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Impact of weather on breeding success of the Eurasian Kestrel *Falco tinnunculus* in a semi-arid island habitat

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In semi-arid ecosystems, rainfall and temperature induce changes in the food chain and affect breeding conditions of raptors. We examined the influence of rainfall and temperature on the breeding success of the Eurasian Kestrel *Falco tinnunculus* inhabiting xerophytic scrub on Tenerife Island, Canary Archipelago. Reproductive performance was recorded during five years, and food availability (arthropods, lizards, mice and birds) was monitored monthly during a wet and a dry breeding season. We found that increased rainfall in the previous autumn was associated with an earlier laying date and a more prolonged breeding season. Mean clutch size showed a positive correlation with rainfall in the month prior to laying. Hatching and fledgling success did not vary significantly between a wet and a dry year. Temperature did not influence breeding parameters. Despite the advanced laying date and larger clutch size observed, high prey availability during egg formation in the wet year did not result in higher overall breeding success. Stable between-year number of fledglings coincided with stable prey availability during the nestling or fledgling periods. Food conditions in the dry year were more stable and attuned to harsh weather conditions regardless of rainfall during the previous autumn and pre-breeding period.

Key words: breeding success, *Falco tinnunculus*, food availability, islands, rainfall, semi-arid, Tenerife, xerophytic scrub

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Because rainfall in arid ecosystems is unpredictable, birds may breed at any season of the year. Serventy (1971) pointed out that rainfall replaced daylength as the supreme *Zeitgeber* for breeding periodicity in regions with unpredictable precipitation. Rainfall is an important factor in determining food availability, and influences the breeding biology of birds living in arid mainland (Rotenberry & Wiens 1991, Lloyd 1999, Morrison & Bolger 2002) and arid island ecosystems (Grant *et al.* 2000, Illera & Díaz 2006, García del Rey & Cresswell 2007). It has been hypothesized that (1) clutch size in arid habitats is positively associated with rainfall during egg formation (Patten & Rotenberry 1999); and (2) rainfall could act as a proximate cue on the physiology and behaviour of birds (Hau 2001). Rainfall in arid regions also induces changes in temperature, affecting the food chain from lower to higher levels (Noy-Meir 1973) and reproductive parameters in birds (Lloyd 1999, Grant *et al.* 2000, Wichmann *et al.* 2006).

Adverse weather, especially heavy rainfall, may reduce hunting success or prey availability and increase mortality in raptors (Newton 1998, McDonald *et al.* 2004). In arid ecosystems rainfall has a positive effect on food availability and consequently on the breeding success of raptors (Wichmann *et al.* 2006). Some studies also found a positive effect on breeding performance, i.e. brood size at fledging (Hustler & Howells 1988, Bahat & Mendelssohn 1996) but others recorded the opposite (Steenhof *et al.* 1999, Macías-Duarte *et al.*

2004, Charter *et al.* 2007). The influence of weather on raptor reproduction in arid island ecosystems is, to our knowledge, poorly documented (del Hoyo *et al.* 1994, but see Carrillo 2005). At temperate and northern latitudes, temperature and rainfall in the months prior to laying influence reproduction in the Eurasian Kestrel (hereafter Kestrel) *Falco tinnunculus* via food availability (Cavé 1968, Kostrzewa & Kostrzewa 1991, Carrillo & González-Dávila 2010). Female kestrels can advance laying date and increase clutch size if food supply during egg formation and laying is sufficiently abundant (Aparicio 1994, Korpimäki & Wiehn 1998).

In the Canary Islands the Kestrel is the most common diurnal raptor, breeding in a wide range of habitats including semi-arid areas (Carrillo 2007) where rainfall might not occur for several years (Santos 1984). Our aim was to examine the influence of weather (i.e. rainfall and temperature in the months prior to laying and during the breeding season), on the reproductive success of the Kestrel under semi-arid conditions.

METHODS

Study area

We examined an area of ≈ 100 km^2 in south-eastern Tenerife (0–400 m a.s.l.), an island situated in the Atlantic Ocean off the west coast of Africa (27°55', 28°4'N, and 16°–17° W) in the Canary Archipelago. Dry conditions are typical of southern Tenerife and most rain usually falls from November to March. High solar radiation throughout the year is normal, with sporadic warm Saharan winds and a mean monthly temperature of 18–25°C. The vegetation is composed of xerophytic scrub, mainly consisting of *Euphorbia canariensis, E. balsamifera, Plocama pendula, Schizogyne sericea, Artemisia thuscula* and *Argyranthemum* spp.

Study species

The Kestrel *Falco tinnunculus* is a single-brooded raptor breeding across a high diversity of habitats (Village 1990), including semi-arid areas (Carrillo 2007). Kestrels in the leeward xerophytic scrub of Tenerife breed as solitary pairs in rock cavities (n = 87 breeding pairs, 1985–94; Carrillo & González-Dávila 2005). Kestrel diet in this environment during the breeding season includes insects 75.7% (Coleoptera 40.1% [Tenebrionidae, Scarabaeidae, Curculionidae], Hymenoptera 18.1% [Formicidae], Orthoptera 12.8% [Acrididae, Gryllidae], Dyptera 1.9%, Odonata 0.5%), Tenerife Lizards *Gallotia galloti* 14.2%, mammals (Muridae) 7.4% and birds 1.1% (n = 1119 items of prey; percent occurrence in 285 pellets; JC, unpubl. data). Nestlings are mainly fed with lizards, which are the prey most often found in the nests (91.1%, n = 550 prey item, Carrillo & Aparicio 2001; 95.8%, n = 377 prey item, 35 nests; JC, unpubl. data).

General methods

Most data were recorded during intensive field work in 1993 and 1994. Although we monitored mating and courtship of 36 Kestrel pairs, we only observed breeding in 29 pairs (18 in 1993 and 11 in 1994). Nest sites were located before the onset of laying by checking for courtship behaviour and regular visits to determine laying date, clutch size, brood size and number of fledglings. In some cases, laying date was estimated from the hatching date by subtracting 30 days, the mean incubation period (Village 1990). Based on previous observations, we considered courtship to occur from mid-January to mid-February, the egg formation and laying as mid-February to mid-March, incubation from mid-March to mid-April, nestling from mid-April to late May, and fledgling period in June. The chicks were ringed when 15–20 days old.

Rainfall and temperature

Data on rainfall and temperature (maximum, minimum and average) were gathered from the Regional Centre of Meteorology for the western Canaries (Santa Cruz de Tenerife). The weather station is situated within the study area at Reina Sofía airport.

Within the period 1985–94, 1993 was among the wettest years with 145 mm of rainfall (Fig. 1A) of which 102 mm were recorded during March. Throughout 1994, only 29 mm was recorded, the driest year of the decade, without any rainfall in March (Fig. 1A). The mean monthly rainfall of 1993 (16.5 mm) exceeded the 95% confidence interval (CI) for 1985–94 (CI 95%: 5.72–14.03) whereas the mean monthly rainfall of 1994 (4.07 mm) was below this interval.

Mean, maximum and minimum temperatures were not significantly different between 1993 and 1994. The highest mean monthly temperature was reached in August (1993: 24°C, 1994: 24.7°C), the lowest in February (1993: 18.0°C, 1994: 18.2°C). The temperature was also stable between 1985 and 1994 (Fig. 1B).

Food availability

We estimated the availability of arthropods (insects, spiders), Tenerife Lizards, terrestrial birds and mice *Mus musculus*, the main prey groups of Kestrels in the Canary Islands (Carrillo *et al.* 1994), every 15 days

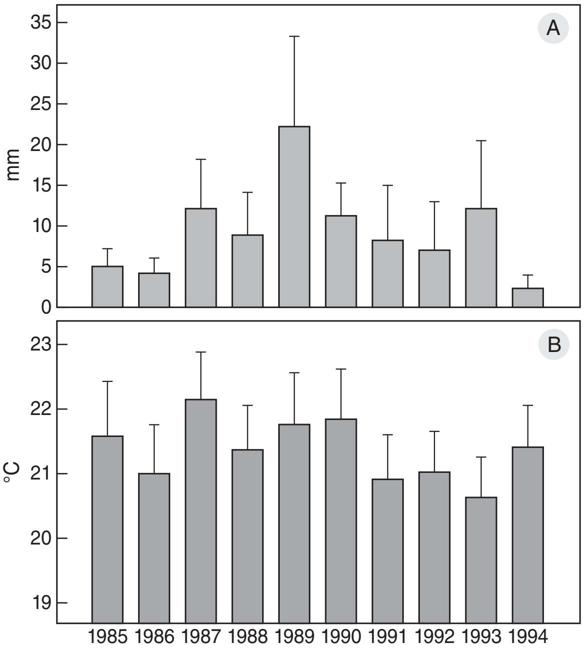

Figure 1. (A) Annual rainfall and (B) mean annual temperature in leeward xerophytic scrub, Tenerife, between 1985 and 1994.

throughout the pre-breeding, breeding and post-breeding periods during 1993 and 1994. Prey data were collected on sunny days in seven plots of 12.5 ha each (Molina 1985, Ausden 1996). No census was carried out when adverse weather conditions prevailed (strong wind, rainfall, thick cloud). Arthropods larger than 5 mm were counted over periods of 2 min, in 15 circular areas with a 1-m radius, each area being separated by 10 steps, in seven plots. We did not register the exact number of insects when this exceeded 20 individuals. Lizards were counted using the number of times one was seen or heard within a 2-m belt from the observer while following perimetric transects of 500 m. Birds seen or heard were counted within a 50-m belt while traversing the plot (Tellería 1986). Mice were sampled at night by installing 70 snap traps per session (traps 5 m apart, two lines of 5 traps in each plot, 140 per month). Prey availability was estimated using the average obtained from the seven plots per visit.

Analysis

We determined breeding success as the number of chicks hatched against the number of eggs laid (Hatching Success, HS), considering nests whose clutch size was known and in which at least one chick had hatched; and as the number of chicks fledged against the number of chicks hatched (Fledgling Success, FS). Student *t*-test was conducted to compare HS and FS between years before using arcsine square root transformation to assess breeding success. We employed Spearman rank correlation coefficients to assess relationships between monthly rainfall and temperature averages vs. prey availability. After confirming the normality of distribution (Kolmogorov-Smirnov), differences between annual laying dates were tested using Student *t*. Pearson's coefficient was used to calculate relationships between laying date and clutch size vs. weather conditions. We report only those relationships that proved statistically significant after applying Bonferroni correction. In order to determine differences between years (1993–94) in clutch size, brood size at hatching and brood size at fledging we used a generalized linear model (Poisson log model). We assessed inter-annual differences in prey availability using two-way ANOVA after normalizing data by logarithmic transformation. We present results as means ± SD. All tests are two-tailed, and statistical significance was set at 0.05. All calculations were carried with SPSS 14.0 (SPSS 2005, Inc., Chicago, U.S.A.) and Statistica 6.0 (Statistica 2001, Inc., Statsoft).

RESULTS

Food availability

Food availability (arthropods, lizards, mice and birds) varied within and between years (Fig. 2, Table 1). Prey availability during courtship ($F_{3,87} = 1.269$, $P = 0.290$), nestling ($F_{3,136} = 0.926$, $P = 0.430$), and fledgling periods ($F_{3,104} = 1.431$, $P = 0.238$) did not differ between 1993 and 1994. Conversely, between-year prey availability differed for the periods of egg formation and incubation ($F_{3,81} = 3.546$, $P = 0.018$; $F_{3,93} = 2.896$, $P = 0.039$, respectively), due to higher lizard availability in the wet year ($F_{1,81} = 2.843$, $P = 0.006$; $F_{1,93} = 3.085$, $P = 0.003$, respectively). Arthropod populations significantly increased three months after rainy periods ($r_s = 0.547$, $P = 0.01$, $n = 21$). Orthoptera abundance was positively correlated with mean monthly temperature ($r_s = 0.455$, $P = 0.029$, $n = 23$), maximum temperature ($r_s = 0.502$, $P = 0.015$, $n = 23$), rainfall three months before ($r_s = 0.541$, $P = 0.01$, $n = 21$) and insolation ($r_s = 0.774$, $P < 0.001$, $n = 23$).

Reproductive traits

In the wet year, 67% of the recorded Kestrel pairs initiated laying during the first two weeks of March (range 26 February to 6 April). In the dry year, 63% started

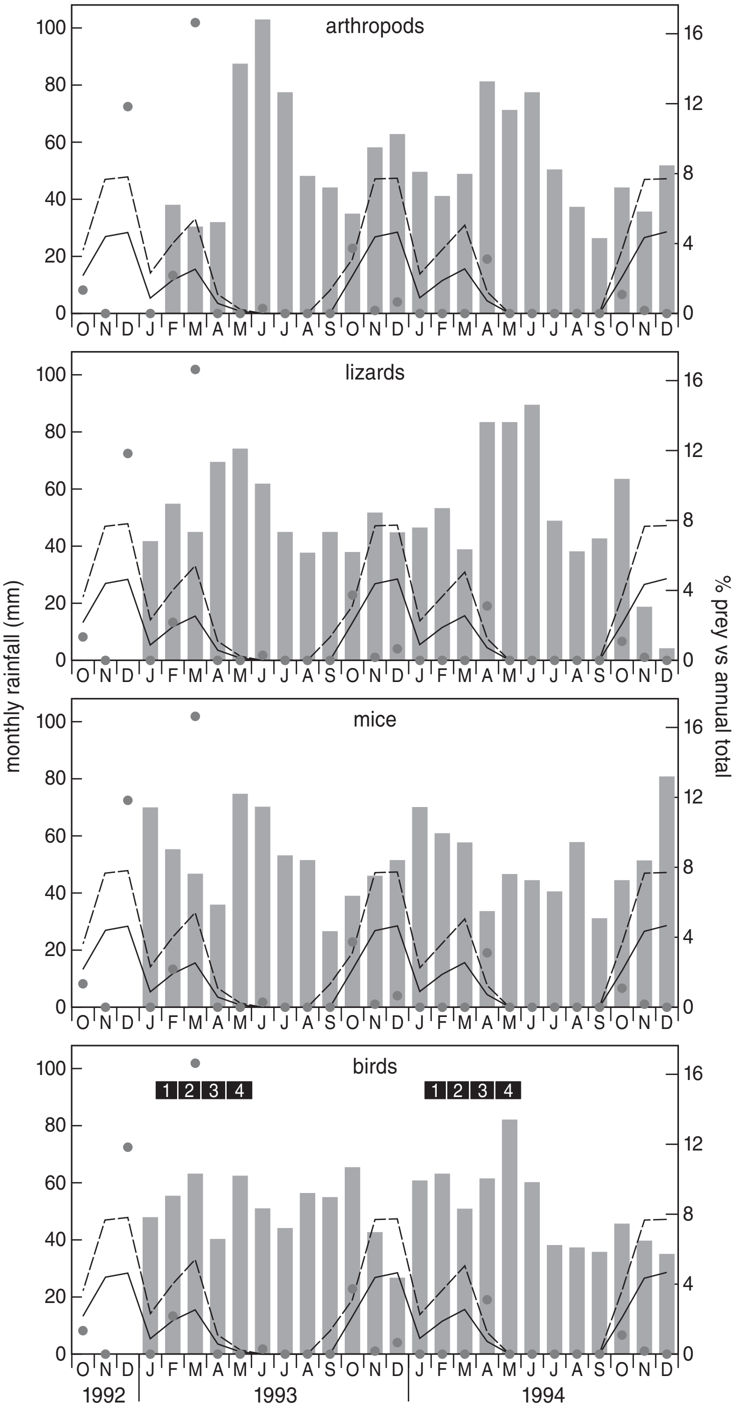

Figure 2. Monthly availability of arthropods (insects and spiders), Tenerife Lizards *Gallotia galloti*, House Mice *Mus musculus*, and birds (bars, expressed as proportion of annual total for each prey group) and monthly distribution of rainfall in leeward xerophytic scrub in Tenerife. Grey dots = monthly rainfall; solid line = 10-year average monthly rainfall for 1985–94; dashed line = upper 90% confidence interval for average rainfall. Breeding season of Kestrels illustrated in lower panel, showing courtship period (1), egg formation and laying (2), incubation (3) and nestling period (4).

laying during the second and the third week of March (range 7 March to 2 April; Fig. 3). Mean laying date differed significantly between 1993 and 1994 (Table 2). During 1990 to 1994, mean laying date correlated negatively with autumn rainfall preceding the breeding season after correcting for the number of nests per year ($R = 0.35$, $P = 0.01$, $n = 60$; intercept = 81.047, slope = –0.095, S.E. = 0.035; Fig. 4).

We found significant differences in mean clutch size between 1993 and 1994 (Wald = 5.55, $P = 0.018$), but not in brood size at hatching, brood size at fledging and breeding success (HS and FS; Table 2). During 1990–94, mean clutch size was not correlated with mean temperature, but showed a positive correlation with rainfall in February ($R = 0.30$, $P = 0.02$, $n = 60$; Fig. 4, Table 3).

Table 1. Mean number of prey items/plot/visit recorded during the various stages of the breeding cycle in leeward xerophytic scrub, Tenerife, in 1993 (wet year) and 1994 (dry year). Total breeding season (January–June): means ± SD and number of plots surveyed.

	Breeding stage	Courtship	Egg-formation and laying	Incubation	Nestlings	Fledglings	Total breeding season
1993	Arthropods (total)	18.37	19.17	25.43	49.76	79.29	44.02 ± 33.50 (63)
	Coleoptera	1.00	2.00	4.71	11.24	16.07	8.68 ± 11.49 (63)
	Orthoptera	1.13	2.33	2.71	19.19	37.14	15.62 ± 11.31 (63)
	Lizards	29.44	39.70	72.54	62.81	61.00	56.39 ± 24.64 (67)
	Mice	1.93	1.64	1.36	1.85	1.86	1.71 ± 1.35 (77)
	Birds	13.37	18.62	17.07	15.05	14.00	15.49 ± 6.37 (65)
1994	Arthropods (total)	28.21	37.83	35.90	40.62	39.21	36.27 ± 18.23 (63)
	Coleoptera	16.79	8.67	16.00	19.54	15.50	15.40 ± 12.77 (63)
	Orthoptera	1.93	6.92	10.00	11.00	17.86	9.57 ± 5.32 (63)
	Lizards	46.29	21.15	38.08	67.14	64.36	48.07 ± 17.47 (67)
	Mice	1.50	1.57	0.50	0.95	0.93	1.08 ± 1.17 (76)
	Birds	12.86	10.58	12.00	14.62	12.29	12.52 ± 4.70 (63)

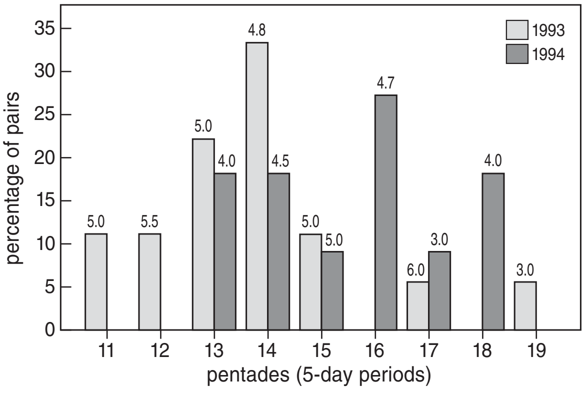

Figure 3. Seasonal distribution of laying dates of Kestrels breeding in leeward xerophytic scrub on Tenerife in 1993 and 1994. Pentade 12 = 1–5 March. Mean clutch size in each pentade is indicated on top of the bars.

Table 2. Reproductive parameters of Kestrels in leeward xerophytic scrub on Tenerife in 1993 (wet year) and 1994 (dry year). Laying date 50 = 19 February. Means ± SD, sample size in parentheses.

	1993	1994	*P*
Laying date	71.17 ± 9.33 (18)	78.82 ± 9.05 (11)	$t_{27} = 2.17$ 0.039
Clutch size	4.94 ± 0.80 (18)	4.27 ± 0.65 (11)	$\chi^2_1 = 5.55$ 0.018[a]
Brood size at hatch	3.67 ± 1.78 (18)	4.09 ± 0.54 (11)	$\chi^2_1 = 0.56$ 0.454[a]
Brood size at fledge	3.39 ± 1.72 (18)	3.45 ± 0.93 (11)	$\chi^2_1 = 0.01$ 0.908[a]
Hatching success	0.84 (16)	0.96 (11)	$t_{25} = -1.80$ 0.084[b]
Fledging success	1.0 (16)	1.0 (11)	- -

[a] Generalized Linear Model.

[b] Arcsine square root transformation.

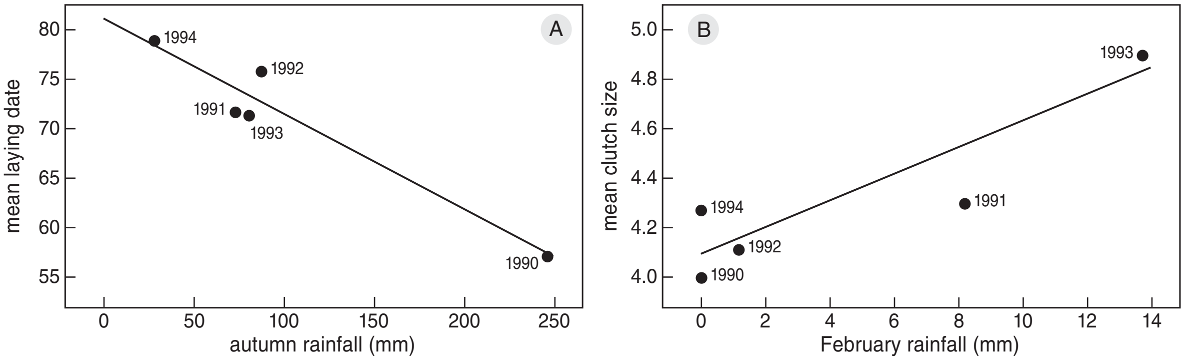

Figure 4. Relationships between (A) mean laying date and rainfall in the previous autumn (laying date 50 = 19 February), and (B) mean clutch size and February rainfall (month prior to laying) for Kestrels breeding in leeward xerophytic scrub on Tenerife in 1990–94. Data weighted by the number of nests per year.

Table 3. Multiple correlation coefficient (*R*) between mean laying date and mean clutch size, and rainfall and temperature. Clutch size was log-transformed. We included year as a random factor. *P*-value in parentheses. Significant values in bold.

	Autumn	Winter	January	February	March
Rainfall					
Laying date	**–0.350**	–0.211	–0.149	–0.192	–0.209
	(0.01)	(0.12)	(0.28)	(0.16)	(0.12)
Clutch size	0.106	**0.312**	0.133	**0.303**	**0.310**
	(0.42)	**(0.02)**	(0.31)	**(0.02)**	**(0.02)**
Temperature					
Laying date	–0.264	–0.145	0.171	–0.162	–0.221
	(0.06)	(0.29)	(0.21)	(0.24)	(0.10)
Clutch size	–0.148	–0.259	–0.230	–0.199	–0.217
	(0.26)	(0.06)	(0.08)	(0.13)	(0.10)

DISCUSSION

Laying date and clutch size of Kestrels inhabiting xerophytic scrub on Tenerife showed inter-annual variations associated with fluctuations in rainfall, but brood size at hatching and number of fledglings did not. Temperature did not correlate with any of the breeding parameters measured.

Our results suggest that high rainfall in the previous autumn is associated with an earlier mean laying date and a more prolonged breeding season. Rainfall during the previous autumn favours plant growth and flowering, and therefore the Kestrel's basic prey species, the Tenerife Lizard *Gallotia galloti*, during the breeding season (JC, unpubl. data). This lizard is especially active in February–March (de los Santos & de Nicolás 2008) when favourable prey conditions increase male Kestrel capture rate during egg formation, which influences the female's condition and advances laying date (Aparicio 1994, Korpimäki & Wiehn 1998). The effects of rainfall on the laying dates of raptors inhabiting arid or semi-arid habitats are variable (MacLean 1970, Steenhof *et al.* 1997, McDonald *et al.* 2004, Macías-Duarte *et al.* 2004). In our study area the variation in mean laying date suggests that the Kestrel breeding season is not regular and depends on previous rainfall. Prey and weather variations have greater impact on small, short-lived raptors, since the relative costs of egg formation are higher for smaller species (Newton 1979).

Several studies carried out in semi-arid islands show the influence of rainfall on clutch size through food availability (Grant *et al.* 2000, Illera & Díaz 2006). We found that abundant rainfall during the month prior to laying increased clutch size, but was not a good predictor of fledging success, which was similar in wet and dry years. Between-year differences in lizard availability were particularly evident in the pre-laying period, but had largely disappeared by the time the eggs hatched. Moreover, the study area contains agricultural greenhouses, open air tomato plots and water tanks, sites where compensatory food can be found when conditions are adverse.

In 1994, seven out of eighteen nest sites were not occupied by a breeding pair, and because our Kestrels are faithful to their nest sites (pers. obs.), we deduce that the unfavourable conditions in this particularly dry year were not conducive to breeding. Under semi-arid conditions, non-breeding has a higher impact on total breeding performance than changes in laying date and clutch size of those pairs that do breed. This is particularly relevant when the harsh conditions in semi-arid regions are further aggravated by drought, as found on various trophic levels in other semi-arid and arid regions (Newton 1998, Macías-Duarte *et al.* 2004, Zwarts *et al.* 2009).

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SAMENVATTING

Klifbroedende Torenvalken *Falco tinnunculus* op Tenerife hebben te maken met de semi-aride condities van de Canarische Eilanden. De weinige regen valt hier van november tot maart, terwijl de gemiddelde maandelijkse temperatuur varieert van 18° tot 25°C. Aan de lijzijde van de kliffen strekken zich droogteminnende struikvegetaties uit waar insecten, spinnen, hagedissen, vogels en Huismuizen *Mus musculus* de voedselbronnen voor de valken vormen. De valken begonnen eerder met eieren leggen als er in de voorafgaande herfst relatief veel regen was gevallen. Bovendien was het broedseizoen in zulke jaren uitgestrekter en deden er meer paren mee aan het broedproces dan onder drogere omstandigheden. De gemiddelde legselgrootte vertoonde een positieve correlatie met de regenval in de maand voorafgaande aan de eileg. Uitkomst- en uitvliegsucces verschilden niet tussen droge en natte jaren. De temperatuur had geen invloed op de broedparameters. Dat laatste had vermoedelijk te maken met het stabiele voedselaanbod in de jongen- en uitvliegfase van de valken. Kennelijk is de variatie in voedselaanbod groter in de eilegfase en de maand daaraan voorafgaand (en voldoende groot om de valken al dan niet te verleiden tot een vroegere start van de eileg en grotere legsels), maar verdwijnt dit voordeel in de loop van het voorjaar. De belangrijkste invloed van regen (niet temperatuur), in termen van reproductie, uit zich in het aantal paren dat tot broeden overgaat: weinig in droge jaren, veel in natte jaren. (RGB)

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