Breeding biology of the Red Kite *Milvus milvus* in Corsica

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The breeding biology of the Red Kite *Milvus milvus* is still little known in the southern part of its range (Mediterranean), despite recent conservation concerns and major declines in most insular populations (Sicily, Sardinia and Balearics). We report here on the breeding biology of the Red Kite in Corsica in 1996–99 and on recent population trends there. In a 42-km^2 study area located in the northwest of the island (Balagne region), breeding density was locally high (1.17–1.78 breeding pairs/km^2). Breeding dispersion ranged from loosely colonial to dispersed, with average nearest-neighbour distance of 444 ± 316 m (range 50–2000) (all data as means ± sd). Kites established breeding territories in January–February, and 92.4% of territorial pairs laid a clutch (*n* = 238). Laying took place between February and May (mean lay date: 27 March ± 16 days, *n* = 147). Clutch size averaged 2.44 ± 0.71 (1–5 eggs, *n* = 96), hatching success 66.9% and fledging success 78.6%. Productivity averaged 1.33 ± 0.88 young per breeding attempt (*n* = 221) and 1.65 ± 0.65 young per successful breeding attempt (*n* = 173). Overall breeding success was 51.4 ± 38.0% (*n* = 88). We describe the growth of young (wing, weight, tarsus and bill) and show a marked seasonal decline in clutch size and breeding performance, with pairs laying earlier producing larger clutches and being more successful than later breeding pairs. Unlike most other insular Mediterranean Red Kite populations that have recently declined, the breeding population in the northwest of Corsica, which accounts for *c.* 25% of the whole island population, increased from 25 to 35 pairs in 1989 to a maximum of 80–90 pairs in 1997. This increase was probably related to the lack of persecution and a local increase in abundance of Rabbits *Oryctolagus cuniculus*, following their introduction in the late 1970s, which provided an important feeding resource for Kites. Finally, we compare our results with those from other Red Kite populations studied in Europe. We found that there is a latitudinal gradient in laying date and productivity across Western Europe populations, but no evidence of an insular syndrome in the Corsican population.

The genus *Milvus* includes two main species of kites, the Black Kite *Milvus migrans* and Red Kite *Milvus milvus*, with the Cape Verde Kite *Milvus* (*milvus*) *fasciicauda* and Yellow-billed Kite *Milvus* (*migrans*) *parasitus* sometimes being considered as full species (see Hille 1998, Sangster *et al.* 2003, Johnson *et al.* 2005). Both Black and Red Kites are opportunistic raptors of open habitats (although they usually need fragmented forests and trees for breeding), which means that they favour extensive agricultural

habitats where they forage and scavenge a wide variety of foods (Carter 2001, Cramp & Simmons 1980, Sergio *et al.* 2003). The Black Kite is widely distributed over Africa and Eurasia and is probably the most abundant raptor in the world (Ferguson-Lees & Christie 2001), whereas the Red Kite is endemic to the western Palaearctic (distributed over only 1.8 million km^2), with a much smaller and declining world population. Red Kite population estimates vary from 10 800–12 500 pairs with probably more than 100 000 individuals (Ferguson-Lees & Christie 2001) to 19 000–25 000 pairs (BirdLife International 2004) and most recently 25 000–29 000 pairs (Gensbol

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2005). The species is breeding in 24 countries, but has disappeared from seven in the 20th century. It is very rare in North Africa (few breeding pairs remain in Morocco; Viñuela 1996) and in the Middle East. Its main population strongholds are found in Germany, Spain and France, which host about 85% of the world population. Across most of its breeding range, the species has been declining in recent years, and especially so in the three countries that hold the bulk of the world population: *c.* 25% decline in Germany (Mammen 2000), 10–15% decline in France (Thiollay & Bretagnolle 2004) and 30–50% decline in Spain (Viñuela *et al.* 1999). Declines have been attributed mainly to habitat degradation and intensification, and to illegal killing through persecution and poisoning (e.g. Villafuerte *et al.* 1998, Viñuela *et al.* 1999, Carter 2001, Wotton *et al.* 2002). Because of the recent population declines in its main population strongholds and in the Mediterranean (Viñuela *et al.* 1999), the Red Kite is now considered as a declining species (BirdLife International 2004). However, some breeding populations have been increasing, for instance in Sweden and in Switzerland (Evans & Pienkowski 1991), and in the UK where the species was re-introduced in England and Scotland (Wotton *et al.* 2002, Carter & Newbery 2004).

Although it is restricted to the Western Palaearctic with an unfavourable conservation status, recent and detailed published material on the breeding biology of the Red Kite is surprisingly scanty (Carter 2001, Ortlieb 1980, Evans & Pienkowski 1991). We particularly lack detailed comparative data from most southern and Mediterranean populations (Patrimonio 1990, Sergio *et al.* 2005). For instance, Red Kites breed on all the major islands of the western Mediterranean: on four of these (Sicily, Sardinia and Menorca and Mallorca), Red Kite populations have suffered dramatic declines during the 1980s or 1990s (Cortone *et al.* 1994, De Pablo & Triay 1996, De Pablo & Pons 1999). Yet, little is known about the breeding biology of the species in Mediterranean continental and island populations (see Patrimonio 1990, Thibault *et al.* 1992). Our aims here are two-fold: first, to provide basic information on the breeding biology of Red Kites in an insular Mediterranean population. For this we provide a detailed description of the breeding biology of Red Kites in Corsica, with particular emphasis on the breeding density, recent population trends and breeding performance. Secondly, we aim to provide an extensive review of the breeding biology of the Red Kite throughout most of its range in Western Europe. By comparing our results with those from other studied populations, we investigate whether reproductive parameters vary with latitude and/or longitude (e.g. Caughley 1988), and discuss whether the Corsican population shows characteristics of a latitudinal or insular syndrome (e.g. expanded niche breadth, higher breeding densities and reduced clutch size), as found in other raptors (Thibault *et al.* 1992).

MATERIALS AND METHODS

Study area and population

In Corsica, the Red Kite is mainly sedentary and breeds from sea-level up to 1400 m, the highest density usually being found at altitudes below 600 m (Thiollay 1968, Patrimonio 1990). It is the only breeding kite species, as Black Kites are occasionally observed but do not breed in Corsica (Thibault & Bonacorsi 1999).

We studied the breeding biology of the Red Kite in the northwestern part of Corsica, in the Balagne province. This region, referred to as the 'gardens of Corsica', has been known as the main stronghold of the Red Kite since 1964 at least (Thiollay 1968). It held 25–35 breeding pairs in 1989, an estimated 25% of the whole Corsican breeding population at that time (Patrimonio 1990). Our 42-km² study area was located in the Reginu valley (Fig. 1), a coastal valley open to the sea in the north with mountain slopes on the south and east. The habitat is characterized by a mosaic of Mediterranean bush, pastures (used mainly for extensive sheep and cattle grazing), oaks and pinewoods, and olive tree plantations. Rabbits *Oryctolagus cuniculus* were introduced locally in
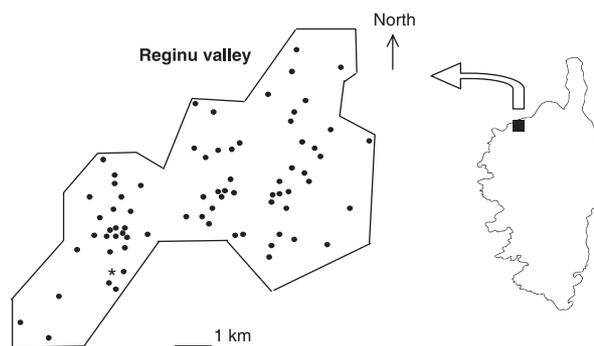

Figure 1. Location of the Reginu valley in Corsica (right) and distribution of breeding pairs (●) within the main 42-km² area in 1997 (left). The location of a main carrion-site (see Fig. 5) is indicated by the star.

the 1970s for hunting purposes, since when they have increased rapidly in numbers, providing an important food supply for breeding Kites. Kites also feed on carcasses left by local butchers and on human refuse (Patrimonio 1990).

Breeding biology

We studied the breeding biology of the Red Kite in 1996–99. Each year, breeding territories and nests were systematically searched for and visited by one of us (F.M.). A more widespread but less intensive nest search was also conducted in the neighbouring Aregnu Valley to increase sample size. Occupied breeding territories were located in January–March, when pairs that establish breeding territories are very vocal and behave conspicuously (nest-building activities, territorial interactions, courtship feeding, copulations; Mougeot 2000). We found nests by observing birds in the pre-laying period and by systematically inspecting all suitable nesting trees within an occupied breeding territory. Most nesting trees were relatively small and could be climbed to check nest contents. Each year, a sample of nests was visited regularly (at least three times during the breeding season) to monitor breeding performance.

During incubation, we recorded clutch size. Nests were visited again after hatching and later during the chick-rearing period. Chicks were individually ringed upon first nest visit. During each nest visit, we measured the following: (1) body mass (g), with an electronic balance for small chicks and with a *Pesola* for older young; (2) flattened wing length (mm), with a ruler, and (3) bill (culmen) length and (4) tarsus length (mm), with a calliper. In 1996, nests of known hatch date, visited during hatching, were re-visited regularly to study the growth of young (body mass, wing and tarsus length). Sample size included 21 young from 12 nests. These measurements were used to model the growth of young and to infer hatching date from nestling measurements. When the young were *c.* 3 weeks old, we wing-tagged them using individual patagial colour tags. The contents of nests that could not be accessed were checked from a viewpoint where possible to determine the number of young at fledging (productivity).

We thus recorded the following breeding parameters, whenever possible: number of territorial pairs; number of territorial pairs that laid (hereafter referred to as breeding pairs); laying date, which was assessed when nests were visited during laying or by backdating nestling age from body measurements; clutch size, hatching success (young hatched/egg laid) and fledging success (young fledged/young hatched); breeding success (young fledged/egg laid) and productivity (number of young fledged/breeding pair, number of young fledged/successful breeding pair and number of young fledged/territorial pair; Steenhof 1987).

We studied the attendance at breeding areas of immature Red Kites by counting the number of adult and first-year birds (aged from plumage traits; see Carter 2001) at a main feeding site. This feeding site (shown in Fig. 1) was used by local butchers to dispose of unused meat and carcasses about every 2 weeks, and it was attracting Kites from the neighbouring breeding areas. Data on post-breeding dispersal were gathered from occasional observations of wing-tagged Kites by a number of observers from the island.

Statistical analyses

We used SAS version 8.01 (SAS 2001) for all statistical analyses. We analysed data using Generalized Linear Models (GLM and Genmod procedure) or Generalized Linear Mixed Models (Mixed and Glimmix procedures) or non-linear regression models (SAS 2001). When combining data from different years in the analyses, we used mixed models with year included as a random effect to account for variation among years. Models were fitted to the data using the following error distributions and link functions: distance to nearest neighbour, laying date, breeding success, fledging success and hatching success – normal error distribution and identity link function; counts of territorial or breeding pairs, eggs, young hatched and young fledged – Poisson error distribution and Log link function (SAS 2001). Combined measurements from all nestlings were fitted to the Richards growth model (Ricklefs 1983, Zach *et al.* 1984). The use of a non-linear least-square regression procedure assumes that residuals are randomly distributed independently of chick age (Zach *et al.* 1984). The Richards general model of growth curve, with four parameters, was used because it provides a way to choose which kind of more simple model fits the data best (Zach *et al.* 1984); three models were compared (logistic, Gompertz, von Bertalanfy). The value of parameter *m* and inspection of the distribution of residuals using the Richards model (Ricklefs 1983, Zach *et al.* 1984) indicated that the Gompertz model was the most appropriate for all growth measurements, and we present only the results from this model for simplification.

We analysed longitudinal and latitudinal variation in population breeding parameters using Spearman

correlations (SAS 2001). All data are expressed as means ± sd and all tests are two-tailed.

RESULTS

Nest-sites and breeding density

During the study, 125 different active nest-sites were fully described. Most nests (84.9%) were built in oak trees (*Quercus viridis* 51.3%, *Q. suber* 19.3%, *Q. pubescens* 14.3%), but Kites used a wide range of tree species for breeding, including Olive *Olea europaea* (10.1%), Alder *Alnus cordata* (2.5%) and pine *Pinus* spp. (2.5%). Most nests were in isolated trees surrounded by Mediterranean bush (42.1%) or in small woods (37.3%), more rarely in forests (14.7%) or alongside streams (5.9%). Nesting tree height averaged 11.8 ± 4.6 m (range 6–20 m) and nest height 8.7 ± 3.7 m (range 5–18 m).

Breeding density was fairly high during the study period (1996–99), with a maximum of 75 breeding pairs within the 42-km^2 study area (Reginu valley) in 1997 (Fig. 1). In the core study area, breeding density estimates were of 1.26, 1.78, 1.17 and 1.40 pairs/km^2 in 1996, 1997, 1998 and 1999, respectively. The distance to the nearest breeding neighbour averaged 444 ± 316 m (range 50–2000 m, $n = 259$ active nest-sites), but the distribution of this variable was skewed, with the most frequent inter-nest distance being *c.* 250 m (Fig. 2). This reflected the tendency of Kites to aggregate into loose colonies (usually of 3–5, but up to 12 pairs).
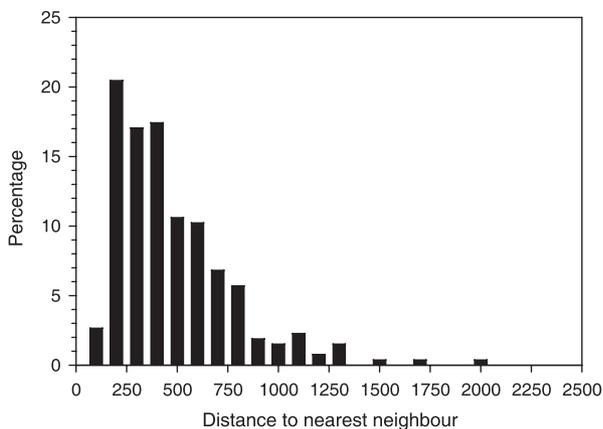
Laying date, clutch size and hatching success

Laying was spread over almost 3 months, with earliest laying recorded on 27 February and the latest on 22 May (see Fig. 3). Overall, 92.4% of territorial pairs laid a clutch ($n = 238$; yearly average range 89.6–96.8%). The mean laying date was 27 March ± 16 days ($n = 147$) and this did not vary significantly among years (GLM: $F_{3,143} = 2.30$, $P = 0.08$), although laying tended to be earlier in 1997 (23 March ± 19 days, $n = 36$) than in other years (1996: 27 March ± 14 days, $n = 45$; 1998: 28 March ± 15 days, $n = 21$; 1999: 29 March ± 14 days, $n = 45$).

Clutch size averaged 2.44 ± 0.71 eggs ($n = 96$ clutches, range 1–5) and varied significantly among years (Genmod: $F_{3,92} = 7.38$, $P < 0.001$). Clutch size was larger in 1997 (2.83 ± 0.79, $n = 35$) than in other years (1996: 2.16 ± 0.45, $n = 32$; 1998: 2.43 ± 0.76, $n = 14$; 1999: 2.13 ± 0.52, $n = 15$). A clutch of five eggs, the maximum observed, was laid in 1997. There was a marked seasonal decline in clutch size (early breeders produced larger clutches; Fig. 3), which was consistent among years (Genmod: year: $F_{3,64} = 10.70$, $P < 0.05$; laying date: $F_{1,64} =$
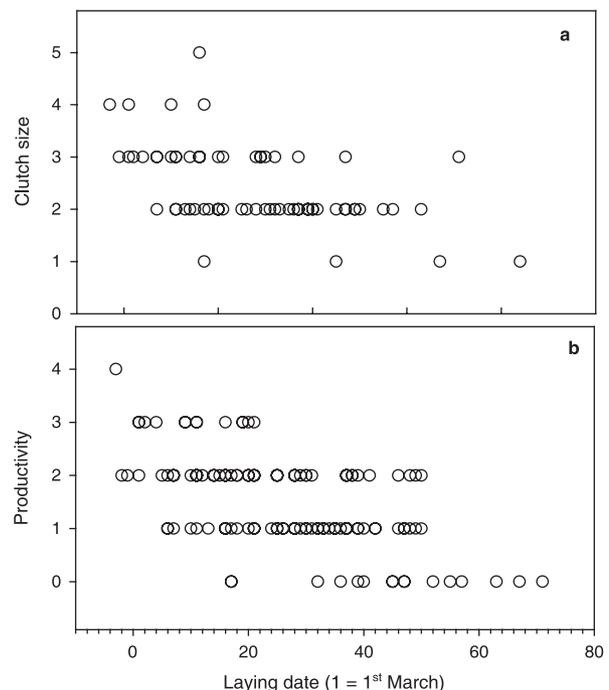

Figure 2. Frequency distribution of average distance (in m) to nearest breeding neighbour of breeding Red Kites in 1996−99. Based on 259 occupied nest-sites. The distribution was skewed, with most nests being 200−300 m from the nearest pair.

Figure 3. Variation in clutch size and productivity according to laying date (1 = 1 March). Data from 1996 to 1999 are combined.

16.69, $P < 0.001$; laying date × year interaction: $F_{3,64} = 1.58$, $P = 0.66$).

Breeding pairs hatched on average 1.77 ± 0.97 chicks ($n = 97$, range 0–4). Hatching success averaged $66.9 \pm 40.3\%$ ($n = 63$) and did not differ significantly among years (Genmod: $F_{3,61} = 0.33$, $P = 0.81$). Hatching success was negatively correlated with laying date (early breeders had a better hatching success; Genmod: $F_{1,46} = 5.45$, $P < 0.05$), and this relationship was consistent among years (non-significant laying date × year interaction: $F_{3,46} = 4.11$, $P = 0.25$).

Growth of nestlings

Figure 4 shows the growth curves for wing, tarsus and culmen length and body weight of 21 young Red Kites. To describe the growth of young Kites, the best-fitted models to the data were Gompertz growth models (see Table 1 for a summary of parameter estimates). These curves allowed us to predict the age of a young Kite from its measurements. Considering young aged between 5 and 20 days, a period when wing, tarsus and culmen growth are linear, we could derive simplified formulas:
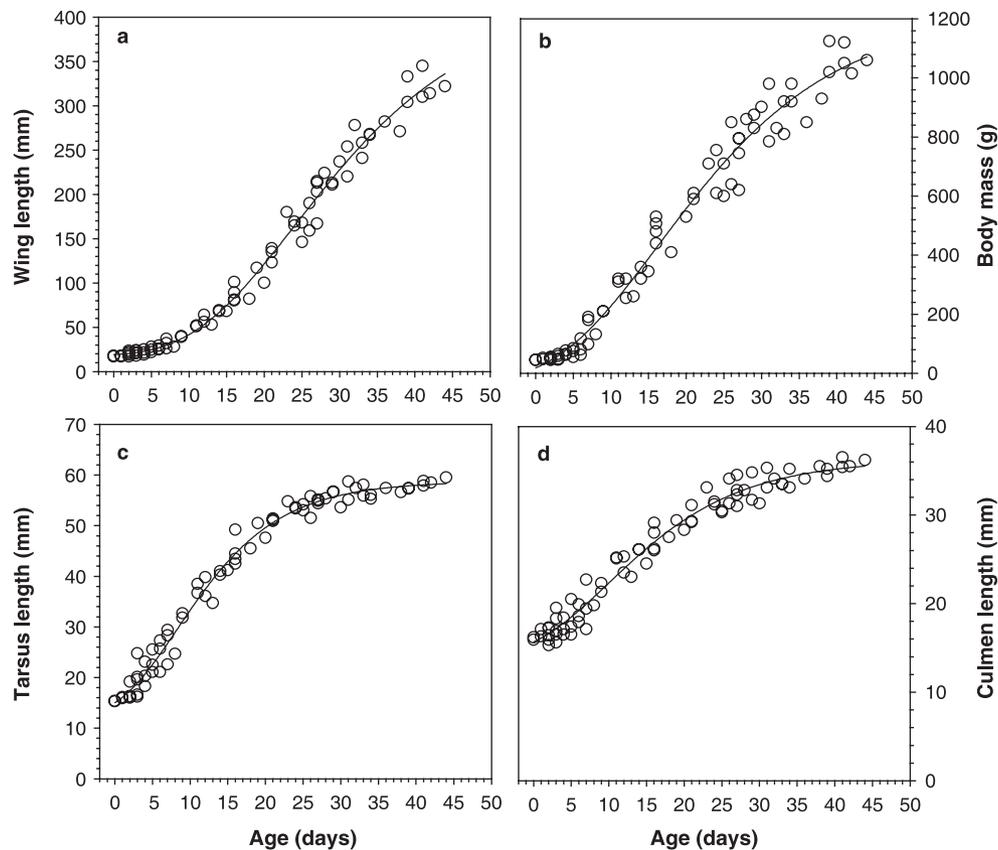

Figure 4. Growth curves of young Red Kites. (a) maximum wing length, (b) body mass, (c) tarsus length and (d) culmen length.

Table 1. Growth model parameters (mean ± se) of Red Kite nestlings ($n = 21$).

	W_0	W_{max}	X_0	b	R^2
Wing length (mm)	18.0 ± 3.6	400.4 ± 25.3	24.1 ± 0.8	13.6 ± 1.17	0.98
Body weight (g)	4.5 ± 2.3	1193.0 ± 73.1	16.7 ± 0.7	12.7 ± 1.3	0.96
Tarsus length (mm)	12.5 ± 2.0	56.2 ± 2.4	8.3 ± 0.7	7.8 ± 0.6	0.98
Culmen length (mm)	14.1 ± 1.5	36.1 ± 2.0	9.9 ± 1.2	10.1 ± 1.3	0.97

Data were fitted to a Gompertz model: $y = W_0 + W_{max} \times \exp(-\exp(-(age - X_0)/b))$. W_0 = measure at birth (day 0); W_{max} = asymptote; X_0 = age at maximum growth rate (days); b = growth rate.

$$Age \ (days) = 0.19 \times wing \ (mm) - 1.92$$
$$(F_{1,26} = 375.2, P < 0.0001, R^2 = 0.94),$$

$$Age \ (days) = 0.54 \times tarsus \ (mm) - 6.34$$
$$(F_{1,26} = 455.5, P < 0.0001, R^2 = 0.94),$$

$$Age \ (days) = 1.21 \times culmen \ (mm) - 15.86$$
$$(F_{1,26} = 231.9, P < 0.0001, R^2 = 0.90).$$

Fledging success, productivity and breeding success

Fledging success averaged $78.6 \pm 32.2\%$ ($n = 80$) and did not vary significantly among years (Genmod: $F_{3,92} = 0.51$, $P = 0.67$). Fledging success decreased with increasing laying date ($F_{1,71} = 17.23, P < 0.001$), but this relationship did not differ between years (non-significant laying date $\times$ year interaction: $F_{3,71} = 2.88, P = 0.15$).

Breeding pairs fledged on average 1.33 ± 0.88 young ($n = 221$, range 0–4). The number of young fledged per breeding pair varied significantly among years (Genmod: $F_{3,217} = 3.86, P < 0.05$): it was highest in 1997 (1.58 ± 0.99, $n = 65$), intermediate in 1996 (1.43 ± 0.87, $n = 53$), and lowest in 1998 (1.24 ± 0.74, $n = 41$) and 1999 (1.01 ± 0.76, $n = 62$). The number of young fledged per breeding pair was also related negatively to laying date within a breeding season (early breeders fledged more young: $F_{1,133} = 39.15$, $P < 0.001$; Fig. 3) and this relationship was consistent among years (non-significant laying date $\times$ year interaction: $F_{3,133} = 0.20, P = 0.90$).

The number of young fledged per successful breeding pair averaged 1.65 ± 0.65 ($n = 175$, yearly average range 1.39–1.87). The number of young fledged per territorial pair (including pairs that did not lay) was 1.23 ± 0.91 ($n = 238$, yearly average range 1.01–1.39). In all, 75% of territorial pairs ($n = 238$) successfully fledged young (yearly average range 73–80%).

Overall breeding success (young fledged per egg laid) averaged $51.44 \pm 0.38\%$ ($n = 88$), and did not differ among years (Genmod: $F_{3,84} = 0.62, P = 0.61$). Breeding success decreased with increasing laying date ($F_{1,62} = 20.62$, $P < 0.001$) in all years (non-significant laying date $\times$ year interaction: $F_{3,62} = 1.10$, $P = 0.36$). Of all breeding attempts ($n = 221$), 80.8% were successful. Successful pairs fledged on average 1.65 ± 0.65 young ($n = 173$, range 1–4).

Post-breeding dispersal

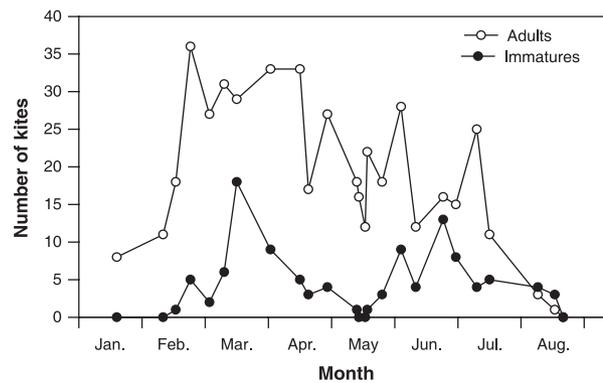Immature Kites frequently visited the study area during the breeding season (February–August).

Figure 5. Seasonal variations in the number of adult and immature Red Kites attending a carrion site for feeding (January–August 1997).

The proportion of immature relative to adult Kites observed at a main feeding site showed a bimodal pattern, with a peak in attendance by immature birds in mid March and a second peak in late June, which coincided with the period when most breeding Kites were laying or fledging their young, respectively (Fig. 5).

Red Kites tagged as juveniles in the study area were frequently observed there in subsequent years. Juvenile Kites tagged in the Reginu valley were also observed elsewhere in Corsica outside the breeding season (winter months), mainly in the centre of the island (near Corte and Poggio di Venaco: observations of five different individuals; 40–50 km from natal site), and more rarely on the east coast (Teghim pass, near Bastia: two observations of two different individuals; *c*. 40 km from the natal site) or west coast (near Galeria: one observation; 30 km from the natal site). Two Kites fledged and tagged in 1996 were observed breeding in the study area (one in 1998 and 1999, the other in 1999). Another fledgling tagged in 1997 bred in the study area in 1999. The distance between the natal and breeding sites within the study area averaged 4.5 km.

Comparative breeding data across the western Palearctic

Published data on the laying date, clutch size and productivity of Red Kites across their range in Western Europe are summarized in Table 2. Laying date increased with latitude ($R_s = 0.77$, $n = 9$, $P < 0.05$) but was not significantly related to longitude ($R_s = 0.65$, $P = 0.11$). Similarly, clutch size did not vary significantly with longitude ($R_s = 0.10$, $n = 17$, $P =$

Table 2. Comparative breeding ecology of the Red Kite in western Europe.

Country, region	Years	Laying date	References
UK, Wales	1946–96	10 April	Newton *et al.* (1996)
Luxembourg	1991–97	11 April	Kiefer (1998)
Germany, Hakel	1958–93	13 April (858)	Mammen and Stubbe (1995)
Germany, Mansfeld-Harzgeroder	–	10 April	Traue 1978, in Ortlieb (1980)
Switzerland, Broye	1995–2003	15 April	A. Aebisher & Groupe Broyard de Recherches Ornithologiques (pers. comm.)
France, Corsica	1996–99	27 March (137)	this study
Spain, Menorca	1993–98	18 March (53)	De Pablo and Pons (1999)
Spain, Mallorca	2000	15 March (7)	Muñoz and Riera (2000)
Spain, Andalucia	1988–89	7 March	Veiga and Hiraldo (1990)

Country, region	Years	Clutch size	References
Sweden	–	2.8 (30)	Rosenius 1974, in Ortlieb (1980)
UK, northern Scotland	1991–2000	3.0 (24)	in Evans *et al.* (1999) and Carter (2001)
UK, northern England	1991–95	2.9 (8)	in Evans *et al.* (1999)
UK, Wales	1946–96	2.3 (746)	Cross and Davies (1998); Newton *et al.* (1996)
Germany, Mansfeld-Harzgeroder	–	3.2 (10)	Traue 1978, in Ortlieb (1980)
Germany, Leipzig	–	2.8 (19)	Meyer 1958, in Ortlieb (1980)
Germany, Nordharz	–	2.7 (10)	Haensel & Konig 1974, in Ortlieb (1980)
Germany, Souabe	1960–69	2.1 (109)	Bauer & Bezzel 1971, in Glutz von Blotzheim *et al.* (1971)
Germany, Braunschweiger	–	2.8 (14)	Warncke 1958, in Ortlieb (1980)
Germany, Hakel	–	2.5 (37)	Stubbe 1961, in Ortlieb (1980)
Germany, Niedersachsen	–	2.8 (9)	Basecke 1938, in Ortlieb (1980)
Germany, Schwäbisch Alb	–	2.3 (–)	Rockenbauch 1967, in Ortlieb (1980)
France, East	1966	2.2 (20)	Thiollay (1967)
France, Corsica	1996–99	2.4 (96)	this study
Italy, Monti Tolfa	1981–87	1.92 (13)	Arca (1989)
Spain, Menorca	1993–98	2.7 (55)	De Pablo and Pons (1999)
Spain, Mallorca	2000	2.4 (7)	Muñoz and Riera (2000)
Spain, Andalucia (Donana)	1989–2000	2.33 (208)	Sergio *et al.* (2005)

Country, region	Years	Productivity		References
		YpBP	YpSBP	
Sweden	–	1.7 (1443)	1.98	Kjellen (1996); Evans *et al.* (1999)
Denmark	–		2.1 (54)	Jorgensen (1989)
UK, northern Scotland	1992–2003	2.1 (257)	2.4 (226)	SOC (2003)
UK, northern England	1991–95	1.9 (59)		in Evans *et al.* (1999)
UK, English Midlands	–	1.6 (31)		in Carter (2001)
UK, Wales	1946–96	0.7 (1061)		Cross and Davis (1998); Newton *et al.* (1996)
UK, Wales	1991–98	0.9 (943)		in Carter (2001)
UK, southern England	–	2.0 (292)		in Carter (2001)
Germany, Eastern	1988	1.8 (491)	2.31 (491)	Stubbe and Gedeon (1989)
Germany, Mansfeld-Harzgeroder	–		1.7 (48)	Traue 1978, in Ortlieb (1980)
Germany, Kyffhausergebirge	–		2.5 (13)	Grimm 1975, in Ortlieb (1980)
Germany, Nordharz	–		2.2 (18)	Haensel & Konig 1974, in Ortlieb (1980)
Germany, Schleswig-Holstein	1974–75	1.7 (51)		in Gensbol (2005)
Germany, Rhine valley	1974–75	2.2 (14)		in Gensbol (2005)
Germany, Brandenbourg	1974–75	2.0 (24)		in Gensbol (2005)
Germany, Hildesheim	–		2.3 (18)	Trillmich 1969, in Ortlieb (1980)
Germany, Souabe	1960–69	1.7 (109)		Bauer & Bezzel 1971, in Glutz von Blotzheim *et al.* (1971)
Germany, Saaleaue	–		2.3 (16)	Koop 1971, in Ortlieb (1980)
Germany, Hakel	1957–67		2.2 (427)	Wuttky 1968, in Ortlieb (1980)
Germany, Mecklenburg	–		2.1 (27)	Pflugbeil 1954, in Ortlieb (1980)
Germany, Schwäbisch Alb	–		2.2 (68)	Rockenbauch 1967, in Ortlieb (1980)
Switzerland, Broye	1995–2003	1.66 (368)	2.15 (284)	A. Aebisher & GBRO (pers. comm.)

Table 2. *Continued*

Country, region	Years	Productivity		References
		YpBP	YpSBP	
Belgium	1985–88		2.32 (19)	in Evans and Pienkowski (1991)
France, East	1966	1.3 (20)		Thiollay (1967)
France, Northeast	1971–82	1.4 (55)		in Mionnet (2004)
France, Champagne	1971–82	1.51	1.86	in Evans and Pienkowski (1991)
France, Alsace	1997–2001	1.9 (17)		in Thiollay and Bretagnolle (2004)
France, Corsica	1996–99	1.3 (217)	1.7 (173)	this study
Italy, North	1980s	0.60	0.77	in Evans and Pienkowski (1991)
Italy, Monti Tolfa	1981–87	0.77 (13)	1.67 (13)	Arca (1989)
Spain, Menorca	1993–98	1.6 (68)	1.9 (57)	De Pablo and Pons (1999)
Spain, Mallorca	2000	1.6 (7)	1.8 (7)	Muñoz and Riera (2000)
Spain, Andalucia (Donana)	1989–2000	0.76 (208)	1.55 (208)	Sergio *et al.* (2005)

YpBP, mean number of young fledged per breeding pair; YpSBP, mean number of young fledged per successful breeding pair.

0.71), but was positively related to latitude ($R_s = 0.55$, $P < 0.05$). Average productivity (number of young fledged per pair) was not related to longitude ($R_s = 0.15$, $n = 20$, $P = 0.60$), but increased significantly with latitude ($R_s = 0.56$, $P < 0.05$). A similar result was found using another productivity measure, the number of young fledged per successful pair (Table 2), which was also significantly, and positively, correlated with latitude ($R_s = 0.66$, $n = 16$, $P < 0.05$). The relationship between latitude and productivity was, however, similar for both productivity measures (i.e. the slopes did not differ significantly: productivity × latitude interaction: $F_{1,35} = 0.08$, $P = 0.79$). Average breeding success tended to increase with latitude, although the relationship was not significant ($R_s = 0.30$, $n = 13$, $P = 0.32$). The laying date, clutch size and productivity observed in the Corsican populations were as predicted from the overall latitudinal trends (Table 2; Fig. 6).

DISCUSSION

Breeding density and nest dispersion

In the northwest of Corsica, Red Kites breed locally at high densities (up to 1.8 pairs/km²). Such breeding densities are remarkably high compared with those found elsewhere (e.g. Cramp & Simmons 1980, Ortlieb 1980). Our study area, and more generally the region of Balagne, seems to be particularly suitable for Kites, which appear always to have bred there at relatively high densities (Thiollay 1968, Patrimonio 1990). In the 1990s, this region held approximately one-quarter of the entire Corsican population (Patrimonio
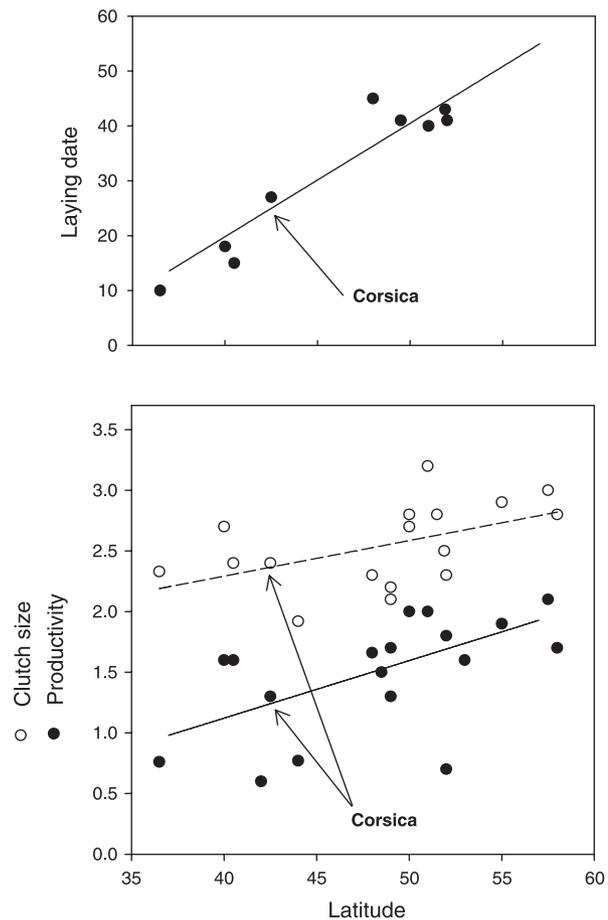

Figure 6. Relationship between latitude and laying date (top; 1 = 1 March), and between latitude and clutch size and productivity (bottom; number of young fledged per pair). Data from Table 2.

1990). In 1996–99, we found breeding densities much higher than those reported previously in the same area, and we could estimate that the population had more than doubled in less than 10 years, from *c.* 25–30 pairs in 1989 (Patrimonio 1990) to a peak of 70–90 pairs in 1997. In 2002, the Red Kite population in Corsica was estimated at 208–277 breeding pairs (Thiollay & Bretagnolle 2004), i.e. 6–8% of the total French population (*c.* 3400 pairs). At this time, the Balagne area held approximately one-third of the Corsican population.

The high breeding density found in this study was associated with a locally very abundant rabbit population. In fact, the increase in Kite density was related to a large increase in the rabbit population during the 1990s (rabbit numbers increased *c.* seven-fold between 1989 and 1996, l'Office National de la Chasse et de la Faune Sauvage unpubl. data). In 1989, rabbits accounted for 39% of the diet of Red Kites, the remainder consisting mainly of carrion and large mammal remains (Patrimonio 1990). During our study, in 1996–98, rabbits largely dominated the diet, and accounted for 67–77% of the prey remains found at nest sites (J.F. Seguin & F. Mougeot unpubl. data). The increase in the Red Kite population was therefore associated with a shift in their diet towards the rabbit, highlighting the fact that Kites clearly benefited from the increase in rabbit abundance. Other studies have shown that Kites rely on rabbit populations (e.g. Viñuela & Veiga 1992), and increases in rabbit populations have been associated with significant increases in population size of other raptor species (e.g. Sim *et al.* 2000, Viñuela & Villafuerte 2003). In 1997, the rabbits were particularly abundant in the study area, and this also coincided with the highest Red Kite breeding density, earliest laying date and largest average clutch sizes (with an exceptionally large clutch of five eggs, which has rarely been reported in the species; see Ortlieb 1980), all of which supports our argument that this prey species plays a key role for the Kites when breeding.

Breeding dispersion was not regular, but appeared typical of a loosely colonial raptor. Unlike its close relative, the Black Kite, which can breed in true colonies (Cramp & Simmons 1980), the Red Kite is a facultative colonial breeder and forms loose breeding aggregations, especially when breeding at high density (e.g. Cramp & Simmons 1980, Ortlieb 1980). In our study area, Red Kites typically formed loose colonies of 2–5 pairs. On average, breeding pairs nested about 450 m apart, but many nests were in fact only 200–300 m apart, and sometimes as close

as 50 m. Red Kites nested in both large and small trees of various species, including isolated trees. They also bred very close to occupied houses and villages. Thus, potential nest-sites were probably available in the whole of the study area, and the aggregated distribution was most probably not constrained by the availability of suitable trees. Such aggregations of Kite territories could be explained by the locally abundant food supply (Viñuela *et al.* 1994) and conspecific attraction, and by potential benefits such as collective nest defence or the sharing of public information (see Sergio & Penteriani 2005).

Breeding performance

We found that the overall breeding success and productivity of Red Kites was relatively low in Corsica, despite an apparently locally abundant food supply (rabbits). Productivity averaged 1.33 young per breeding pair (1.01–1.58, depending on years), which is lower than most studies of productivity have found elsewhere (see Table 2). A number of factors could explain this. As young Red Kites have a poorer breeding success than older birds (Evans *et al.* 1999), the low productivity could be due to the fact that the population recently increased and contains many young, inexperienced breeders. Hatching success was particularly low in the Corsican population, which could also be explained by the inexperience of these young breeders. Although food supply appeared locally to be abundant, and probably contributed to the population increase, it is also possible that density-dependent regulation of breeding success is currently taking place (e.g. Sinclair 1988, Thibault *et al.* 2001), either through competition for food or through interference with conspecifics. Lastly, Mediterranean lowlands may not be the most suitable habitat for the Red Kite (see Seoane *et al.* 2003), as also suggested by the comparative analysis of breeding parameters across the distribution range of the species (see below).

Laying was spread over a long period, as found in another Corsican raptor, the Osprey *Pandion haliaetus* (Thibault & Patrimonio 1991), but not in several others (see Thibault *et al.* 1992). Such long laying periods are unusual for raptors. We also found a marked seasonal decline in clutch size, productivity and breeding success of Red Kites. Kites breeding earlier laid larger clutches and had a better breeding success than those laying later in the season. Such seasonal declines in breeding performance have been reported in other raptors (e.g. Newton 1979,

Newton & Marquiss 1984, Thibault & Patrimonio 1991), but have seldom been documented in Red Kites (Davies & Newton 1981). This seasonal decline usually reflects either a difference in the quality of individuals breeding earlier vs. later in the season, or a degradation of environmental conditions, with poorer breeding conditions (less or lower quality food, poorer weather conditions) later in the season. In some cases, breeding performance declines despite an increase in food supply, with seasonal variation in breeding performance being mainly due to local variation in prey availability and individual variation in hunting success (see Newton & Marquiss 1984). Younger raptors typically have a poorer breeding performance than older, more experienced individuals, and also tend to breed later in the season than older birds (e.g. Newton 1979). In our study area, rabbit abundance seems to increase during the Kites' breeding season with a peak in abundance in June–July, when most Kites raised their young. This was also associated with an increase in the number of young rabbits, which appeared more frequently as prey items for Kites (our unpubl. data). It seems unlikely therefore that food abundance decreased during breeding, and thus the observed marked seasonal decline in breeding performance might best be explained by differences in the quality of individuals breeding earlier vs. later or by a breeding population mainly comprising young, inexperienced breeders.

Growth curves are highly reliable as a means of ageing young Kites. We did not distinguish between the growth of male and female nestlings, but there is very little sexual dimorphism in size in adult Red Kites (Cramp & Simmons 1980). Fledging age in Doñana, southern Spain, was 54–58 days (average 55.8) (Viñuela & Bustamante 1992). At that age in Spain, the asymptotic body mass of Red Kites was about 850 g (see Viñuela & Ferrer 1997) to *c.* 950 g (Viñuela & Bustamante 1992). Both values are lower than that found in Corsica (1190 g). This might indicate that the birds in Corsica are either larger or heavier at fledging. The latter is more likely, because the asymptotic tarsus length found in Corsica (Table 1) was similar to that found in Doñana (Viñuela & Ferrer 1997), and because there is an important local food supply in Corsica.

Philopatry and mobility

The Red Kite is believed to be sedentary in Corsica (Thibault & Bonacorsi 1999), and our results with wing-tagged fledglings supported this. Young Kites wing-tagged in the study area were regularly observed near the breeding areas, and elsewhere in the centre of the island throughout the winter. It is possible, however, that only part of the population remains in Corsica year round. We also observed immature Kites tagged as juveniles and breeding in the study area at a young age. In one instance, a first-year bird was found breeding, although it failed to produce young (see also Evans *et al.* 1998). These observations, although few, are consistent with an important degree of natal philopatry, as documented elsewhere (Newton *et al.* 1994), and a relatively young age at first breeding, as seen in the recovering UK populations (Evans *et al.* 1998, Carter 2001). Interestingly, immature Kites visited the breeding areas at two main periods, which coincided with peak laying and peak fledging times. Recent work has highlighted the possibility that birds use public information to decide where to settle to breed for the first time (Doligez *et al.* 2004). Such suggested use of public information was supported in the Black Kite (Sergio *et al.* 2005), and this might explain the pattern of attendance seen in immature Red Kites: young birds might visit breeding grounds first to assess where other Kites breed, and later during fledging time to assess where breeding was most successful.

Breeding of Red Kites in Corsica compared with continental populations

Thibault *et al.* (1992) analysed the insular pattern of Corsican raptors compared with their continental counterparts at both the community and the population levels, and concluded that only the forest species of Corsica (the two *Accipiter* and the *Buteo* species, all being represented by endemic subspecies) showed at least one sign of the insular 'syndrome', i.e. expanded niche breadth (*Buteo*), higher breeding densities (*Buteo*) and reduced clutch size (*Accipiter*). Although the Red Kite was included in their analysis, very few data were available at that time (Thibault *et al.* 1992). We found that Red Kites breed in Corsica at higher densities (up to 1.8 pairs/km²) than reported elsewhere (e.g. Cramp & Simmons 1980, Ortlieb 1980). Moreover, as suggested by Thibault *et al.* (1992), Red Kites in Corsica show a larger niche breadth (breeding up to 1400 m asl) than their continental counterparts. However, both these traits could result from the absence of Black Kites in Corsica.

Using more data from Corsica, and comparing them with a much larger data set from other European

localities, we found that average clutch size in Corsica (2.4) was close to the overall European clutch size (2.6), as it is in Menorca (2.7), another Mediterranean island, suggesting no evidence of an insular reduction of clutch size. There is, however, a noticeable latitudinal trend in breeding effort: Red Kites in northern populations lay slightly more eggs and produce more young on average than those in southern populations (see Fig. 6, lower). Moreover, lower productivity in southern populations is not only related to smaller clutches but also to slightly higher brood reduction (Fig. 6). The low productivity in Corsica might thus be explained because the Mediterranean habitats and climate are not the most suitable for this species, which has the bulk of its population further north, in continental Europe, rather than being a consequence of an insular syndrome. Productivity data from Sardinia or Sicily may help to resolve this issue. The Red Kite, although reported to breed over a wide range of climate and landscapes (Seoane *et al.* 2003), shows a more restricted breeding range in terms of latitude than many other European raptors, including the Black Kite. The latitudinal trend in clutch size and productivity might also reflect a trade-off between survival and breeding, rather than habitat suitability. Red Kite populations in the south are mainly sedentary, and might survive better than migratory populations. If survival is improved, breeding effort might not need to be as high as further north to maintain populations.

Red Kite conservation and the importance of Mediterranean populations

All Mediterranean Red Kite populations other than the Corsican one, continental as well as insular, are currently declining (see Viñuela *et al.* 1994, 1999). Red Kites breed on four main islands within the Mediterranean. On Sardinia and Sicily, they were common until the 1970s, but declined dramatically during the 1980s with small populations remaining in the 1990s (Cortone *et al.* 1994). In Sardinia, the breeding population decreased from 20–30 pairs in 1976 to 10–15 pairs in 1990–92, and in Sicily from 100–150 pairs in 1980 to 10–12 pairs in 1990–92 (Cortone *et al.* 1994). In the Balearic islands (Menorca), the breeding population declined from *c.* 135 pairs in 1987 to 23 pairs in 1993 and eight pairs in 1998 (De Pablo & Pons 1999). The breeding population also declined on another Balearic island (Mallorca). Corsica still holds a significant population of Red Kites, which was estimated at about

100–180 pairs in 1989 (25–30 pairs in the Balagne region). The breeding population increased during the 1990s, with 70–90 breeding pairs in the Balagne region alone. The island population was probably closer to 200–270 pairs in the late 1990s, and currently is probably stable. The increase in Kite density in the Balagne region might be due to a number of factors: little persecution, suitable habitats and extensive sheep and cattle farming, and the recent increase in the rabbit population that has provided an important feeding resource. Persecution and habitat degradation have been identified as the main causes for the population declines in Mediterranean populations. As Kites appear to benefit from abundant rabbit populations, as recorded in previous studies (Viñuela *et al.* 1992, 1994, Villafuerte *et al.* 1998), this prey species could also play an important role in the conservation of Red Kites and other threatened carnivores in the Mediterranean. Our study highlights the fact that the Corsican population is of particular importance for the conservation of sedentary Red Kites breeding in Mediterranean islands, as it has not suffered the dramatic declines observed on other islands, and is the last such remaining significant population.

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