

Effect of abiotic factors on reproduction in the centre and periphery of breeding ranges: a comparative analysis in sympatric harriers

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Variables such as weather or other abiotic factors should have a higher influence on demographic rates in border areas than in central areas, given that climatic adaptation might be important in determining range borders. Similarly, for a given area, the relationship between weather and reproduction should be dissimilar for species which are in the centre of their breeding range and those that are near the edge. We tested this hypothesis on two sympatric ground-nesting raptors, the hen harrier *Circus cyaneus* and the Montagu's harrier *Circus pygargus* in Madrid, central Spain, where the hen harrier is at the southern edge of its breeding range in the western Palearctic and the Montagu's harrier is central in its distribution. We examined the reproductive success of both species during an 8-yr period, and looked at the influence of the most stressful abiotic factors in the study area (between-year variation in rainfall and within-year variation in temperature) on reproductive parameters.

In the hen harrier, low levels of rainfall during the breeding season had a negative influence on annual fledging success and thus on population fledgling production. The relationship between rainfall and reproduction was probably mediated through food abundance, which in Mediterranean habitat depends directly on rainfall levels. In the Montagu's harrier, no negative effect of dry seasons on productivity was found. Additionally, in the hen harrier, the proportion of eggs that did not hatch in each clutch increased with higher temperatures during the incubation period. No such relationship was found in the Montagu's harrier. We interpret these between-species differences in terms of differences of breeding range and adaptations to the average conditions existing there. Hen harriers, commonest at northern latitudes, are probably best adapted to the most typical conditions at those latitudes, and have probably not developed thermoregulatory or behavioural mechanisms to cope with drought and high temperatures in Mediterranean habitats, in contrast to Montagu's harrier. Thus hen harrier distribution might be constrained by these variables, due to lower reproductive success or higher reproductive costs. Accordingly, a logistic regression analysis of the presence or absence of both species in 289 random points throughout the western Palearctic showed that the distribution of both species was related to temperature, but the relationship was in opposite directions for the two species: hen harriers had lower probability of breeding in areas with higher temperature (as expected in a species with a more northerly distribution).

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Explaining species distribution and the limits of geographic ranges is one of the main questions in ecology (Krebs 1985). Many studies have shown correlative relationships between the distribution or abundance of a given species and certain biotic or abiotic factors (e.g. Mehlman 1997), but these do not indicate which traits are actually responsible in determining a border (Hoffmann and Blows 1994). For this it is necessary to evaluate whether demographic rates (mortality, fecundity or dispersal) change from the centre towards the edge of a species range (Randall 1982, Rogers and Randolph 1986, Caughley et al. 1988, Lawton 1993, 1996), and whether any such change is related to a decrease in habitat or environmental suitability (Brown 1984, 1985, Brown et al. 1996). Knowledge of reproductive and population parameters at the edge of species ranges may thus indicate the traits involved in limiting species distribution.

Distribution patterns may be determined by biotic factors, like predation or competition (Andrewartha and Birch 1954), or abiotic factors, such as weather (MacArthur 1958). However, the relative importance of abiotic (usually density independent) and biotic factors (usually density dependent) on population limitation is likely to change according to the position within the geographical range (Randall 1982). At the edge of an animal's distribution, abiotic factors are likely to be extremely important, as climatic conditions often represent a first step in delimiting a species range, and several studies have shown the importance of climatic adaptation in determining range borders (Root 1988, Hersteinsson and Macdonald 1992). Therefore, variables such as weather or other abiotic factors should logically have a greater influence on demographic rates in border areas than in central areas (Hoffmann and Blows 1994).

The latter hypothesis might ideally be tested through comparisons among different populations of the same species in different locations of the species' range (Rogers and Randolph 1986, Caughley et al. 1988). However, these types of studies are very costly and, in general, comparative reproductive or survival data from a number of populations of a given species in widely separated localities are relatively rare. Interspecific comparisons provide another means to test this hypothesis (Hoffmann and Blows 1994) in that, for a given area, the relationship between weather and reproduction should be dissimilar for species which are in the centre of their breeding range (and therefore probably better adapted to prevailing conditions), and for species for which this area is peripheral to their overall breeding range.

In the Iberian Peninsula, located in the southwestern part of the Palearctic, climate changes from the wetter and temperate conditions of the Eurosiberian Region in northern Europe, to the xeric and hot conditions in the southernmost areas of the Mediterranean region. In

this area, therefore, the southern limit of distribution ranges of northern (central-European) species falls within the ranges of typical peninsular species. This geographical scenario provides an ideal framework to test, through interspecific comparisons, whether the influence of weather on population limitation depends on relative position within the breeding range. For such purpose, we have chosen as models two avian species, hen harrier *Circus cyaneus* and Montagu's harrier *C. pygargus*, which are close related and have similar breeding habitat and food niches (Schipper 1973, 1978). Central Spain constitutes the southern limit of the breeding range of the hen harrier in the western palearctic, but the core of the breeding distribution of Montagu's harrier in western Europe (Hagemeijer and Blair 1997).

In this paper, we evaluate the relative effect of weather on the reproductive parameters of sympatric hen harriers and Montagu's harriers in central Spain over an 8-yr period. We predicted that weather should be more important in explaining among and/or within year variation in the reproductive parameters of hen harriers (at the edge of their breeding range) than of Montagu's harriers (more central in their breeding range). The most stressful abiotic factor(s) should negatively affect reproductive success of hen harriers, but these same factors might not necessarily affect Montagu's harriers. Finally, if the observed relationship between weather and reproductive success is not specific to the study area, it should hold at a larger geographical scale; therefore, the southern limit of breeding hen harriers could be constrained by the variable with the strongest negative effect on reproductive success.

Methods

Study area and species

The study area covers 195 km² of agricultural habitat (extensive cereal crops and ploughed fallow land), on the eastern flood plains of the river Jarama, Madrid province (Spain, 40°38'N, 3°30'W), at an altitude of 600–822 m a.s.l. The climate in central Spain is mesomediterranean (Peinado and Rivas-Martínez 1987), characterised by high spring and summer temperatures and a marked summer drought (Mooney 1981).

The hen harrier has a northern breeding range, occupying high to mid-latitudes (Cramp and Simmons 1980), from arctic to temperate climates (Harrison 1982). The breeding population in central Spain represents the southern limit to the breeding range in the western palearctic (Hagemeijer and Blair 1997). In contrast, the Montagu's harrier has overall a more southern breeding distribution, breeding south to northern Morocco and with 60°N as the northern limit (Hage-

meijer and Blair 1997). The Iberian Peninsula, together with France, constitutes the core of the breeding distribution in Europe (excluding Russia). Both species are migratory, but the hen harrier probably stays within the Iberian Peninsula in winter, whereas the Montagu's harrier winters in Africa south of the Sahara (Cramp and Simmons 1980).

Both species are similar in size, the hen harrier being slightly heavier than the Montagu's harrier (Del Hoyo et al. 1994). The length of the breeding cycle is very similar: incubation period per egg is estimated to be 28–30 d in the Montagu's harrier and 30 d in the hen harrier (Cramp and Simmons 1980). Nestlings make their first flights at ca 30–35 d in Montagu's harriers (Cramp and Simmons 1980, Arroyo 1995, unpubl.), and between 31–34 (males) and 35–38 d (females) in hen harriers (Scharf and Balfour 1971, unpubl.). Both species are ground-nesting and, in the study area, breed primarily in cereal croplands.

Reproductive data

The study was conducted from 1991 to 1998. We searched for breeding pairs of both species beginning in late March. Searching effort was strong and similar among years, and we are confident that we detected all breeding pairs each year (except 1991). Number of breeding pairs in the study area ranged between 39 and 53 Montagu's harriers, and 6–18 hen harriers. Reproductive values from 1991 for hen harrier were excluded from the analyses due to the small sample size (2 nests) and partial data, which arose from deficiencies in searching effort that year. Therefore, we included 7-yr data for hen harrier, and 8-yr data for Montagu's harrier. We considered the number of breeding pairs (and thus density) each year, as the number of pairs that produced a clutch. We visited nests frequently (between 2 and 5 visits per nest) to determine reproductive parameters, including laying date, clutch size, hatching success (number of chicks hatched/number of eggs laid), fledging success (number of chicks fledged/number of chicks hatched), productivity (number of chicks fledged). Not all data were obtained for every nest, so sample sizes vary slightly among variables analysed. Nests destroyed intentionally by humans ($n = 1$ in hen harriers, and $n = 5$ in Montagu's harrier, all years pooled) were excluded from the analyses. Additionally, eight hen harrier nestlings from six different nests, and 51 Montagu's harrier nestlings in 38 nests (all years pooled) died due to cereal harvesting activities. However, we considered them as fledged for the analyses because they were > 20 d old and in good condition (mass) for their age. In Madrid, nestlings over that age have never been found to die naturally before fledging except when their mass was extremely low

(Arroyo and García unpubl.). Laying date was obtained directly (if visits had taken place when clutch size was not completed) or estimated through nestling measurements (Saunders and Hansen 1989, Arroyo 1995).

Weather data

We analysed the effect of weather on reproduction at two different time scales (Allen and Star 1982, Rotenberry and Wiens 1991): between years (large-scale weather variation), and within years (short-scale weather variation). We considered rainfall to be a more important determinant of large-scale weather variation, as annual variation in precipitation is related to habitat productivity in Mediterranean habitats (Herrera 1980, Soriguer 1981, Lucio 1990, Suárez et al. 1992, Tellería 1996, Borralho et al. 1998). In contrast, for short-scale weather variation, we considered that day-to-day differences in temperature (a stressful abiotic factor in Mediterranean climates) are more likely to affect time and energy budgets of breeding pairs and their offspring than are day-to-day differences in rainfall. We therefore chose maximum daily temperature as an indicator of short-term weather conditions.

The Spanish Meteorological Inst. provided daily rainfall data from 1 March to 31 July (1991–1997) from the weather station of Fuente El Saz del Jarama, located in the middle of the study area. From these data we calculated the total amount of rainfall from March to July each year. Daily temperature data, which were not available from the above-mentioned station, were obtained from the meteorological station of Talamanca del Jarama, located 7 km to the north of Fuente el Saz, in the northern edge of the study area. To describe short-term (within-season) weather variation, we divided the reproductive cycle of each pair into three periods: pre-laying period (30 d before the onset of laying), incubation period (onset of laying to 30 d later), and nestling period (hatching to 31 d later). Periods for both species were estimated similarly. Average maximum temperatures during each period were calculated separately for each pair, according to their particular laying date.

Geographical distribution data

From a total of 300 random points generated by IDRISI (Geographic Information System program) throughout the western palearctic, 289 random points were chosen after removing points that were in lakes or other large water bodies. For each random point, we determined the presence or absence of both

Montagu's and hen harriers as breeding species; it was considered that the species were "present" if they were described as such in the 50 × 50 km quadrat including the random point in the distribution maps published in Hagemeyer and Blair (1997). Additionally, an index of temperature was estimated for each random point from NOAA-AVHRR (Advanced Very High Resolution Radiometer) weather imagery. Data from the AVHRR carried on board the NOAA polar-orbiting satellites are widely used for environmental analysis at large scales (see Fjeldsø et al. 1997). Data were available from 1985 to 1991 (except 1988). AVHRR senses in five spectral bands, 1: 0.58–0.68 µm, 2: 0.73–1.10 µm, 3: 3.55–3.93 µm, 4: 10.30–11.30 µm and 5: 11.50–12.00 µm. Calibrated temperature (Ts) is a geophysical parameter which can be extracted from AVHRR data quite precisely by the use of channels 4 and 5. Monthly surface temperature data are presented, and we calculated the average for the spring period (April–June), corresponding to the incubation and brooding period throughout the range.

Statistical analyses

Between-year effects of rainfall on annual reproductive parameters were analysed with non-parametric (Spearman) correlations. The effect of within-season weather variation on reproduction was analysed by ANCOVA analyses, using temperature in a given period (incubation or nestling) as a covariate, and year as a main factor (to control for annual differences due to variables other than weather). Variables that were percentages (hatching and fledging success) were normalised through arc-sine transformations (Zar 1984). To assess the effect of temperature during the breeding period on the distribution of breeding Montagu's and hen harriers, we used logistic regressions (CATMOD procedure; Anon. 1988), with breeding probability (presence or absence) as the dependent variable. As latitude and temperature are correlated, and to evaluate whether temperature had an effect independently of latitude, we also included latitude and the interaction latitude × temperature in the original (complete) model. We looked for the most parsimonious significant explanatory model, eliminating sequentially each variable or interaction, starting by the least significant. For each effect removed, the increase in deviance in the new model was tested with a χ^2 test, the χ^2 value and degree of freedom being obtained by the difference between the deviances and the degrees of freedom of the two models to be compared. This operation was conducted until the increase in deviance was no longer significant. All means are expressed ± SD. Analyses were made with STATISTICA 4.5 and SAS 6.03 (Anon. 1988) packages.

Results

Weather variation in the study area

Average total rainfall during the breeding season (March–July) in the years of the study was 137 ± 34 mm, a figure similar to that found in 1961–1990 (148 mm, Instituto Nacional de Meteorología). Total annual rainfall ranged between 97.3 and 187.5 mm, with 1992 and 1993 being the wettest years, immediately followed by the driest years (1994 and 1995) (Table 1). Rainfall did not have a clear within-year pattern: this variable was highly unstable and unpredictable, both between and within years.

Maximum temperatures increased more or less regularly with date throughout the breeding season, from an average of $19.0 \pm 4.6^\circ\text{C}$ in March to $34.1 \pm 4.2^\circ\text{C}$ in July (all years pooled). There were, however, significant between-year differences in temperature (ANCOVA, $F_{1,1215} = 1819$, $p < 0.0001$ for date, $F_{7,1215} = 11.3$, $p < 0.0001$ for year). Overall, rainfall and temperature were inversely related, but the relationship was not significant (Table 1, $r_s = -0.59$, $n = 8$, $p = 0.12$).

Annual reproductive variables and rainfall

Average annual reproductive parameters in the study area for hen harriers and Montagu's harriers are presented in Table 2 and Table 3, respectively. In the Montagu's harrier, all considered parameters except fledging success varied significantly among years (Table 3). In contrast, no breeding parameter considered varied significantly among years in the hen harrier (Table 2), possibly due to the fact that sample sizes were small and standard deviations each year were large. Nevertheless, annual variation in fledging success in the hen harrier was positively (and significantly) related to total rainfall in the breeding period (Table 4, Fig. 1). As a consequence, annual mean productivity was also significantly related to total rainfall (Table 4, Fig. 2). No other reproductive variable (breeding density, clutch size, hatching success) was significantly related to annual variation in rainfall (Table 4). Thus between-year differences in reproductive success in the

Table 1. Annual weather parameters during the breeding season (March–July) in the study area in different years.

Year	Total rainfall (mm)	Average maximum temperature ($^\circ\text{C}$)
1991	118.4	24.24
1992	172.2	24.46
1993	187.5	24.42
1994	97.3	26.64
1995	99.9	27.77
1996	143.3	25.07
1997	163.5	25.09
1998	114.2	24.75

Table 2. Annual breeding parameters of hen harriers in the study area. All means \pm SD, sample size in brackets. CV = coefficient of variation of annual values = $100 \times \text{SD}/\text{mean}$. F and p values for the ANOVA of among-year variation. ANOVA of percentage variables (hatching success, fledging success) with transformed data.

	No. of breeding pairs	Clutch size	Hatching success	Fledging success	Productivity (fledglings/pair)
1992	7	4.42 \pm 1.27 (7)	0.80 \pm 0.19 (6)	0.75 \pm 0.43 (5)	3.0 \pm 2.12 (5)
1993	6	5.25 \pm 0.96 (4)	0.86 \pm 0.13 (3)	0.83 \pm 0.29 (3)	2.83 \pm 1.60 (6)
1994	11	4.37 \pm 1.06 (8)	0.74 \pm 0.35 (8)	0.60 \pm 0.34 (7)	1.88 \pm 1.53 (9)
1995	9	4.66 \pm 0.58 (3)	0.93 \pm 0.11 (3)	0.65 \pm 0.40 (3)	2.33 \pm 1.50 (6)
1996	11	4.75 \pm 1.48 (8)	0.70 \pm 0.44 (8)	0.65 \pm 0.13 (6)	2.54 \pm 1.57 (11)
1997	18	4.87 \pm 0.88 (16)	0.76 \pm 0.24 (16)	0.76 \pm 0.35 (15)	2.94 \pm 1.64 (17)
1998	10	4.75 \pm 0.88 (8)	0.89 \pm 0.19 (7)	0.54 \pm 0.30 (7)	2.25 \pm 1.83 (8)
CV	38%	22%	10%	14%	16%
F		0.45	0.54	0.51	0.48
p		0.84	0.77	0.79	0.82

Table 3. Annual breeding parameters of Montagu's harriers in the study area. All means \pm SD, sample size in brackets. CV = coefficient of variation of annual values = $100 \times \text{SD}/\text{mean}$. F and p values for the ANOVA of among-year variation. ANOVA of percentage variables (hatching success, fledging success) with transformed data.

	No. of breeding pairs	Clutch size	Hatching success	Fledging success	Productivity (fledglings/pair)
1991	39	3.67 \pm 0.71 (30)	0.83 \pm 0.28 (30)	0.74 \pm 0.42 (26)	1.88 \pm 1.75 (34)
1992	48	3.74 \pm 0.76 (38)	0.59 \pm 0.46 (38)	0.70 \pm 0.37 (26)	1.41 \pm 1.47 (46)
1993	49	4.18 \pm 0.76 (39)	0.84 \pm 0.29 (39)	0.74 \pm 0.30 (36)	2.44 \pm 1.49 (48)
1994	36	4.34 \pm 0.86 (29)	0.79 \pm 0.28 (28)	0.70 \pm 0.39 (26)	2.37 \pm 1.63 (35)
1995	51	4.00 \pm 0.81 (44)	0.81 \pm 0.29 (41)	0.69 \pm 0.35 (37)	2.13 \pm 1.58 (46)
1996	53	3.56 \pm 1.01 (32)	0.78 \pm 0.34 (30)	0.67 \pm 0.34 (28)	1.79 \pm 1.45 (52)
1997	45	4.11 \pm 0.69 (27)	0.87 \pm 0.20 (27)	0.71 \pm 0.36 (27)	2.39 \pm 1.48 (43)
1998	39	3.73 \pm 1.07 (22)	0.91 \pm 0.23 (21)	0.75 \pm 0.29 (18)	2.50 \pm 1.24 (26)
CV	17%	7%	12%	4%	18%
F		3.55	3.11	0.19	2.74
p		0.001	0.004	0.98	0.009

hen harrier were related to the fact that wetter (i.e. higher primary and secondary productivity) years significantly increased nestling survival. In the Montagu's harrier, in contrast, annual variations in reproductive parameters were not significantly related to variations in rainfall (Table 4).

Within-season weather variation and reproduction

Due to the variation in weather throughout the season, different individuals nesting during the same year, but at different dates, also experienced a wide range of temperatures in each given reproductive period (see large standard deviation bars in Fig. 3).

In the hen harrier, maximum temperature during the incubation period had a negative influence on hatching success (Table 5): the proportion of eggs that did not hatch increased with higher temperatures during the incubation period. Additionally, there was a significant effect of temperature in the incubation period, but not during the nestling period, on fledging success (Table 5). In the Montagu's harrier no significant relationship was found between temperature and egg survival, and a trend was only weakly suggested between temperature in the incubation period and chick survival (Table 5).

Overall, Montagu's harriers were exposed on average to higher maximum temperatures in both the incubation and the nestling periods, although differences were small (1.05°C and 2.68°C, respectively).

Temperature and geographical distributions of Montagu's and hen harriers

Table 6 presents the results of the logistic regression analyses performed to investigate the probability of finding hen or Montagu's harriers as a breeding

Table 4. Spearman correlation analyses between total rainfall throughout the breeding season (March–July), and average annual breeding parameters in the hen harrier and the Montagu's harrier in Madrid.

Reproductive variables	Hen harrier		Montagu's harrier	
	r_s	p	r_s	p
No. of breeding pairs	-0.53	0.21	0.22	0.59
Clutch size	0.63	0.13	-0.14	0.73
Hatching success	0.00	1.00	0.07	0.86
Fledging success	0.83	0.02	0.37	0.36
Productivity	0.86	0.01	-0.29	0.78

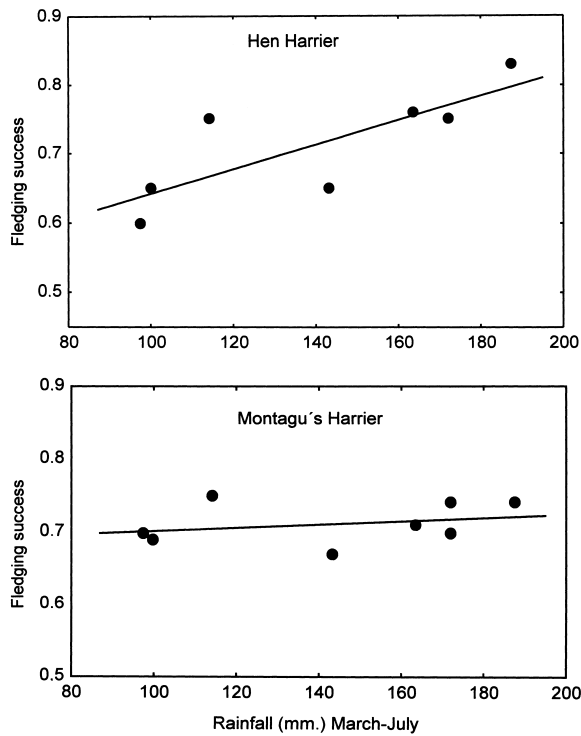


Fig. 1. Relationship between total rainfall during the breeding season (March–July) and average annual fledging success (number of chicks fledged/number of chicks hatched) of hen harriers (above) and Montagu's harriers (below) in Madrid, Spain. Sample sizes (number of nests each year) in Tables 2 and 3.

species at random points. Both variables and their interaction had a significant explanatory effect in both species (Table 6). The distribution of both species was significantly related to temperature (Fig. 4), but the relationship was in opposite directions for the two species: the probability of breeding decreased with increasing temperature in hen harrier, but it increased in Montagu's harrier (Fig. 4).

Discussion

The results of this study confirmed the prediction that abiotic factors might be important in explaining both between-year and within-year variation in the reproductive performance of a species in the periphery of its range (hen harrier in Madrid), but less important for a species in the centre of its range (Montagu's harrier). Stressful abiotic factors, which in our study area were low rainfall and high temperatures, negatively affected reproductive success of hen harriers at different temporal scales.

Annual variation in hen harrier nestling survival depended strongly on rainfall levels during the breed-

ing season, whereas no such relationship was observed in Montagu's harriers. As a result, population productivity in hen harriers was lower in drier years. The relationship between rainfall and productivity was probably related to food abundance, as documented in a wide range of other birds (Newton 1998). In Mediterranean and dry climates, such as in our study area, primary and secondary productivity are directly related to rainfall levels: with high rainfall increasing grass biomass and the abundance of insects, passerines and gamebirds (Herrera 1980, Soriguer 1981, Lucio 1990, Suárez et al. 1992, Tellería 1996, Borralho et al. 1998), all of which form part of the diet of hen harriers (García and Arroyo unpubl.). The fact that productivity of Montagu's harriers, which also feed on those prey (Arroyo 1997), was not dependent on rainfall, suggests the existence of other factors not contemplated in this study. A potential explanation is that there exist between-species differences in foraging behaviour: Montagu's harriers might be better able than hen harriers to catch prey or to switch to alternative prey, when main prey are scarce (García and Arroyo unpubl.). Alternatively, populations at the centre of their breeding range might be

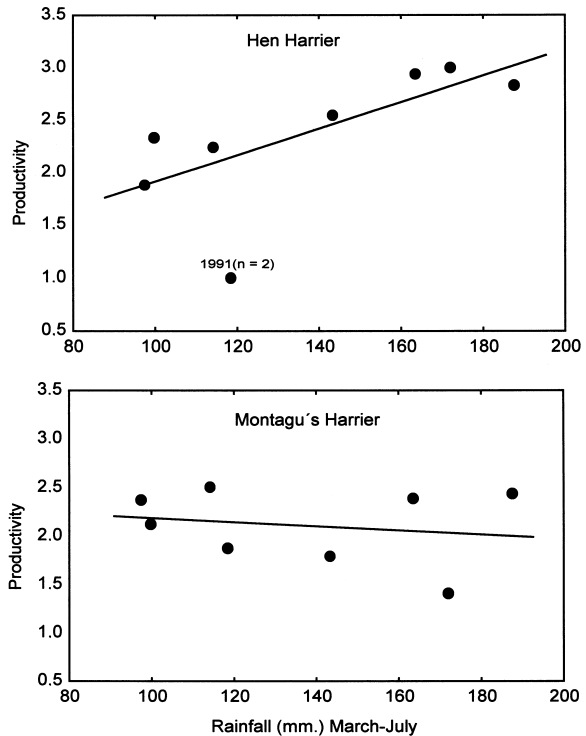


Fig. 2. Relationship between total rainfall during the breeding season (March–July) and average annual productivity (number of chicks fledged/pair) of hen harriers (above) and Montagu's harriers (below) in Madrid, Spain. Sample sizes (number of nests each year) in Tables 2 and 3. Average productivity of hen harriers in 1991 based on two nests.

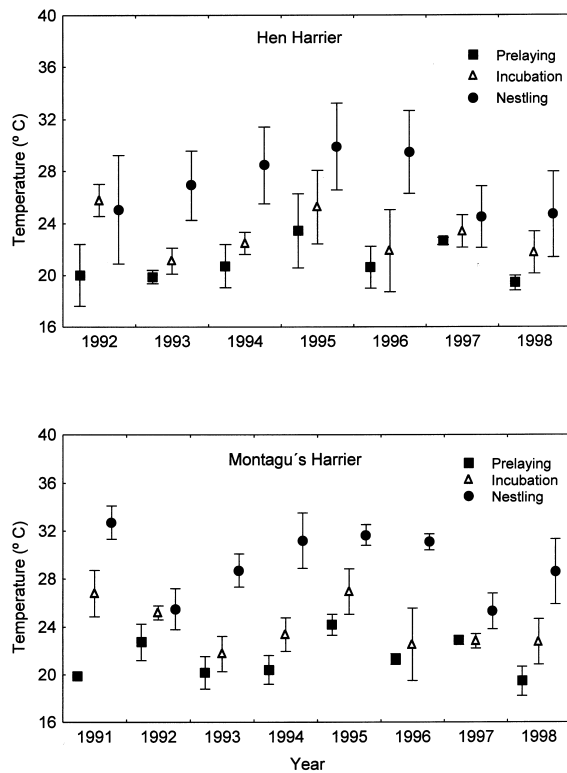


Fig. 3. Average (\pm SD) maximum temperatures experienced by breeding hen harrier (above) and Montagu's harrier (below) pairs in each of the periods of the breeding cycle in Madrid, Spain. Sample sizes (number of pairs) in Tables 2 and 3. Note the large standard deviations showing the different conditions experienced by different individual pairs.

more affected by density-dependent regulating factors than density-independent factors (such as weather) (Randall 1982). Thus, the effect of rainfall on reproductive parameters in the Montagu's harriers in Madrid might be masked by density-dependent factors, although we could not test for the latter.

In any case, the main conclusion is that annual productivity of hen harriers in the study area, at the edge of their breeding range, was related to an abiotic unpredictable variable, namely rainfall. The implications of this result on local population viability might be important. When population size is small and highly variable between years, such hen harriers

Table 6. Results of the logistic regression analyses (CAT-MOD procedure, maximum likelihood analysis, Anon. 1988) for the variables affecting the probability of presence/absence of Montagu's harriers (a) and hen harriers (b) as breeding species throughout 289 random points in Western Palearctic, according to temperature, latitude, and their interaction. Temp = average temperature index for April–June obtained from NOAA-AVHRR weather imagery. Lat = latitude (decimal degrees).

Source	DF	χ^2	p
(a) Lat	1	30.35	0.0001
Temp	1	19.74	0.0001
Lat \times Temp	1	25.34	0.0001
Likelihood ratio	283	296.91	0.27
(b) Lat	1	3.44	0.064
Temp	1	9.15	0.0025
Lat \times Temp	1	5.03	0.025
Likelihood ratio	283	317.01	0.08

in our study area, local extinction probability is relatively high (Pimm et al. 1988, Lesica and Allendorf 1995), particularly when productivity depends on an unpredictable variable. Prolonged droughts may affect negatively many species through reduced food availability (Newton 1998). Frequently, such factors act in a density-independent way, and may affect a large proportion of the population, and after a long drought period population decrease might be irreversible (examples in Newton 1998). Alternatively, after a number of rainy years, increased productivity may cause a substantial population increase, which will influence dispersal. At the edge of the geographic range, such phenomena are common, and the geographic limits of the species may retract or expand, according to changes in climatic conditions.

Adaptation and reproduction in marginal populations

As well as finding differences between the two species related to large-scale weather variation, we also found differences related to short-scale weather variation. High temperatures in the incubation period reduced egg survival in the hen harrier, but not in the Montagu's harrier. We interpret the negative effect of heat

Table 5. Results of the analysis of covariance (random 1-way ANCOVA) of year (factor) and maximum temperatures (T^{\max} , covariates) on egg and nestling survival in the hen harrier and the Montagu's harrier.

Variables	Hen harrier		Montagu's harrier	
Hatching success				
Year	$F_{6,44} = 1.76$	$p = 0.13$	$F_{7,230} = 2.17$	$p = 0.038$
Incubation T^{\max}	$t_{44} = -5.60$	$p < 0.0001$	$t_{230} = -0.45$	$p = 0.65$
Fledging success				
Year	$F_{6,38} = 1.14$	$p = 0.36$	$F_{7,209} = 0.72$	$p = 0.65$
Incubation T^{\max}	$t_{38} = -2.03$	$p = 0.05$	$t_{209} = -1.79$	$p = 0.08$
Nestling T^{\max}	$t_{38} = -0.38$	$p = 0.71$	$t_{38} = -1.03$	$p = 0.30$

on hen harrier hatching success as a consequence of the lack of adjustment of this species to the high temperatures of the study area. The range of endurable temperatures over optimal incubation temperature may be strongly limited, and hyperthermia is more harmful to the developing embryo than is hypothermia (Webb 1987). The fact that harriers nest on the ground likely exacerbates the potential harmful effect of high environmental temperatures on egg viability, as nests are less sheltered than those of hole-nesting species (Elkins 1983). Ground-nesting birds in hot environments have to employ behavioural and physiological mechanisms to prevent overheating of their eggs, and attentive behaviour at the nest is particularly important for maintenance of egg temperatures below lethal levels in these environments (Grant 1982, Ward 1990). If temperatures are too high, even short exposures to very strong heat may reduce embryo survival (Wink et al. 1982). In both species, eggs are exposed to ambient temperatures several times each day while females are feeding. However, feeding absences from the nest in the incubation period in both species were similar (1–23 min, $n = 39$ in Montagu's harrier and 2–27 min, $n = 20$ in hen harrier, Garcia unpubl.), and the range of temperatures experienced during the incubation period were also similar. Thus, the fact that Montagu's harriers did not suffer from within-season weather variations in relation to hatching success, suggests that this species is better adapted to the conditions in central Spain, given that this area is part of the main breeding range, where the bird may have developed mechanisms to avoid overheating of the eggs. Interestingly, the relationship between weather and reproduction of these same two species in The Netherlands (a northern area of the breeding distribution for Montagu's

harrier and a central area for the hen harrier) was opposite to what we found in this study (Schipper 1978): Montagu's harrier fledging success was significantly (and negatively) influenced by rainfall, which was thought to reduce the number of prey supplied per day, and to chill unprotected nestlings. In contrast, no effect was found in The Netherlands between rainfall and hen harrier reproduction, suggesting that hen harriers are better able to cope with wet and cool climates, typical of those found in the main range of this species (Schipper 1978). Bird species are usually adapted to the average weather conditions found in the main geographical range (Brown 1984). In cold areas, thermoregulatory or behavioral mechanisms may develop to resist low temperatures (Wink et al. 1980), while in hot areas other mechanisms may develop to cope with heat and insulation (Dawson and Bennett 1973, Kendeigh and Blem 1974, Weathers 1979, Wasser 1986).

The lack of adaptation to the conditions found at the edge of the distribution range may have important effects, reducing reproductive success or other demographic variables, or increasing reproductive costs and thus limiting the distribution of a species. This hypothesis is supported by the observed relationship between harrier distribution and temperature. The results of presence/absence of both species in random points through Europe suggest that the reduced productivity in adverse weather conditions might hold through a wider geographical scale, and that the scarceness of hen harrier as a breeding species in southern latitudes might be at least partly explained by temperature alone. The abundance of a species depends on the existence of suitable conditions for breeding within the geographical range (Hanski 1982). In our example, suitability of breeding conditions for hen harriers decreases with increasing temperature, so this factor may limit the species distribution.

Most studies which state that temperature (and thus energy constraints) influence distribution limits, are only based on presence or abundance data (e.g. Root 1988), which are easier to obtain than demographic data. However, only data on demographic rates may reveal the mechanisms involved in limiting distribution. The results presented here support existing theories on the importance of weather on populations at the edge of their range, not only on species' abundance and distribution, but on their reproductive success. They support the hypothesis that abiotic factors have a stronger influence on population limitation in marginal areas than in central areas, through an effect on demographic parameters, and that range borders may be explained by the lack of adaptation to conditions found at edge areas.

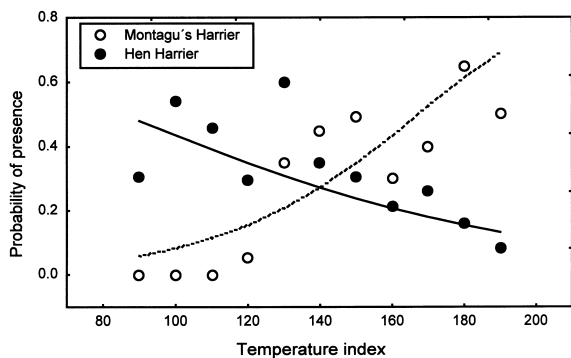


Fig. 4. Observed (dots) and predicted (lines) probability of presence of hen and Montagu's harrier according to the estimate of temperature taken from NOAA-AVHRR satellites. Predicted values are calculated with the following equations: $\ln(PB/[1 - PB]) = 1.54 - 0.018 \times \text{Temp}$ (hen harrier); and $\ln(PB/[1 - PB]) = -6.02 + 0.036 \times \text{Temp}$ (Montagu's harrier), where PB is probability of breeding, and Temp is average temperature.

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