of a UK-ringed Montagu's Harrier in Africa occurred in Senegal in 1995 (1995 Norfolk Bird & Mammal Report). Indeed, these are over-wintering grounds for vast numbers of Palearctic-African migrant birds and the region is notorious for the depth of international concern for its environmental problems.

A crash in numbers of common summer migrant birds in western Europe in 1969 alerted ornithologists to the problem of drought in the Sahel region. The Common Bird Census, launched by the British Trust for Ornithology in 1962, provided the first widely-based measure for identifying problems in the population levels of these birds. The connection between drought in the Sahel and migrant numbers was originally made by WINSTANLEY et al. (1974). The data they presented showed that a sudden dip in Sahel rainfall 1968 and a further dip in the 1970s seemed to account for the crash in numbers of migrants returning to breed in Europe in 1969 and a continued depression in their numbers. In the 1980s and 1990s, Sahel rainfall remained below average, with particularly pronounced droughts in 1983 and 1984 which were mirrored by lows in populations of birds such as Common Whitethroat *Sylvia communis*, Sedge Warbler *Acrocephalus schoenobaenus* and Sand Martin *Riparia riparia* breeding in Britain (Marchant et al. 1990).

Montagu's Harrier is a generalist predator that can switch between small reptiles, mammals and birds. However, in the winter range these are probably less reliable as prey than locusts and large grasshoppers (in the rest of this paper referred to collectively as 'locusts') because they require considerably more effort to catch. I have researched harrier winter roosting and feeding ecology in India (e.g. CLARKE 1996a, 1996b, 1999, CLARKE & PRAKASH 1998, CLARKE et al. 1998), where Montagu's Harrier predominates at the largest harrier roosts in the world (up to 3000 birds). Its dependence on locusts as food there soon became clear. Harriers wintering in India originate from the mid Asian breeding population. However, my findings on their feeding ecology in India seem equally applicable to the West European birds wintering in West Africa. Indeed, locusts (largely the Desert Locust *Schistocerca gregaria*) have been identified as the main prey for the birds attending large Montagu's Harrier roosts documented in Senegal (CORMIER & BAILLON 1991, ARROYO et al. 1995).

In India, at similar latitudes to the West African wintering grounds, my observations have indicated that the time windows for hunting each day are quite brief. Leaving the roost soon after first light, harriers spend a certain amount of time post-roost loafing and travelling to hunting grounds in cotton fields and shrub lands. Hunting in earnest begins at about an hour after sunrise and ceases at about three hours after sunrise, when the sun has gained enough altitude to make its full heat felt. There is a lull in hunting activity during the heat of the midday period, when harriers tend to circle up in the sky in ones and twos and individual birds can be seen standing in the shade under bushes. A few more harriers can be seen hunting by the middle of the afternoon. About four hours before sunset, a more general evening hunting session begins. Winter foraging therefore seems to be timed to coincide with the cooler parts of the day. The reason for this is not known for certain, but Montagu's Harriers have been noted to rest similarly at midday during the breeding season (GLUTZ et al. 1971, KHAN in CRAMP & SIMMONS 1980), and similar midday lulls in activity are characteristic of many species in warm weather, including grasshoppers (Belovsky et al. 1990). Movement is thought to be necessary to reveal cryptically coloured / patterned Orthoptera in their natural habitat to raptors (INGLES 1940). A harrier has to achieve a run of success with small prey in two limited time spans each day, and so a good density of easy prey may be a necessity despite reduced energy requirements in the warm climate.

The principal harrier roost that I have studied, at Velavadar in Gujarat, Northwest India, occurs annually. However, my experience whilst leading a birding holiday tour there in January 1994 brought the true dynamics of the situation home to me. It was a strange winter for birds due to a lack of autumn monsoon rain, and I had the embarrassment of having just a handful of harriers to show at what, on the experience of previous winters, had been billed as 'the largest harrier roost in the world' We still saw Pallid Harriers *C. macrourus*, which principally hunt for larks, but virtually no Montagu's. Links between poor rainfall, much reduced cropping in the area, straggly cotton bushes and lack of locusts were easy to suspect. Clearly, it is not unreasonable to hypothesise that the amount of rainfall influences the density of locusts, because it governs the extent of foliage available for them to eat. Such a mechanism could also explain any link between Sahel drought and numbers of Montagu's Harriers returning to breed in Western Europe. Reportedly, the African roosts have been less consistent than the ones that I have studied in India, which could indicate even greater vulnerability to drought there.

In this paper I examine breeding season diet in Britain, winter feeding ecology in India, and the applicability of knowledge of the latter to Palearctic-African migrant Montagu's Harriers breeding in Britain. I also discuss some conservation issues related to diet.

Methods

Determining harrier diet

Determination of diet was based on pellet analysis methods developed by CLARKE (1999). In the breeding season, pellets were collected from nests and roosting places around nests, mainly after the young had fledged. In winter, samples of pellets were collected in February 1992 and December 1995 from grassland night-roost areas at Velavadar. The roost was comprised mainly of Montagu's Harriers, but included 15-25 % Pallid Harriers. Analysis results were compared to those from a batch of pellets collected at a Senegal Montagu's Harrier roost by CORMIER AND BAILLON (1991).

In the Indian pellets, care was taken to select the correct durable part to count locusts by. Some parts are discarded by harriers; remains collected from one well-used 'plucking place' consisted of wings representing about six locusts, five pronotums, seven whole and three part hind-leg femurs (six with the rest of the leg attached), and three heads (one with the gut trailing from it). Because it was almost certain that the abdomen of every locust caught was consumed, sets of ovipositor valves were taken as providing the most complete counts, but of course only of the females in the population. In order to convert that into an estimate of total number consumed, a locust sex ratio had to be used. This was not determined in the field, as locusts proved difficult (for humans!) to find and catch, and insufficient time was available to amass an adequate sample of locusts to determine the sex ratio with confidence. However, both female and male locusts were caught and in the Desert Locust, POPOV (1954) showed that the sexes were about equal in numbers, which only changed as females died off more quickly towards the end of the egg-laying period. It was unlikely that egg laying was taking place in winter, as it is facilitated by rainfall which is then scarce, and so it was assumed that the sex ratio was even and that only adult locusts were involved. A further assumption was made that each harrier produced two pellets in 24 hours, and that these were equal in size (discussed in CLARKE 1999).

Daily locust consumption calculated from sets of ovipositor valves found in purely locust remains pellets × 2 for sex ratio and × 2 for two pellets in 24 hours was compared with the number of locusts calculated to be required by a harrier from its gross energy intake needs, and conclusions were drawn about the likely accuracy of each method of calculation.

Calculating the energy content of a diet of locusts

As the locusts in India were similar in size to the Desert Locust reported as food in Africa, dry mass (water content has no bearing on energy content) of a typical locust was taken from measurement data for Desert Locust by DUDLEY in UVAROV (1966). DUDLEY showed that dry mass in the locust body increases significantly over the first few weeks as the adult insect matures after fledging. His values for dry mass in five-week old females (1592 mg) and males (992 mg) were therefore selected to reflect the adult state expected of locusts at Velavadar. These were averaged to give a dry mass value, assuming an even sex ratio, of 1292 mg. The proportion lost in wings, legs, pronotums, and sometimes heads and guts discarded by harriers was difficult to assess. The value of 1292 mg was rounded down to 1 g in further calculations as an allowance for this.

The only data on caloric value of Orthoptera available from the literature were those of BIRD et al. (1982) for the Spur-throated Grasshopper *Melanoplus f. femurrubrum*, a very much smaller species. However, fat content of the grasshopper was particularly low (6.03 % of dry mass) compared to that found in locusts (e.g. Migratory Locust: female 13.5-15.0 % of dry mass, male 23.4 %, CHEU 1953). Fat plays a key role in locust physiology as fuel for flight (UVAROV 1966) and strongly influences calorific value of food (GESSAMAN in PENDLETON et al. 1987). A more normal value for raptor foods (in e.g. BIRD et al. 1982, WIJNANDTS 1984) was therefore used (23 kJ per gram of dry matter) rather than the value for small grasshopper (21 kJ, 1 kilojoule = 0.239 kilocalories).

The energy value of a whole locust implied by the calculations, multiplied by the numbers of locusts eaten as determined from pellet analysis, was compared with predicted daily gross energy intake for Montagu's Harrier calculated by means of the equations of KENDEIGH et al. (1977), which are perhaps the most widely used in avian energetics. I interpolated the results from their equations for 'existence metabolism' (energy used by caged birds) in non-passerines in winter/migration with 10+ hour photoperiods at 0° and 30 °C, to arrive at a value for a bird the size of Montagu's Harrier in a mean ambient temperature of 22 °C (taken from metero-logical station data in Ranjitsinh [1989] at the nearest town for the core of the season, November to February). The result was multiplied by two to gross up for the energy costs of wild existence (assessed from a range of multiples in raptors given in KIRKWOOD 1981), and adjusted for over-prediction of KENDEIGH et al. equations in harriers by 24% (CLARKE 1999) and digestion efficiency of about 75% (KIRKWOOD 1981, TOLLAN 1988, NEWGRAIN et al. 1993). The size of bird used in the equations was based on mean weights of 261 g (male) and 370 g (female) (Glutz et al. 1971) and an even sex ratio. Difficulty was encountered in checking the sex ratio in the field. Many harriers, even perched on the ground at pre-roost, could not be successfully separated by telescope beyond greys (adult males) and browns (ringtails and juveniles) due to the distances, light and attitudes. At pre-roost, successive time-spaced counting (to lessen the effect of any arrival time differential between the sexes) over four evenings in February 1992 and January 1993 showed that 30.5% of harriers were greys (total $n = 397$). This agreed well with the proportion of greys (27/91 = 29.7%) in photographs taken at random of harriers foraging in cotton fields. If the sex ratio of adults were even, this would imply that about 40% of the birds present were juveniles. Casual observation suggested that this was roughly correct.

As an additional check on energetic demands, the time-budget formula constructed by KOPLIN et al. (1980) (working on the energetics of American Kestrels *Falco sparverius* and White-tailed Kites *Elanus leucurus*) was used. The flight coefficient (multiple of basal metabolism to reflect the energy cost of flight and influential in their formula) used was 8.0, because due to light wing-loading and other adaptations for sustained flight in Montagu's Harrier, it probably is less than the 9.5 predicted by WIJNANDTS (1984) for Long-eared Owl *Asio otus*.

The proportions of locust-only pellets in the February 1992 (40%) and December 1995 (37%) collections at Velavadar were similar (table 1). An assumption of 50% locust specialist harriers was adopted in the calculation of total locust consumption by the roost to reflect birds practising mixed foraging and the likely lesser durability and therefore frequency of the fragile locust-only pellets in batches collected.

Testing for a relationship between rainfall and breeding numbers

I tested the hypothesis that Sahel summer rainfall, through its effect on the extent of foliage and therefore the density of locusts each winter, influences the number of breeding attempts in Britain in the following years over the period from 1966-67 (a point pre-dating the crash noticed in other summer migrants) to 1994-95 (the latest years for which it was practicable to obtain the data). The numbers of Montagu's Harrier nests in Britain each year amount to tiny sample sizes, but they may be particularly responsive to overall population expansion and contraction because they are on the very north-western edge of the breeding range. Breeding habitat in the Britain could be sub-optimal and only used when numbers are higher.

The rainfall measure used was a 'Western Sahel standardised anomaly index', produced by the Climatic Research Unit at the University of East Anglia. Calculated from rainfall measured at 12 weather stations in West Africa, located between latitudes 10°N and 17°N and from the west coast to 5°E and encompassing much of the south-west Sahel, it is the extent to which annual rainfall (mainly occurring in the annual rainy season May to October) falls above or below a long-term mean of annual rainfall, that for the period 1961-1990, divided by the overall standard deviation. The resulting value shows by how many standard deviations each year's rainfall deviates from mean rainfall.

The data for numbers of nests in Britain were taken from UNDERHILL-DAY (1990), supplemented by Rare Breeding Birds Panel data for the latest years. Care was taken to deduct re-nests by the same female from the figures.

These two sets of data were tested for correlation using the Spearman rank correlation coefficient (r_s) corrected for tied observations (SIEGEL & CASTELLAN 1988), on a one-tailed basis.

Results

Harrier diet

Analysis of pellets from nests occurring in east and south England in the period 1996 to 2000 indicated that the diet in Britain is comprised mainly of small birds. Of 117 pellets collected, 77 (66 %) were purely of bird remains, and the most frequent prey was Skylark *Alauda arvensis*, which occurred in 70 % of all pellets collected (Tab. 1).

In winter, locusts were the principal prey in pellets from both the Indian and African roosts (Tab. 2). Locusts occurred in 60 % of pellets from the Indian roost and 97 % of pellets from the African roost in the two similar-sized samples. There was a highly significant difference between the contents of those two samples, on the basis of pellets sorted into three classes: locust, mixed locust and other prey, and purely other

Table 1: Composition of Montagu's Harrier pellets collected at nests in Britain. – *Bestandteile in Wiesenweihengewöllen von Nestaufsammlungen in Großbritannien.*

	WASH		CAMBS	WILTSHIRE		HAMPSHIRE			TOTAL
	1999	2000	1995	1998	2000	1995	1996	1997	
Avian	**6**	**4**	**23**	**14**	**6**	**4**	**7**	**13**	**77**
pure *Alauda arvensis*	2	1	16	11	1	1	5	12	49
A.arvensis & other	4	1	8	12	3	1	4		33
Mammal	**1**		**3**	**4**	**1**	**1**	**1**	**1**	**12**
pure *Microtus*				3	1			1	5
Microtus & other	5	2		6	1		1	1	16
pure lagomorph			4	1		1			6
lagomorph & other		1	3	2			1		7
Avian/Mammal Mix	**2**	**2**	**6**	**9**	**2**		**3**	**2**	**26**
Vegetable Matter			**1**					**1**	**2**
n **Pellets**	**9**	**6**	**33**	**27**	**9**	**5**	**11**	**17**	**117**

Note: figures in bold add to 100 % of each sample.

prey ($\chi^2_2 = 49.77$, $P < 0.001$).

At the Indian roost, birds were the second most frequent prey and 24-35 % of the pellets contained purely bird remains. Larks were again the most common bird prey, with pellets containing up to three of their bills. There was no equivalent of this in Africa, where mammals were the second most frequent prey.

Two species of locust were present in the Indian pellets. The Tree Locust *Anacridium rubrispinum*, a species very similar to the more widely known Egyptian Locust *A. aegyptium*, and the slightly larger Black-spotted Grasshopper *Cyrtacanthacris ranacea* occurred in the pellets in a ratio of about 9:1.

Indian pellets comprised solely of locust remains contained a mean of 6.99 sets of ovipositor valves. Multiplied by two for an even sex ratio in locusts, and again by two for number of pellets assumed produced in 24 hours, this implies daily consumption of 28 locusts by a locust-specialist harrier.

The caloric value of 28 locusts was calculated as:

1 g DM per locust × 23 kJ per gram of dry matter × 28 locusts = 644 kJ per day

Predicted consumption calculated from the KENDEIGH et al. (1977) equations gave:

236 kJ / day for a male

290 kJ / day for a female.

The mean value of 263 g, × 2 for wild existence, × 76 % to adjust for over-prediction of KENDEIGH et al. equations in harriers, and × 100 / 75 for assimilation efficiency = 533 kJ / day

Intake calculated by the pellet route therefore exceeded predicted consumption by 111 kJ (20.8 % of predicted consumption).

Although following individual birds throughout the day to measure their time budgets proved impossible, an approximate picture was simple to build up. Daylight lasted for about 11 hours during the period from November to February. Early morning and late afternoon hunting sessions lasted for about 2 hours each. Added to a further hour's travelling and roost attendance flight, flight activity occupied about 5 hours. Resting therefore amounted to about 6 hours, of which some time could be seen to be spent at post-roost, about 4 hours during the heat of mid day and the rest at pre-roost. Building this into the equation from KOPLIN et al. (1980), the daily energy budgets calculated were:

348 kJ / day for a male

441 kJ / day for a female.

The mean value of 394.5 kJ / day, grossed up by 100 / 75 for assimilation efficiency = 526 kJ / day.

Table 2: Composition of pellets collected at communal winter roosts of harriers in Gujarat, India (mixed Montagu's and Pallid Harriers) and Senegal, Africa (solely Montagu's Harriers, after CORMIER & BAILLON 1991). – *Bestandteile von Gewöllen aus gemeinschaftlichen Winterrastplätzen in Gujarat, Indien (gemischt Wiesen- und Steppenweihe) und Senegal, Afrika (nur Wiesenweihe, nach CORMIER & BAILLON 1991).*

	Gujarat		Senegal
	Feb '92	Dec '95	Dec'88/ Jan '89
Number of pellets	134	46	113
Containing:	%	%	%
Locust only	40	37	74
Locust and bird	4	4	3
Locust and mammal	6	4	18
Locust and reptile	7	–	2
Locust, bird and reptile	2	–	–
'Absence of locusts'	n/a	n/a	3
Bird only	24	35	–
Bird and mammal	2	4	–
Bird and reptile	4	–	–
Bird, mammal and reptile	2	–	–
Bird, mammal and beetle	–	2	–
Mammal only	6	9	–
Mammal and reptile	2	4	–

This value closely approximates to the predicted intake calculated from KENDEIGH et al. equations.

A tentative calculation of the number of locusts taken from the surrounding fields by the birds attending the Velavadar roost each winter is given below. In view of the many assumptions made, the two values given above for predicted consumption (equivalent to 23 locusts per day) and consumption calculated from pellets (28 locusts) are close enough to lead to the conclusion that a consumption rate calculated from pellet contents could be reasonably accurate with care. A problem with half pellets could have inflated the count of locusts in pellets (e.g. by counting them as halves when they may be the larger sections of pellets), and so the pellet figure of 28 was rounded down to 25 as a working estimate for further calculations.

This figure squares well with my assessment of foraging time available. During runs of the most productive hunting for locusts, the time between strikes was about six minutes. At that rate it would take 2.5 hours of foraging time for a harrier to catch and consume 25 locusts. Taking into account movement between cotton fields, often widely separated by fields in fallow, and far less productive foraging at times, this would still fit comfortably into the observed early and late foraging sessions of 2-3 hours each.

Assuming a mean number of 1000 harriers (calculated from an assumed linear progression from nil at the beginning of the season, up to a peak of 2000, and down to nil at the end) over a period of 182 days (October to March), and half of them were locust specialists consuming 25 locusts per day, total consumption of locusts would amount to 2.28 million. Taking into account the potential for error in the assumptions made, actual consumption is likely to fall within the range of 2-2.5 million.

Relationship between drought and breeding numbers

The standardised anomaly index of rainfall in West Africa in each year 1966-94 and the numbers of nests in Britain in the following seasons 1967-95 (Fig. 1) showed significant positive correlation ($r_s = 0.38$, $n = 29$, $P < 0.025$).

Discussion

The breeding season diet of birds in Britain is in contrast to the vole-rich diet in, for example, the Netherlands where protection has seen sustained recolonisation in the north (B. KOKS & E. VISSER pers. comm.). The principal vole in Britain, *Microtus agrestis*, is more of a surface-dwelling animal and therefore more vulnerable to agricultural practices than the continental, burrowing *M. arvalis*. Hence there may be food problems for breeding Montagu's in Britain, although fledging rates appear to be comparable to those on mainland Europe. Data from the Norfolk Bird & Mammal Report over the period 1988-1999 show a mean fledging rate of 2.19 young from each started nest, similar to rates elsewhere in Europe (see CLARKE 1996a). Nesting in wide expanses of arable farmland not frequented by bird watchers, the nests of some pairs are undoubtedly vulnerable to harvesting and early cuts in silage grass fields which are often used. These local factors could be important, but situated at the very edge of the range, numbers of breeding Montagu's Harriers in Britain may be particularly responsive to range-wide factors.

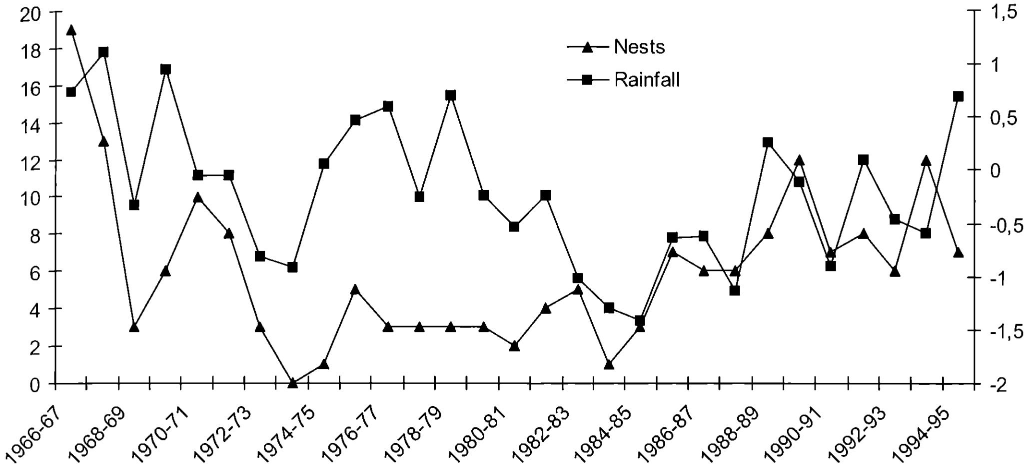

Fig. 1: Relationship between annual Western Sahel rainfall index (y-axis right) and number of Montagu's Harrier nests (y-axis left) in Britain in the following year, 1966-67 to 1994-95. – *Korrelation zwischen jährlichem Niederschlagsindex im West-Sahel (rechte Y-Achse) und der Anzahl von Wiesenweihennestern (linke Y-Achse) im darauffolgenden Jahr in Großbritannien der Jahre 1966 bis 1995.*

Prey specialisation

In the winter range, observation of harriers leaving roosts in the morning emphasised the difference in flight actions of at least the readily recognisable males of the two principal harrier species. Montagu's Harriers left at very first light, intermittently flapping gently and gliding out towards the croplands on their proportionately larger wings (NIEBOER 1973), whereas Pallid Harriers tended to leave slightly later (assessed as about five minutes) and flapped more vigorously, often at lower altitude. SCHIPPER (1977) found that Montagu's Harrier ranged further from the nest than the other species of harrier sympatric with it in western Europe, and that it obtained enough return for hunting effort from smaller prey. This appears to be due to its lighter wing-loading (NIEBOER 1973). 'Grasshoppers' were the principal prey when Montagu's Harriers roosted in their thousands in France in late summer in the nineteenth century (BARBIER MONTAULT 1838).

Analysis of the pellets collected at Velavadar revealed a polarisation between a large proportion of the harriers foraging solely for locusts (37-40 % of pellets) and a significant but lesser number of harriers foraging solely for birds (24-35 %). As the roost was of mixed harrier species and Montagu's Harriers predominated, it seems reasonable to conclude that this was further evidence of the prey niche separation between Montagu's (locusts) and Pallid Harriers (birds) that I found by observing foraging behaviour. A preference for locusts by Montagu's Harrier is further supported by the fact that locusts were far more predominant in the pellets (occurring in 97 %) from Senegal, where only Montagu's Harriers were present, and birds occurred in very few (3 %). Of those pellets from Velavadar containing a mix of prey types (28-36 %), proportionately few (5-6 %) contained a mix of locust and bird despite the fact that birds were more common than mammals or reptiles in the batch of pellets as a whole. This could indicate that hunting for locusts and birds was rarely mixed by any individual harrier.

I gained the impression, from low beating of the wings as Montagu's Harriers struck at locusts, that there is an element of flushing out of prey. Locusts clasp their legs around the cotton bush branches, lying lengthways in a very concealed position. It seems likely that the harriers can detect them by hearing when they are feeding and simply pinpoint the immediate spot to test out. In experiments on the ability of Northern Harriers to pinpoint prey solely from auditory cues, RICE (1982) played vole sounds and prompted a harrier to 'beat the vegetation with its wings, apparently attempting to flush the simulated vole' The low flight of Montagu's Harrier might therefore indicate some dependence on auditory cues. Harriers are very agile at catching prey that they flush at very close quarters – certainly, when once I was close enough to a male Montagu's striking at a locust in open grassland I saw the insect fly and the harrier surge forward and pluck it out of the air with ease well before the insect had flown a metre at grass-top height. No pursuits clear of vegetation were seen, although in Senegal, CORMIER & BAILLON (1991) saw locusts caught from within swarms or after pursuit, and SYMENS (1990) saw them both caught and eaten in flight in Saudi Arabia.

Locust consumption

The largest Senegal roost materialised for one winter only (A. Leroux verbally) in response to the largest explosion in the population of the Desert Locust in the area for 20 years, with large swarms south of Dakar. The Velavadar roost, however, has been known since the mid 1980s (S. Rooke in litt.) and has recurred each winter, indicating that the harriers rely on a stable food source there. Harrier predation on locusts is in effect an integral part of the agricultural economy around Velavadar.

What is the impact on locust population dynamics and agriculture? There is good evidence that avian predation at medium to low Orthoptera infestation levels can reduce Orthoptera densities by 30-50 % (see review in KIRK et al. 1996). At places such as Velavadar, therefore, where harriers feed on non-swarming locusts, biological control of locusts by birds could be significant. Even if locust damage were not evident at the population levels being experienced, it could become an issue were there no suppression of locust numbers by harrier predation and the population increased beyond the threshold where trade off of cost of damage exceeded cost of spraying. Instances of severe damage to crops, including cotton, are on record as caused by the similar Egyptian Locust (ANON. 1992).

Relationship between drought and breeding numbers

Correlation between Sahel drought and breeding numbers was established over a period of 29 years since the Montagu's Harrier population has been faltering in Britain. Looking back at the peak in the British population, which occurred in the 1950s (CLARKE 1996a), it is noticeable that Sahel rainfall was well above average from 1950 after a rather average performance in previous decades. After 1957, however, it was again consistently closer to average and numbers of harriers breeding in Britain soon began to falter.

In addition to the well-known crash in small passerine summer migrants in 1969, after a sudden sharp dip in Sahel rainfall in 1968, there was also a sudden low in the number of nests of Montagu's Harrier that year in Britain. An overall downward trend in the rainfall index from 1969 to 1972/1973 saw the number of Montagu's Harrier nests fall from ten in 1970 to none and temporary extinction of the species as a breeding bird in Britain in 1974. Throughout the late 1970s and early 1980s, rainfall was unpredictable and there were few Montagu's Harrier nests, with lows in both in the mid 1980s. Both rainfall and numbers of nests improved a little over the subsequent period.

A prime candidate for a confounding factor in this relationship is the effect of organochlorine pesticide and PCB contamination on breeding numbers. The low in numbers of nests occurred in the mid 1970s. However, the low in the Sparrowhawk *Accipiter nisus* population due to pesticides occurred much earlier, between 1960 and 1963 (NEWTON 1986). At the beginning of the worst period of its decline from the late 1950s to the early 1970s (CLARKE 1996a), Montagu's Harrier was first lost from East Anglian strongholds, where pesticide contamination was more likely from the predominantly arable farming. Farmland birds form the bulk of the breeding season diet there (UNDERHILL-DAY 1993, CLARKE 1996a). However, subsequent losses occurred largely in westerly and northerly regions (CLARKE 1996a), where the Sparrowhawk did not disappear. Drought on the wintering grounds could have had a major impact on the Montagu's Harriers breeding in Wales, the West Country and the north of England, although the effect of habitat changes too cannot be discounted. The more easterly-biased Marsh Harrier *C. aeruginosus* also reached a low in the early 1970s, and recovered, although initially very gradually, from that point in time with the withdrawal of organochlorine seed dressings and dispersive uses for PCBs (CLARKE 1995). In recent years the breeding population of Marsh Harrier in Britain has grown considerably. Montagu's Harrier has not shown nearly so strong a recovery.

The most readily available medium-term study data on breeding density in other west European breeding populations of Montagu's Harrier are from the marshes of western France over the period 1986 to 1992 (BUTET & LEROUX 1993). The effect of specialisation in voles as prey is also likely to be part of the equation there. BUTET & LEROUX concluded that density of Montagu's Harrier nests in their study areas was linked to vole density at the start of the breeding season. However, the lowest density recorded was in 1991, the season following a sharp drop in Sahel rainfall. This was also a vole-low year, but a vole low of similar magnitude in 1986 had not produced nearly such a pronounced crash. The exact mechanism and timing of the effect of drought on locusts and Montagu's Harrier breeding density may not be as simple as this suggests. The ways in which rain triggers locust invasions, and the differences in the life-cycles of other potential insect prey require careful analysis. However, Desert Locust swarms, although spectacular, may not be as important as more steady and widespread populations of solitary locusts and other large Orthoptera such as the Senegalese Grasshopper *Oedaleus senegalensis*. Their numbers may be governed more directly by whether it is a good year for rain-fed agriculture or not. Also, swarms, at least of Desert Locust, do not occur over much of the western Sahel after November, only in the far west, in Gambia, Senegal and Mauritania, and infrequently (STEEDMAN 1990). Within the harrier population itself, there may be further complexities such as the effect that drought has on the survival of second-calendar-year birds which over-summer in Africa.

Is the Sahel drought a temporary, normal fluctuation, taken in the long term context, or is it part of climate change to which we must be reconciled? Rainfall has in truth only been about 20 % down since the 1970s, but was rather above normal prior to that. The effect of such 'drought' on habitat and bird numbers appears to have been exacerbated by the effects of rapid growth in the human population. The concomitant vast increase in livestock (in Tsetse-free areas), firewood cutting and unsustainable agricultural practices has led to widespread degradation of natural vegetation, soil erosion and consequential expansion of the desert. The lower annual rainfalls in the more northerly of the Sahel/Sudan zones make them more susceptible to variation in that rainfall, to which the ecology of the wildlife is adapted. If recent droughts are not in the long term unusual, the difference now may be that habitat degradation by the human population has reduced the ability of the fauna and flora to bounce back.

The problems for wild birds cannot be viewed in isolation. The shortfall in resources for the human population and their livestock is the underlying problem, and this has being addressed with varying degrees of success. Some schemes touted as panaceas, such as the damming of rivers and irrigation can badly disrupt finely-tuned traditional systems, and the lessons from such mistakes need to be remembered in future action. The widespread lack of economic and industrial development in West Africa also needs addressing, as it perpetuates subsistence farming which harms the environment. The issue of whether repayment of debt owed to developed countries should be waived is pertinent to this. The effect on Montagu's Harriers is the loss of acacia savanna and wetland vegetation where they used to forage for insects, and they may be forced into shifting their distribution to the south. In common with other overwintering Palearctic raptors, Montagu's Harriers are suspected to move south through the winter with the shifting abundance of food (Thiollay in Meyburg & Chancellor 1989). This response may now be more marked and triggered earlier in the winter, forcing them to move further south into sub-optimal habitat already occupied by resident species. Some Montagu's Harriers may therefore be penetrating further down into cleared areas in the Guinea Zone and the effects on the Montagu's Harrier population could be reductions in both winter survival and breeding condition.

Harriers and the locust control issue

There is an urgent need for the potential of harriers themselves as biological control agents to be further researched and for the information to be disseminated. However, although predation by birds may have a significant effect on solitary locusts, it has long been known that it has little effect once major locust infestations have developed, such as that occurring in Senegal (Cormier & Baillon 1991), as avian predators have the capacity to remove only a small percentage of such large swarms (Moreau 1930, Smith & Popov 1953).

It is important to be aware of the programme to control locusts and other insects in Africa and India as a possible source of pesticide poisoning in Montagu's Harriers, because of the potential use of organochlorines there to protect rice, cotton and other crops. Of all the pests involved, the Desert Locust has had the highest profile from biblical times. The worst 'plague' of Desert Locusts in recent times built up to a peak in the winter of 1988-89 in the semi-arid regions of the northern half of Africa, leading to international debate about whether to use Dieldrin, an organochlorine pesticide of the type known to build up in raptors, reduce their breeding success and in high doses cause direct mortality. Such compounds were used in some areas, whereas in others the more internationally acceptable (and less powerful) organophosphorates such as fenitrothion were used. The roost of one thousand Montagu's Harriers in Senegal, the highest concentration on record in Africa, was discovered that winter (CORMIER & BAILLON 1991). There is little doubt that this aggregation of birds was caused by the local swarming of the Desert Locust. Observations were actually obtained of harriers feeding on locusts that had been killed by spraying. However, the direct mortality of harriers did not seem to be high. Only three corpses were found in the roost, although the extent to which they were searched for is not stated. Published figures show that the area sprayed to control Desert Locust was markedly reduced in the following three winters, but was stepped up in 1993, 1994 and 1995, especially in response to a locust problem in Senegal and south-east Mauritania.

Such locust plagues in the late 1980s, and the dilemma of whether to use persistent insecticides, stimulated international research into less environmentally harmful locust control technology (see KRALL et al. 1997). The avenues explored included more sophisticated delivery systems for synthetic insecticides, and the use of biological agents such as plant extracts and fungi. This has led to the first commercial releases of host-specific fungi in South Africa (ANON. 1999), which are sprayed and gradually incapacitate and then kill target locusts over a number of days. In the very short term, this seems benign to the environment and provides a glut of dying locusts susceptible to predation. As such technology is developed further and becomes more widely used, however, there must be the fear that there is danger of further loss of the prey base for Montagu's Harrier.

Abstract

In Britain, the status of Montagu's Harrier *Circus pygargus* has remained tenuous over the past few decades, whilst the Marsh Harrier *C. aeruginosus* population has grown considerably. Is breeding effort of Montagu's Harrier in Britain governed by factors in breeding or wintering areas? Breeding attempts can go unnoticed in arable farmland, where harvesting is a threat and increased use of silage grass fields for nesting has made the species vulnerable to early cutting. However, despite close protection from farming operations, and a mean fledging rate in a core area for the species in Norfolk (2.19/started nest) comparable to those on mainland Europe, numbers show no sign of increase. The prey base is currently mainly avian in Britain; the Skylark *Alauda arvensis* is the most important prey. This is in contrast to the vole-rich diet in, for example, the Netherlands where protection has seen a sustained recovery in numbers. The principal vole in Britain, *Microtus agrestis*, is a surface-dwelling animal and therefore more vulnerable to agricultural practices than the continental, burrowing *M. arvalis*.

Montagu's Harrier specialises in locusts and large grasshoppers as prey on its wintering grounds in both India and Africa. An individual harrier requires about 25 locusts per day. In the winter range, abundance of locusts and large grasshoppers is regulated by rainfall and vegetation growth. Over a period spanning 29 years, annual rainfall in the Western Sahel and numbers of Montagu's Harrier nests in Britain each following summer have shown positive correlation ($r_s = 0.38$, $n = 29$, $P < 0.025$), providing strong circumstantial evidence that a link

exists between drought and the weak breeding status of Montagu's Harrier in Britain. Do recent advances in locust control, including biological methods beginning to come on the market, add to threats to the winter prey base?

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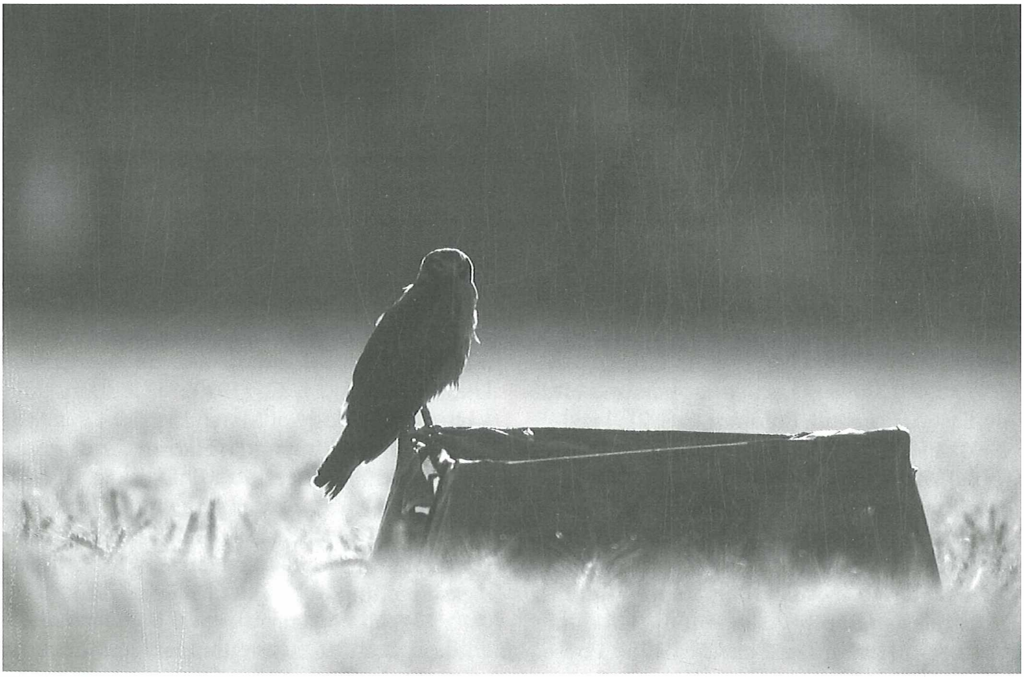

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