

# Breeding biology and nest characteristics of the Eurasian Kestrel in different environments on an Atlantic island

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We studied reproductive parameters, nest-site characteristics and breeding success of the Eurasian Kestrel (*Falco tinnunculus canariensis*) on Tenerife Island, Canary Archipelago. Kestrels typically breed in cliffs cavities (79.4%), and were present in all habitats from sea level to 2,400 m, except in shrubby heaths (rich in *Myrica faya* and *Erica arborea*) and laurel forests. The breeding cycle was variable and dependent on altitude. Mean laying date for the island was 21 March and we found a significant delay of  $31 \pm 7$  days in mean laying dates in habitats above 1,000 masl, probably due to weather conditions. No interannual differences were found in mean laying dates between habitats. We found no differences in clutch size (mean 4.41,  $n = 133$ ) between habitats or altitude. Laying date and mean clutch size were correlated under 1,000 masl. Mean brood size at hatching was 3.48 ( $n = 124$ ). Mean brood size at fledging was 2.99 ( $n = 124$ ) with no differences between habitats or years. Our results suggest that the stability of the island habitats of Tenerife favours stability of reproductive parameters between years.

## 1. Introduction

Island birds, compared with those of continental populations, are characterized by having smaller clutch sizes and later laying dates (Cody 1966, Wiggins et al. 1998). Habitat type (Grant 1965), weather conditions (Blondel 1985), genetic factors (Frankham 1997), island size and its isolation from the continent (Wiggins et al. 1998), as well as parasites (Møller 1997) and predators (Williamson 1981) have been suggested as potential factors responsible for island effects on the reproductive ecology of birds. The birdlife of the Canary Islands is characterized by reduction in sexual dimorphism (Volsøe 1955) and clutch size compared to mainland populations (Lack 1947). These differ-

ences likely apply to the kestrel (*Falco tinnunculus*), whose subspecies *F. t. canariensis* is the most numerous and widely distributed diurnal raptor inhabiting in the western Canary Islands (Martín & Lorenzo 2001).

In general, the breeding biology of kestrels is well-known (Village 1990) but has not been studied in detail in islands (Balfour 1955, de Naurois 1987, Carrillo et al. 1988, Carrillo & Trujillo 1989). We studied the breeding biology of the Kestrel in Tenerife, the highest island of Canary Archipelago. Our aim was to describe the breeding biology (timing of breeding, clutch size, breeding success), nest site characteristics and to analyse island effects on the reproductive variables. We examined if clutch size and timing of kestrel's breed-

ing seasons may differ geographically with altitude (Immelmann 1971, Perrins & Birkhead 1983).

## 2. Material and methods

### 2.1. Study area and species

Tenerife (27° 55' and 28° 40' N, 16 – 17° W) is a volcanic island situated in the Atlantic Ocean, some 292 km (at the closest point) from the NW of the African continent. This island is the largest (2058 km<sup>2</sup>) and highest (3718 m above sea level [masl]) of the Canary Archipelago. The mean annual rainfall varies between 100 and 1,100 mm and the mean temperatures from 9.5° C at high elevation areas to 18.5–21° C in coastal areas (Marzol 2000). There is a large and diverse flora in arid and semi-arid habitats (coastal halophile vegetation, xerophytic scrub of *Euphorbia*), woodland communities or thermophile bushes, laurel forests, shrubby heaths (rich in *Myrica faya* and *Erica arborea*), pine forests (*Pinus canariensis*), and subalpine scrub (1,900–3,000 masl). More information on the study area and its climate are reported by Santos (1984).

Kestrels breed in rocky cavities and mainly feed on Coleoptera (Scarabaeidae, Tenebrionidae) and Orthoptera, although in terms of biomass mice and lizards are also important (Carrillo et al. 1994, 1995). In the south of Tenerife lizards (*Gallotia galloti*) are a common prey item in the diet of nestlings (Carrillo unpub. data). Man is the main predator of kestrel nests, destroying clutches or robbing nestlings (Carrillo & Aparicio 2001).

### 2.2. General methods

We monitored 145 nests during 1985–1994 in the following habitats: (ES) southern *Euphorbia*-habitat, characterized by *Euphorbia* spp.; (EN) northern *Euphorbia*-habitat, characterised by *E. canariensis* and *Aeonium* spp.; (PS) northern pine forests (*Pinus canariensis*) and subalpine scrub, characterised by *Spartocytisus supranubius* and *Descurainia bourgaeana* (Santos 1984; Table 1).

Nest searching effort differed among the different cover types (ca. 60% ES, 25% EN and 15%

PS) due to the steep topography of Tenerife (Espigado 2000). Nests were found by observing the kestrels' behaviour (Village 1990). Not all nests were visited regularly, thus the sample sizes differ in different analyses. Measures of reproductive success are reported for those nests in which at least one egg was laid.

With respect to nest characteristics, we measured nest cliff orientation, nest cavity dimensions (maximum width and height of the entrance hole, cavity depth, width and height interiors for the mid-depth of the nest), height above the ground, distance from the nest to the top of the cliff.

Whenever possible, we climbed to nests to determine laying dates, clutch sizes, hatching dates, brood sizes, numbers of fledglings and mortality (number of dead chicks per nest). We measured distance of the clutch from the entrance hole (from the entrance to the nearest egg), egg length (L) and breadth (B) to the nearest 0.1 mm with Vernier caliper and calculated the mean egg volume according to Hoyt (1979):  $V = 0.51 LB^2$ . We used the mean measures of the eggs of each nest as the sample unit. Laying date was recorded in Julian dates and was estimated from the hatching date by subtracting 30 days, the median incubation period (Village 1990). Laying interval was assumed to be 2 days (Village 1986, Hasenclever et al. 1989). The chicks were ringed at 15–20 days old.

### 2.3. Analysis

We used three rates to determine the breeding success: (HR) Hatching rate was the number of chicks hatched against the number of eggs laid, considering nests whose clutch size was known accurately and in which at least one chick was hatched; (NDR) Nest desertion rate was the number of pairs that lost a clutch against the number of pairs that started to breed; (FSR) Fledglings success rate was the number of chicks fledged against the number of chicks hatched. HR and FSR were compared between the nests oriented to the north and south respectively using a Student's *t*-test, according to Cochran (1977).

Comparisons between samples of the rest of variables were carried out by means of *t*-tests, ANOVA's and ANCOVA (differences a posteriori between pairs with Scheffé test; Fisher & van

Table 1. Habitats and nests characteristics of the kestrel *Falco tinnunculus* in Tenerife island. ES, southern *Euphorbia*-habitat; EN, northern *Euphorbia*-habitat and rural anthropogenic environments; PS northern pine forests and subalpine scrub. The means are shown  $\pm$  S.D.

	ES (n)	EN (n)	PS (n)	Island (n)
<b>Habitats characteristics</b>				
Altitude	75–500	100–300	1,200–2,400	0–3718
Climate	aridity, high solar radiation	wet, low solar radiation, steep hillside	low rainfall, dry wind, winter snow	diversity
Typical vegetation	xerophytic scrub	xerophytic scrub	pine forests, subalpine scrub	diversity
<b>Nests characteristics</b>				
Entrance width (cm)	41.28 $\pm$ 35.39 (77)	42.78 $\pm$ 31.58 (23)	21.47 $\pm$ 12.59 (15)	39.00 $\pm$ 33.07 (115)
Entrance height (cm)	33.10 $\pm$ 20.68 (78)	23.17 $\pm$ 7.48 (15)	30.53 $\pm$ 11.88 (15)	31.36 $\pm$ 18.58 (108)
Interior width (cm)	47.98 $\pm$ 34.62 (52)	51.13 $\pm$ 14.48 (15)	43.75 $\pm$ 29.86 (12)	47.94 $\pm$ 30.85 (79)
Interior height (cm)	32.37 $\pm$ 23.13 (54)	20.09 $\pm$ 7.45 (11)	33.00 $\pm$ 13.34 (14)	30.77 $\pm$ 20.47 (79)
Depth of cavity (cm)	114.14 $\pm$ 93.67 (83)	55.04 $\pm$ 40.01 (23)	68.10 $\pm$ 26.16 (19)	96.27 $\pm$ 82.65 (125)
Height of cliff (m)	6.85 $\pm$ 3.38 (80)	11.40 $\pm$ 6.20 (24)	22.80 $\pm$ 21.79 (19)	10.20 $\pm$ 10.82 (123)
Height nest-ground (m)	3.83 $\pm$ 1.96 (87)	7.38 $\pm$ 5.13 (39)	15.71 $\pm$ 19.67 (19)	6.34 $\pm$ 8.56 (145)
Nest-cliff top (m)	3.00 $\pm$ 2.40 (80)	4.64 $\pm$ 3.66 (22)	7.44 $\pm$ 5.28 (20)	47.51 $\pm$ 34.95 (122)

Belle 1993). All tests are two tailed and statistical significance was set at 0.05. Data were analyzed using SPSS 11.0 (SPSS Inc. 2001) and STATISTICA 5.0 (STATISTICA 1984–1995).

### 3. Results

#### 3.1. Nest sites

Nests were mostly in cavities and on ledges of cliffs (79.4%,  $n = 145$ ), buildings (14.9%,  $n = 145$ ), and old nests in rocks used by ravens (*Corvus corax*) or doves (*Columba livia*) (4.5%,  $n = 145$ ). The maximum altitude of used nests was 2,400 m on lava flows.

There were significant differences between habitats in the depth of the nest, in the height of the wall where the nest is located, the height from the ground to the nest and the distance from the nest to

top of cliff. Nests are deeper in the ES than in other habitats (Scheffé test); they are situated at a greater height above the ground and located in higher walls in PS (Table 1).

#### 3.2. Breeding success

The mean laying date in the whole island was 21 March (S.D. = 17.44,  $n = 120$ ), 17 February being the earliest and 27 May the latest (Table 2). We observed differences in mean laying dates for the different habitats ( $F_{2,117} = 40.99$ ,  $P < 0.001$ ). The pairs below 1,000 masl (EN and ES) laid  $31 \pm 7$  days earlier ( $t_{117} = -8.72$ ,  $P < 0.001$ ) than those breeding above this altitude (Fig. 1). We did not find interannual differences in the mean laying date (ES from 1985 to 1994,  $F_{8,59} = 1.74$ ,  $P = 0.11$ ; EN from 1985 to 1991,  $F_{6,19} = 0.67$ ,  $P = 0.67$ ; PS from 1988 to 1991,  $F_{3,12} = 0.66$ ,  $P = 0.59$ ).

Table 2. Reproductive parameters of kestrel *Falco tinnunculus* for the different habitats studied in Tenerife island. ES, southern *Euphorbia*-habitat; EN, northern *Euphorbia*-habitat and rural anthropogenic environments; PS northern pine forests and subalpine scrub. Laying date 1 = 1 January. The means are shown  $\pm$  1 S.D.

	ES (n)	EN (n)	PS (n)	Island (n)
<b>Reproductive parameters</b>				
Laying date	74.28 $\pm$ 12.42 (72)	79.68 $\pm$ 16.51 (31)	107.18 $\pm$ 11.59 (17)	80.33 $\pm$ 17.44 (120)
Clutch size	4.36 $\pm$ 0.96 (84)	4.71 $\pm$ 0.59 (31)	4.11 $\pm$ 0.76 (18)	4.41 $\pm$ 0.88 (133)
Distance clutch– entrance hole (cm)	49.67 $\pm$ 39.16 (24)	43.00 $\pm$ 27.26 (7)	42.50 $\pm$ 21.89 (4)	47.51 $\pm$ 34.95 (35)
Length eggs (mm)	38.48 $\pm$ 1.39 (50)	38.34 $\pm$ 1.28 (12)	37.95 $\pm$ 1.07 (8)	38.40 $\pm$ 1.34 (70)
Breadth eggs (mm)	30.97 $\pm$ 0.95 (50)	31.17 $\pm$ 0.86 (12)	30.10 $\pm$ 0.82 (8)	30.91 $\pm$ 0.96 (70)
Eggs volume (cm <sup>3</sup> )	18.85 $\pm$ 1.43 (50)	19.04 $\pm$ 1.62 (12)	17.55 $\pm$ 1.15 (8)	18.73 $\pm$ 1.48 (70)
Brood size at hatch	3.36 $\pm$ 1.64 (81)	3.82 $\pm$ 1.44 (28)	3.53 $\pm$ 1.06 (15)	3.48 $\pm$ 1.54 (124)
Brood size at fledge	2.95 $\pm$ 1.64 (81)	2.89 $\pm$ 1.71 (28)	3.40 $\pm$ 1.06 (15)	2.99 $\pm$ 1.60 (124)
<b>Breeding success</b>				
Hatching rate	0.87	0.88	0.88	0.87
Nest desertion rate	0.12	0.06	0.00	0.09
Fledglings success rate	0.90	0.85	0.93	0.89

Laying date was not related to the number of young hatched ( $r = -0.13$ ,  $P = 0.20$ ,  $n = 104$ ), nor to the number of fledglings ( $r = -0.09$ ,  $P = 0.36$ ,  $n = 114$ ). There is only a slight tendency in ES (young hatched:  $r = -0.21$ ,  $P = 0.08$ ,  $n = 66$ ; young fledged:  $r = -0.21$ ,  $P = 0.08$ ,  $n = 66$ ). Mean clutch size across all populations was 4.41 (S.D. = 0.88, min. 2, max. 6,  $n = 133$ , Table 2), clutches of 4 eggs (41%) and 5 eggs (39%) being the most frequent and there were no significant differences between habitats ( $F_{2,130} = 3.08$ ,  $P = 0.05$ ).

Seasonal trends in clutch size were different between habitats ( $F_{2,99} = 5.56$ ,  $P = 0.005$ ). We did not find differences in EN and ES (habitats < 1,000 masl). Clutch size and laying date were correlated negatively in EN and ES ( $r = -0.28$ ,  $P = 0.008$ ,  $n = 92$ ) but there was a positive correlation in PS ( $r = 0.65$ ,  $P = 0.015$ ,  $n = 13$ ; Fig. 2). We found significant differences in clutch size between years (EN 1987 to 1991,  $F_{4,16} = 5.70$ ,  $P = 0.005$ ; ES 1988 to 1994,  $F_{6,63} = 2.86$ ,  $P = 0.016$ ). In PS there are no

significant differences (data from 1988 to 1991,  $F_{3,11} = 1.29$ ,  $P = 0.33$ ).

The mean brood size at hatching was 3.48 (S.D. = 1.5, min. 0, max. 6,  $n = 124$  clutches) and there were no differences between habitats ( $F_{2,121} = 1.04$ ,  $P = 0.36$ ). The mean brood size at fledging was 2.99 (S.D. = 1.6, min. 0, max. 6,  $n = 124$ ) and there were no differences in the number of fledglings between habitats ( $F_{2,121} = 0.32$ ,  $P = 0.72$ ), nor were there interannual differences either (ES,  $F_{8,72} = 1.7$ ,  $P = 0.12$ ). To calculate these two parameters those nests in which both variables were not accurately known were omitted.

The orientation of the entrance of the nests in the whole island, grouped in categories of 90° (N–NE, E–SE, S–SW, W–NW) was not related to hatching rate (HR) ( $F_{2,108} = 0.07$ ,  $P = 0.94$ ), or with fledglings success rate (FSR) ( $F_{2,94} = 0.14$ ,  $P = 0.87$ ). The same was done for the orientation of the wall of the nest, finding that this variable did not influence these three rates.

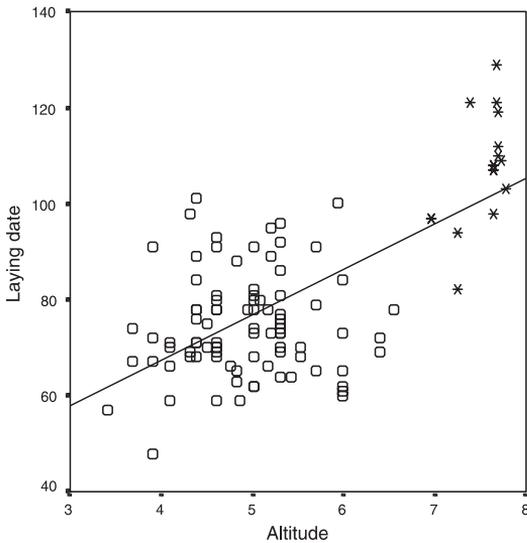


Fig. 1. Relationships between laying date of kestrels *Falco tinnunculus* and altitude (logarithmic scale) in Tenerife island. Nests below 1,000 masl (o), and above 1,000 masl (\*).

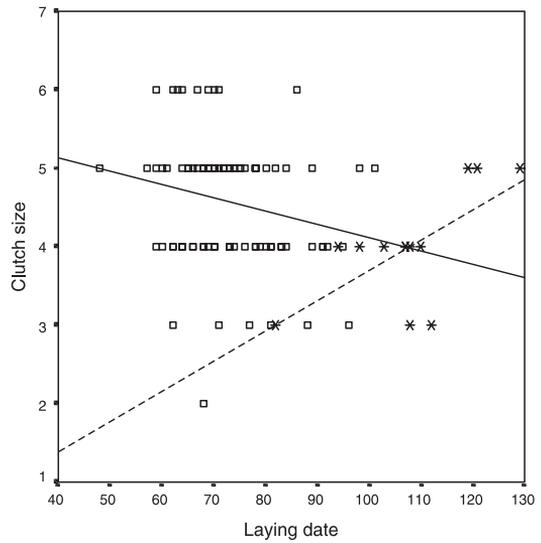


Fig. 2. Seasonal trend in clutch size of kestrels for different years in all habitats below 1,000 masl (o) (intercept = 5.948, slope =  $-0.019$ , S.E. = 0.007) and above 1,000 masl (\*) (intercept =  $-0.124$ , slope = 0.038, S.E. = 0.013) in Tenerife island. Date 40: February 9.

### 3.3. Nests failures

Of the 145 nests studied, 27 (18.6%) failed partially or totally. Main causes of failures included: 1. Human predation on eggs and young (14 nests), 2. No hatching due to unknown causes (9), 3. Desertion of eggs due to heavy rains (1), 4. Breakage of eggs (probably the pollutant DDE, see Mateo et al. 2000) (1), 5. Large young died due to unknown causes (1) and 6. Nest failure (death of a complete family, probably DDE, see Mateo et al. 2000) (1).

## 4. Discussion

### 4.1. Nest sites

On Tenerife, kestrels nests generally in rocky cavities in all the habitats, ranging from from sea level to 2,400 m, except in laurel forest and in shrubby heaths. However, in northern latitudes, kestrels generally breed in old nests of crows, raptors or other birds, but also on cliffs (Village 1990). The rough relief of the island and the scarcity of crows' nests, commonly used by kestrels in other latitudes (Village 1990), are the likely factors that lead kes-

trels to breed in rocky cavities in the Canary Islands. In certain islands of the north of England and Scotland, where there is a lack of other structures they also breed in rocky cavities (Brown 1976).

Although kestrels probably select natural cavities with particular shapes and sizes to breed, only studies made in nestboxes demonstrate that both size and orientation are important factors for the choice of nest (Valkama & Korpimäki 1999). We found that only nest depths differed between habitats such that nests located in the southern *Euphorbia*-habitat are the deepest. Nest depth might be an important characteristic because the deepest nests are probably not easily reached by the main predator, man (Carrillo & Aparicio 2001). Our study suggests that breeding success was not affected by the location of the nest.

### 4.2. Breeding success

The breeding cycle of kestrels in Tenerife is variable and depends on the altitude. Our results suggest that the mean laying date for the pairs that live below 1,000 masl moves forward with respect to

northern latitudes of the Palearctic (Village, 1990). In North African regions near the Canary Islands, laying peaks in April, although the laying period ranges from March to May (Bergier 1987). The pairs that live in habitats above 1,000 masl lay approximately one month later compared to those that breed below this level. Weather affects kestrel breeding by reducing the availability of prey and suppressing hunting behaviour (Cavé 1968, Village 1990).

Low winter temperatures and snow in subalpine scrub in Tenerife (Marzol 1984) may decrease insects and lizards activity, thereby influencing the laying date through availability of prey. Moreover, we assumed that the costs of thermoregulation in cold weather may also increase food demands. If so, delay in breeding season in subalpine scrub could be explained by the delay of fat reserves in females prior to laying (Village 1990). This variation could corroborate the hypothesis of the delay in breeding seasons according to altitude (Immelmann 1971, Perrins & Birkhead 1983) and has been observed for the Kestrel in different regions (Switzerland, G eroudet 1978; Morocco, Bergier 1987; England, Shrubbs 1993).

In many raptors the latitudinal variations of clutch size are well-known (Newton 1979). Carrillo and Gonz alez-D avila (2003) observed a latitudinal decrease (from N to S) in clutch size of the Kestrel in the western Palearctic. Mean clutch size of the Kestrel population on Tenerife was smaller than that of other more northern western Palearctic populations (Carrillo & Gonz alez-D avila, 2003). Nevertheless, these data must be interpreted with caution because clutch size reduction in island birds is generally assumed to be adaptive (Lack 1968, Cody 1971, Isenmann 1982). Moreover, insularity affects the breeding biology (timing, clutches and broods) of birds of prey in different way. For example, the Kestrel breeds roughly at the same time and with similar clutch sizes on the island of Corsica as in the rest of temperate Europe. However, Sparrowhawks (*Accipiter nisus*) on Corsica breed later and laid fewer eggs than mainland populations (Thibault et al. 1992). So, the data for clutch size of kestrel populations that live in islands shows different patterns (Brown 1976, Kuusela 1983, Thibault et

al. 1992, Shrubbs 1993, A. Mestre & S. Vidal unpubl.).

We did not find differences in the number of fledglings produced per pair, nor between habitats or years. At northern latitudes in the western Palearctic the production of young is variable and depends on fluctuations in vole densities (Kostrzewa & Kostrzewa 1990, Korpim aki & Norrdahl 1991), weather (Kostrzewa & Kostrzewa 1990) and the total density of pairs (Village 1990). In Mediterranean environments, no differences in productivity were found between years (Gill-Delegado et al. 1995) or habitats (Avil es et al. 2001). In northern and central Palearctic voles (Microtinae) form the basis of the Kestrel's diet, whereas Murinae, Insecta and Reptilia are preyed upon more frequently in more southern regions (Carrillo et al. 1994, Aparicio 2000). On the Canary islands, insects are the most frequent prey captured by kestrels (Carrillo et al. 1994, 1995) while the nestlings are fed mainly on lizards (*Gallotia galloti*, 89.2%, n = 907 prey, Carrillo unpubl. data from Tenerife), which are plentiful and distributed over all the habitats in Tenerife (B aez 1984). Prey availability may be the main reason for the observed stability between years and habitats in productivity.

Previous studies in northern latitudes show that the availability of preferred habitats was important for hunting success (Village 1982, Pettifor 1984, Valkama et al. 1995) and reproductive parameters (Village 1990, Valkama & Korpim aki 1999, Avil es et al. 2001). Our results suggest that habitat characteristics did not influence clutch size, brood size and number of fledglings on Tenerife. The breeding density appears to vary between areas (Carrillo & Delgado 1996 for the eastern Canary Islands) and this may indirectly affect the availability of food for the pairs (Perrins & Birkhead 1983).

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## Tuulihaukan *Falco tinnunculus* pesimisbiologiaa Kanarian saarilla

Tuulihaukka pesi Teneriffalla tyypillisesti kaliojyrkänteen onkalossa (79,4 %). Tuulihaukkoja tavattiin kaikenlaisissa ympäristöissä merenpinnan tasolta 2 400 m:iin lukuun ottamatta pensaikkaisia kellokanervikkoja ja laakeripuumetsiä. Pesinnän ajoittuminen vaihteli korkeudesta riippuen. Keskimääräinen muninnan aloittamispäivä saarella oli 21.3, mutta yli 1 000 m:n korkeudessa pesivillä pareilla pesinnän ajoittuminen erosi merkittävästi lähempänä merenpintaa pesivistä. Yli 1 000 metrissä muninta aloitettiin  $31 \pm 7$  päivää myöhemmin. Tämä johtuu luultavasti sääolosuhteiden eroista. Muninnan aloittamisajankohta ei eronnut elinympäristöjen välillä. Pesyekoko (k.a. 4,41,  $n = 133$ ) ei vaihdellut habitaattien tai korkeuden mukaan. Alle 1 000 m:n korkeudessa pesyekoko korreloi muninnan aloittamisajankohdan kanssa. Keskimääräinen pesäpoikuekoko oli 3,48 ( $n = 124$ ) ja lentopoikuekoko 2,99 ( $n = 124$ ). Pesimävuosi tai -habitaatti ei vaikuttanut pesyekokoihin. Tulokset viittaavat siihen, että Teneriffan pesimäympäristön vakaus suosii lisääntymiseen liittyvien ominaisuuksien vaihtelemattomuutta.

## References

- Aparicio, J.M. 2000: Differences in the diets of resident and non-resident Kestrels in Spain. — *Ornis Fennica* 77: 169–175.
- Avilés, J.M., Sánchez, J.M. & Parejo, D. 2001: Breeding rates of Eurasian Kestrels (*Falco tinnunculus*) in relation to surrounding habitat in southwest Spain. — *Journal of Raptor Research* 35: 31–34.
- Báez, M. 1984: Anfíbios y reptiles. — In *Fauna marina y terrestre del Archipiélago Canario* (ed. Edirca): 259–273. Las Palmas de Gran Canaria.
- Balfour, E. 1955. Kestrels nesting on the ground in Orkney. — *Bird Notes* 26:245–253.
- Bergier, P. 1987: Les rapaces diurnes du Maroc. Statut, répartition et ecologie. — *Annales du C.E.E.P.* (ex – C.R.O.P.) n° 3. Aix-en-Provence.
- Blondel, J. 1985: Breeding strategies of the Blue Tit and Coal Tit (*Parus*) in mainland and island Mediterranean habitats: A comparison. — *Journal of Animal Ecology* 54:531–556.
- Brown, L. 1976: *British Birds of Prey*. — Collins Sons and Co Ltd. London.
- Carrillo, J., Nogales, M. & Padrón, M. 1988: Nesting of *Falco tinnunculus* in natural sites in Canary pines on El Hierro island. — *Journal of Raptor Research* 22: 85–88.
- Carrillo, J. & Trujillo, N. 1989: Ponte de remplacement inhabituelle chez le Faucon crécerelle *Falco tinnunculus*. — *Alauda* 57: 227–228.
- Carrillo, J., Hernández, E.C., Nogales, M., Delgado, G., García, R. & Ramos, T. 1994: Geographic variation in the spring diet of *Falco tinnunculus* L. on the islands of Fuerteventura and El Hierro (Canary Islands). — *Bonner Zoologische Beiträge* 45: 39–48.
- Carrillo, J., García, R. & Nogales, M. 1995: Contribution à l'étude du spectre alimentaire de *Falco tinnunculus* (Aves: Falconidae), dans l'île de El Hierro (Iles Canaries). — *Boletim do Museu Municipal Funchal* 47: 7–22.
- Carrillo, J. & Delgado, G. 1996: Patrones de distribución y abundancia relativa de *Falco tinnunculus dacotiae* (Hartert, 1913) en las Islas Canarias. — In *Biología y conservación de las rapaces mediterráneas, 1994* (ed. Muntaner, J. & Mayol, J.): 471–476. Monografía n° 4 SEO/Birdlife, Madrid.
- Carrillo, J. & Aparicio, J.M. 2001: Nest defence behaviour of the Eurasian Kestrel *Falco tinnunculus* against human predators. — *Ethology* 107: 865–875.
- Carrillo, J. & González-Dávila, E. 2003: Geographic variation in the clutch size of the Eurasian Kestrel *Falco tinnunculus*. — *Proc. IV Congresso Português de Ornitologia e II Jornadas Ibéricas de Ornitologia*: 154.
- Cavé, A. J. 1968. The breeding of the Kestrel, *Falco tinnunculus* L., in the reclaimed area Oostelijk Flevoland. — *Netherlands Journal of Zoology* 18: 313–407.
- Cochran, W.R. 1977: *Sampling techniques*. — Wiley and sons, New York.
- Cody, M.L. 1966. A general theory of clutch size. — *Evolution* 20: 174–184.
- Cody, M.L. 1971: Ecological aspects of reproduction. — In *Avian Biology Vol. I* (ed. Farner, O.S. & King, J.R.): 461–512. Academic Press, London.
- Espiago, J. 2000: El relieve. — In *Gran atlas temático de Canarias* (ed. Interinsular Canaria): 41–54. Santa Cruz de Tenerife.
- Fisher, L.D. & van Belle, G. 1993: *Biostatistics: A methodology for the health sciences*. — Wiley and sons, New York.
- Frankham, R. 1997: Do island populations have less genetic variation than mainland populations? — *Heredity* 78: 311–327.
- Géroudou, P. 1978: Les rapaces diurnes et nocturnes d'Europe. — Delachaux et Niestlé, Paris.
- Gil-Delgado, J.A., Verdejo, J. & Barba, E. 1995: Nestling diet and fledgling production of Eurasian Kestrels (*Falco tinnunculus*) in eastern Spain. — *Journal of Raptor Research* 29:240–244.
- Grant, P.R. 1965: The adaptive significance of some size trends in island birds. — *Evolution* 19: 355–367.
- Hasenclever, H., Kostrzewa, A. & Kostrzewa, R. 1989: Brutbiologie des Turmfalken (*Falco tinnunculus*): 16 jährige Untersuchungen in Westfalen. — *Journal für*

- Ornithologie 130 (2): 229–237.
- Hoyt, D.F. 1979: Practical methods of estimating volume and fresh weight of birds eggs. — *Auk* 96: 73–77.
- Immelmann, K. 1971: Ecological aspects of periodic reproduction. — In *Avian Biology*, Vol. I (ed. Farner, D.S. & King, J.R.): 341–389. Academic Press, London.
- Isenmann, P. 1982: The influence of insularity on fecundity in tits (Aves, Paridae) in Corsica. — *Acta Oecologica* 3: 295–301.
- Korpimäki, E. & Norrdahl, K. 1991: Numerical and functional responses of Kestrels, Short-Eared Owls and Long-Eared Owls to vole densities. — *Ecology* 72: 814–826.
- Kostrzewa, A. & Kostrzewa, R. 1990: The relationship of spring and summer weather with density and breeding performance of the Buzzard *Buteo buteo*, Goshawk *Accipiter gentilis* and Kestrel *Falco tinnunculus*. — *Ibis* 132: 550–559.
- Kuusela, S. 1983: Breeding success of the Kestrel *Falco tinnunculus* in different habitats in Finland. — *Proceedings of the third Nordic Congress in Ornithology* 1981: 53–58.
- Lack, D. 1947: The significance of clutch size. — *Ibis* 89: 302–352.
- Lack, D. 1968. Ecological adaptations for breeding in birds. — Methuen and Co. Ltd, London.
- Martín, A. & Lorenzo, J.A. 2001: Aves del Archipiélago canario. — In *Aves del Archipiélago Canario* (ed. Lemus, F.): 231–236. San Cristóbal de La Laguna, Tenerife.
- Marzol, M.V. 2000: El clima. — In *Gran atlas temático de Canarias* (ed. Interinsular Canaria): 87–106. Santa Cruz de Tenerife.
- Mateo, R., Carrillo, J. & Guitart, R. 2000: p,p'-DDE residues in eggs of European Kestrel *Falco tinnunculus* from Tenerife, Canary Islands, Spain. — *Bulletin of Environmental Contamination and Toxicology* 65: 780–785.
- Møller, A.P. 1997: Parasitism and the evolution of host life history. — In *Host parasitism evolution: General principles and avian models* (ed. Clayton, D.H. & Moore, J.): 105–127. Oxford University Press, Oxford.
- Naurois, R. de 1987: Contribution à la connaissance de l'écologie de la Crécerelle (*Falco tinnunculus* Linné) dans l'Archipel du Cap Vert. — *Bolletino di Museo Regionale di Scienze Naturali Torino* 5:195–210.
- Newton, I. 1979: Population ecology of raptors. — T & A D Poyser, Berkhamsted.
- Perrins, C.M. & Birkhead, T.R. 1983: *Avian Ecology*. — Blackie, Glasgow.
- Pettifor, R.A. 1984: Habitat utilisation and the prey taken by kestrels in arable fenland. — *Bird Study* 31: 213–216.
- Santos, A. 1984: Flora y vegetación. — In *Geografía de Canarias. Geografía física* (ed. Interinsular Canaria): 258–294. Santa Cruz de Tenerife.
- Shrubbs, M. 1993: *The Kestrel*. — Hamlyn, London.
- Thibault, J.C., Patrimonio, O. & Torre, J. 1992: Does the diurnal raptor community of Corsica (Western Mediterranean) show insular characteristics? — *Journal of Biogeography* 19: 363–373.
- Valkama, J. & Korpimäki, E. 1999: Nestbox characteristics, habitat quality and reproductive success of Eurasian Kestrels. — *Bird Study* 46 (1):81–88.
- Valkama, J., Korpimäki, E. & Tolonen, P. 1995: Habitat utilization, diet and reproductive success in the Kestrel in a temporally and spatially heterogeneous environment. — *Ornis Fennica* 72: 49–61.
- Village, A. 1982: The diet of kestrels in relation to vole abundance. — *Bird Study* 29: 129–138.
- Village, A. 1986: Breeding performance of kestrels at Eskdalemuir, south Scotland. — *Journal of Zoology* (London) 208: 367–378.
- Village, A. 1990: *The Kestrel*. — T & AD Poyser, London.
- Volsøe, H. 1955: The breeding birds of the Canary Islands. II. Origin and History of the Canarian Avifauna. — *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening* 117:117–178.
- Wiggins, D.A., Møller, A.P., Sørensen, M.F.L. & Brand, L.A. 1998: Island biogeography and the reproductive ecology of great tits *Parus major*. — *Oecologia* 115: 478–482.
- Williamson, M. 1981: *Island populations*. — Oxford University Press, Oxford.