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Geo-environmental influences on breeding parameters of the Eurasian Kestrel (*Falco tinnunculus*) in the Western Palaearctic

José Carrillo & Enrique González-Dávila

*J. Carrillo, Department of Animal Biology (Zoology), Faculty of Biology, University of La Laguna, 38206 Tenerife, Spain (current address: Department of Ecology, Faculty of Biology, University of La Laguna, E-38206 La Laguna, Tenerife, Spain). * Correspondent author's e-mail: jchidal@ull.es*
E. González-Dávila, Department of Statistics, O.R. & Computation, Faculty of Mathematics, University of La Laguna, 38206 Tenerife, Spain. E-mail egonzale@ull.es

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Geographic location largely determines environmental factors such as photoperiod and primary productivity. Breeding effort in birds may reflect different responses to these geographic-related conditions. We studied geographic variation in mean laying date (LD) and mean clutch size (CS) of the Eurasian Kestrel (*Falco tinnunculus*) in relation to photoperiod, seasonality of resources, temperature and rainfall during the previous winter and breeding season. We assumed that actual evapotranspiration (AE) varies in direct proportion to primary plant production and food resources. Using published data on 23 Western Palaearctic regions (28–65° N) we found that variation in LD was related to photoperiod. Also, Kestrels bred earlier where winter and spring temperatures were higher, spring rainfall was lower and winter AE was higher. The variables that most affected CS were nest type (box/natural), winter AE and spring temperature. CS was directly related to the ratio between spring and winter AE. Moreover, CS was unrelated with spring AE but inversely related to winter AE. The effect of scarce resources (low AE) during the previous winter on CS supports Ashmole's hypothesis (Ashmole 1961). The data available are not sufficient to verify the influence of density of breeding adults on CS.

1. Introduction

Geographic location largely determines environmental factors, such as photoperiod and primary productivity. Birds use photic and non-photic cues (weather conditions and food) to regulate reproductive functioning; this changes with latitude and environmental conditions (Lambrechts & Perret 2000, Sanz 2003). In temperate regions, birds generally breed when cues suggest that there will be sufficient food for nestlings and favourable weather conditions (Lack 1968). Food availability is one of the main determinants of reproductive success in birds (Drent & Daan 1980, Martin 1987) and may influence the onset of egg laying (Daan *et al.* 1988, Aparicio 1998) and clutch size (Daan *et al.* 1988, Aparicio & Bonal 2002). However, other factors such as weather conditions (Dawson 2008), habitat type (Sanz 1998, Fargallo 2004) and photoperiod (Lambrechts *et al.* 1997, Dawson *et al*. 2001) influence reproductive effort to a greater or lesser extent depending on geographic location (Phillips *et al.* 1985, Sanz 1998).

In avian breeding ecology, geographic variation in timing of laying (Perrins & Birkhead 1983, Cockrem 1995) and in clutch size (Lack 1968, Ricklefs 2000, Cooper *et al.* 2005) is well known. Differences in the timing of laying between populations might reflect responses to changing photoperiod and not to any other proximate factor (Lambrechts *et al.* 1997). However, other non-photic stimuli also affect the timing of laying, e.g., food resources, temperature and rainfall (Dawson 2008). Regarding clutch size, seasonality of resources is hypothesized as being among the main factors explaining geographic variation, as the so-called Ashmole's hypothesis (Ashmole 1961, Lack 1968).

This hypothesis predicts that, during the breeding season, the effect of food resources on clutch size depends on population density. Furthermore, the hypothesis predicts that, if population density is conditioned by the scarcity of food during the winter season, the pairs that survive the winter will more likely have sufficient food for larger clutches. Therefore, environments with greater seasonal fluctuation in resources should favour larger clutch sizes. Ashmole's hypothesis predicts that clutch size should be (1) positively correlated with the ratio between summer and winter resource levels, (2) negatively correlated with winter resource levels, and (3) independent of spring resource levels.

However, potential problems for verifying this hypothesis occur in (a) partially migratory populations, because the exact proportions of residents and migrants in different geographic areas are usually not known, and (b) migratory populations, because the over-wintering locations may vary and are not known for all individuals.

Wide geographic range, single-broodedness and remarkable variation in laying date and clutch size (Village 1990) make the Eurasian Kestrel (*Falco tinnunculus*) a suitable species for examining variation in breeding parameters. This species is a small open-country raptor that breeds in a wide variety of nesting sites, and occupies most environments all over the Western Palaearctic. It is a territorial spring breeder, raising a single brood per season and hunts a wide variety of prey (Village 1990). Kestrels breed early and lay large clutches in years of high vole density (Cavé 1968, Dijkstra *et al.* 1988). This species shows different patterns of migratory behaviour depending on nesting geographic location (Village 1990).

Geo-environmental factors affect the breeding ecology of Kestrels at least in some Palaearctic areas. Observational studies performed in small isolated locations in the Netherlands (Oostelijk Flevoland and Lauwersmeer), Finland (Kauhava and Lapua), and Israel (Jordan Rift Valley) found that (1) high spring temperature tends to advance mean laying date, (2) high rainfall or low previous-winter or spring temperature are associated with delayed laying date and reduced mean clutch size (Cavé 1968, Meijer *et al.* 1988, Charter *et al.* 2007), (3) increased availability of food in winter and in spring is associated with advanced laying date (Cavé 1968), and (4) clutch size tends to be larger in years of increased vole populations (Korpimäki & Wiehn 1998).

In addition, photoperiod appears a determinant factor for laying date in captive Kestrels (Meijer *et al.* 1992). Despite these studies, however, the effects of photoperiod, food resources and weather conditions remain to be confirmed for larger geographic areas. We studied the influence of photoperiod, food resources and weather conditions on two breeding parameters, viz. laying date and clutch size, of the Kestrels over the Western Palaearctic. Specifically, we tested the main predictions of Ashmole's hypothesis, i.e., the correlations between clutch size and levels of seasonal resources.

2. Methods

2.1. Kestrel data

We obtained published data on laying date and clutch size from 23 different areas within 28–65° N and 17–28° E (Table 1). Latitude, longitude and altitude were either obtained from the literature or determined from topographical maps. For extensive areas we considered the central point of the region as a reference point. Regarding experimental studies, only data for the control group (unmanipulated nests; see below) were used. We only considered data from those regions where the number of controlled nests exceeded thirty during more

Table 1. Country, latitude (Lat), longitude (Lon), altitude of the study area (Alt, m asl), daylight in hours (Day), mean laying date and sample size (LD; 1 = 1 January, and nLD), mean clutch size and sample size (CS and nCS) and nest type (Nest; NN = natural nest, NB = nest-box) of Eurasian Kestrel populations in the Western Palaearctic region. – = data not available, * = data known but not used (see text), 1 = data for 1943 were excluded because this study reported only one breeding pair for that year, 2 = mean values for Tenerife, and 3 = data from two habitat types in Tenerife.

Country	Lat	Lon	Alt	Day	LD	nLD	CS	nCS	Nest	Period	Reference
Finland	65º	28º	–	*	–	–	5.12	233	NN	1963–66, 1974–77	Kuusela (1983)
Finland	63º	23º	300	17.13	127	287	5.46	287	NB	1985–96	Korpimäki & Wiehn (1998)
Finland	61º	24º	–	*	–	–	4.79	43	NN	1963–66, 1974–77	Kuusela (1983)
Norway	61º	9º	511	*	–	–	4.93	31	NN	1942–46[1]	Hagen (1969)
Scotland	56º	–3º	200–540	15.23	122	129	5.00	120	NN	1976–79	Village (1986)
Scotland	55º	–3º	200–540	15.23	123	127	5.00	139	NN	1976–79	Village (1990)
The Netherlands	53º	5º	0	15.04	122	213	5.12	213	NB	1977–86	Meijer *et al.* (1988)
England	53º	–1º	50	15.39	132	263	4.50	247	NN	1981–87	Village (1990)
Germany	53º	16º	0–1	15.02	114	155	4.54	130	NN	1986–94	Kostrzewa & Kostrzewa (1997)
The Netherlands	52º	6º	0	14.46	119	492	5.27	492	NB	1960–64	Cavé (1968)
Germany	52º	9º	4–463	14.54	120	486	5.22	1510	NB	1985–94	Kostrzewa & Kostrzewa (1997)
Czech Republic	50º	16º	200	14.44	121	268	4.68	268	NN	1986–89	Pikula *et al.* (1984) in Village (1990), Plesník & Dusík (1994)
Germany	49º	9º	53–263	14.28	118	556	5.26	560	NB	1982–94	Kostrzewa & Kostrzewa (1997)
France	47º	4º	400	14.07	115	82	4.72	82	NN	1973–80	Bonin & Strenna (1986)
Switzerland	46º	8º	–	*	–	–	4.98	100	NN	–	Géroudet (1978)
France	45º	1º	488	*	–	–	4.77	45	NN	1976–79	Nore (1979)
Italy	41º	12º	43–139	13.41	110	464	4.46	464	NB	1999–2007	Costantini *et al.* (2009)
Spain (Iberian P.)	40º	–4º	1300	14.09	123	82	5.00	84	NB	1993–98	Fargallo *et al.* (2001)
Spain (Iberian P.)	40º	–4º	1300	14.09	129	34	4.87	31	NN	1993–98	Fargallo *et al.* (2001)
Mallorca island	39º	3º	10–250	13.40	116	101	4.47	83	NN	1988–93, 2000–03	Mestre & Vidal (unpubl. data)
Algeria &Tunisia	32º	6º	–	*	–	–	4.53	32	NN	–	Heim de Balsac & Mayaud (1962)
Israel	32º	35º	-(150–250)	12.38	*	*	4.70	50	NB	1999–2006	Charter *et al.* (2007)
Israel	32º	35º	-(150–250)	12.38	*	*	4.06	32	NN	1999–2006	Charter *et al.* (2007)
Morocco	31º	–4º	–	12.54	104	40	4.80	40	NN	1979–82	Bergier (1987)
Tenerife island[2]	28º	–17º	0–2400	12.09	80	120	4.41	133	NN	1985–94	Carrillo & González-Dávila (2005)
Tenerife xerophytic scrub[3]	28º	–17º	75–500	12.04	77	103	4.45	112	NN	1985–94	Carrillo & González-Dávila (2005)
Tenerife subalpine scrub[3]	28º	–17º	1200–2400	12.53	107	17	4.11	18	NN	1985–94	Carrillo & González-Dávila (2005)

than four years. This was to minimize the variation resulting from inter-annual differences in productivity due to fluctuations in food resources, an aspect particularly relevant in unstable environments (Korpimäki & Norrdhal 1991). We also included data from Kestrel nest-box populations to test the effect of nest type (Carrillo & González-Dávila 2009). The effects of climate change (i.e., increasing spring temperatures) over the last two decades may affect the breeding biology of birds by advancing the laying date or affecting the breeding success (Crick 2004). Hence, we considered the mean year of the study period in each population to be representative in terms of temperature.

Here, laying date is the mean laying date of a given population over all study years, and was recorded in Julian dates. In Tenerife Island, there is a gradient in laying date along altitude; therefore, laying date had two different values to reflect a one-month delay in laying date above 1,000 m altitude, as compared with laying date of the sea level (Carrillo & González-Dávila 2005). Clutch size is here the weighted average of the annual mean clutch size values per number of clutches. We used mean laying date and clutch size values for all

Table 2. Ten best models explaining (a) laying date (LD) and (b) clutch size (CS) using generalized linear models with quasi-Akaike's Information Criterion (AIC_c). df = degrees of freedom, $\Delta_i = (AIC_c)_i – \min AIC_c$, $w_i = \exp(–\Delta_i/2)/\Sigma \exp(–\Delta_r/2)$. For parameter abbreviations, see text.

Model								df	AIC_c	Δ_i	w_i
a) Laying date (LD)											
1	PHOT	TEMP SPRI	TEMP WINT	RAIN SPRI	RAIN WINT			5	128.07	0.00	0.0352
2	PHOT	AE WINT	TEMP SPRI	TEMP WINT	RAIN SPRI	RAIN WINT		6	129.27	1.21	0.0193
3	PHOT	AE SPRI	TEMP SPRI	TEMP WINT	RAIN SPRI	RAIN WINT		6	129.49	1.42	0.0173
4	PHOT	YEAR	TEMP SPRI	TEMP WINT	RAIN SPRI	RAIN WINT		6	129.73	1.66	0.0153
5	PHOT	AE SPRI						2	129.78	1.71	0.0150
6	PHOT	AE WINT	AE SPRI	TEMP SPRI	TEMP WINT	RAIN SPRI	RAIN WINT	7	129.78	1.72	0.0149
7	PHOT	TEMP SPRI	RAIN SPRI					3	129.79	1.73	0.0148
8	PHOT	TEMP SPRI	TEMP WINT	RAIN SPRI	RAIN WINT	NEST TYPE		6	129.99	1.93	0.0134
9	PHOT	RAIN SPRI						2	130.12	2.06	0.0126
10	PHOT							1	130.15	2.09	0.0124
b) Clutch size (CS)											
1	NEST TYPE	TEMP SPRI						2	–6.82	0.00	0.0156
2	NEST TYPE	TEMP SPRI	RAIN SPRI	RAIN WINT				4	–6.66	0.17	0.0143
3	NEST TYPE	TEMP SPRI	RAIN SPRI	RAIN WINT	AE SPRI			5	–6.21	0.61	0.0115
4	NEST TYPE	TEMP SPRI	AE WINT					3	–6.01	0.82	0.0103
5	NEST TYPE	TEMP SPRI	AE SPRI					3	–5.88	0.94	0.0097
6	NEST TYPE	TEMP SPRI	RAIN WINT					3	–5.77	1.05	0.0092
7	NEST TYPE	TEMP SPRI	RAIN SPRI					3	–5.68	1.14	0.0088
8	NEST TYPE	TEMP SPRI	TEMP WINT					3	–5.67	1.15	0.0087
9	NEST TYPE	TEMP SPRI	AE SPRI	RAIN SPRI				4	–5.65	1.17	0.0087
10	NEST TYPE	TEMP SPRI	AE SPRI	AE WINT				4	–5.58	1.24	0.0084

study areas except for Norway and Switzerland with missing values (Table 1).

2.2. Environmental variables used in the analyses

We considered the main abiotic environmental variables influencing Kestrel breeding ecology as being the following (Cavé 1968, Meijer *et al.* 1988, Kostrzewa & Kostrzewa 1991, Charter *et al.* 2007): (1) mean spring temperature (TEMP SPRI; in °C × 10); (2) mean winter temperature (TEMP WINT; in °C × 10); (3) mean spring rainfall (RAIN SPRI; in mm × 10) and (4) mean winter rainfall (RAIN WINT; in mm × 10). These were obtained from the Climatic Research Unit of the University of East Anglia (data from 1961 to 1990; Climatic Impacts Link Project; http://ipcc-ddc.cru.uea.ac.uk/obs/get_30yr_means.html).

The variation in actual evapotranspiration (AE) depends on the relationship between primary plant production and Kestrel food resources (Ricklefs 1980). We used estimates of relative resource abundance based on AE, separately for spring and winter months (AE SPRI and AE WINT, respectively).

For northern populations, i.e., those above 44º N, we considered April and May as spring and February and March as winter months; for Mediterranean populations, i.e., areas below 44º N, March and April represented spring January and February winter months. We calculated photoperiod (PHOT; in hours) using the Lammi formula (Lammi 1996–2001) and applied the mean laying date of the year of publication. AE SPRI and AE WINT were obtained from the United Nations Environment Programme (http:// www.grid.unep.ch/data).

We included the AE data provided by Thornthwaite-Mather method to supplement the lack of information on Mallorca and Tenerife islands (http://personales.com/colombia/manizales/BALANCEHIDRICO). We obtained all environmental variables according to the geographic coordinates of the study areas, except for Switzerland

Table 3. Model averaging under AIC_c selection for laying date (LD; a) and clutch size (CS; b). The effects with $P < 0.10$ are bolded. Estimate = effect estimate, SE = standard error for that, WALD = Wald statistic. For parameter abbreviations, see text.

Variable	Estimate	SE	WALD	*P*
(a) Laying date (LD)				
Intercept	0.882	3.017	0.085	0.7701
YEAR	0.001	0.001	0.826	0.3635
AE SPRI	–0.001	0.001	1.763	0.1843
AE WINT	–0.001	0.001	2.252	0.1334
TEMP SPRI	**–0.004**	**0.001**	**9.595**	**0.0020**
TEMP WINT	**0.004**	**0.001**	**9.594**	**0.0020**
RAIN SPRI	**0.023**	**0.008**	**8.889**	**0.0029**
RAIN WINT	**–0.016**	**0.006**	**7.495**	**0.0062**
PHOT	**0.103**	**0.027**	**14.481**	**0.0001**
NEST TYPE	0.005	0.014	0.131	0.7178
(b) Clutch size (CS)				
Intercept	10.3053	9.4246	1.1956	0.2742
YEAR	–0.0043	0.0047	0.8178	0.3658
AE SPRI	–0.0006	0.0004	1.9813	0.1593
AE WINT	–0.0004	0.0007	0.2886	0.5911
TEMP SPRI	**–0.0014**	**0.0008**	**2.8857**	**0.0894**
TEMP WINT	0.0003	0.0006	0.1820	0.6697
RAIN SPRI	**0.0061**	**0.0027**	**5.1558**	**0.0232**
RAIN WINT	**–0.0026**	**0.0015**	**3.2003**	**0.0736**
PHOT	0.0170	0.0179	0.9111	0.3398
NEST TYPE	**–0.0979**	**0.0173**	**31.8585**	**0.0000**
LD	–0.0029	0.0024	1.4594	0.2270

with an unspecified study area we considered the central point of the region as a reference point.

2.3. Statistical analysis

Generalized linear models of breeding parameters (laying date and clutch size), using quasi Akaike's Information Criterion (AIC_c), were performed by introducing the following explanatory variables: TEMP SPRI, TEMP WINT, RAIN SPRI, RAIN WINT, AE SPRI, AE WINT, YEAR, PHOT and NEST TYPE (nest-box or natural nest) into the candidate models. AIC_c is a measure of the goodness-of-fit of an estimated statistical model which simultaneously balances its precision against its complexity (Burnham & Anderson 2002). The final model was the average of all models using Akaike weights among those models (Burnham & Anderson 2002).

We used the ratio between breeding-period resources (AE SPRI) and non-breeding-period resources (AE WINT) to test if clutch size consistently varies along a gradient of AE SPRI : AE WINT ratio, as predicted by Ashmole's hypothesis. We used generalized logarithmic equations and AIC_c to analyse the effects of AE SPRI and AE WINT on the breeding parameters. We employed Pearson's correlation coefficient to determine relationships between any two continuous variables, such as AE SPRI and clutch size, and for partial correlations intended to take into account the effects of a third variable. All tests were two-tailed, and a P value of < 0.05 was considered statistically significant. All numerical values are presented as means ± 1 S.D. Data were analyzed using SPSS 17.0 (SPSS Inc., Chicago, U.S.A.) and STATISTICA 6.0 (STATISTICA Inc.; Statsoft, www.statsoft.com.).

3. Results

According to AIC_c, the best model explaining mean laying date included PHOT, TEMP SPRI, TEMP WINT, RAIN SPRI and RAIN WINT

Table 4. (a) Pearson's correlation coefficients between environmental variables and breeding parameters: mean laying date (LD, from 18 regions) and mean clutch size (CS, from 25 regions) in Eurasian Kestrel populations from the Western Palaearctic region. (b) Partial correlations between LD *versus* temperature and rainfall variables after controlling for photoperiod (PHOT). Significant correlations after adjusting P values with sequential Bonferroni correction are bold-faced. For abbreviations of environmental variables, see text.

a) Pearson	LD	TEMP SPRI	TEMP WINT	RAIN SPRI	RAIN WINT	AE SPRI	AE WINT	PHOT
CS	**0.543**	**–0.571**	**–0.592**	0.067	–0.301	0.106	**–0.519**	**0.588**
LD		**–0.730**	**–0.644**	**0.241**	0.001	**0.561**	**–0.630**	**0.759**
TEMP SPRI			**0.912**	–0.314	0.121	–0.244	**0.565**	**–0.842**
TEMP WINT				–0.102	0.332	–0.211	**0.676**	**–0.889**
RAIN SPRI					**0.701**	0.378	–0.018	0.095
RAIN WINT						0.355	0.293	–0.393
AE SPRI							**–0.391**	0.260
AE WINT								**–0.672**

b) Partial	PHOT	TEMP SPRI	TEMP WINT	RAIN SPRI	RAIN WINT
LD	–0.316	0.031	0.304	0.143	

(Table 2). Table 2 shows ten best models, and Table 3a shows model averaging under AIC_c selection for laying date. After controlling for the variable with the greatest weight (i.e., PHOT), partial correlations between laying date and the other variables of the best model were non-significant (Table 4). With PHOT as the only variable affecting laying date (model 10 in Table 2), we found that laying date = 8.191 + 7.599 PHOT ($F_{1,16}$ = 21.68, R^2 = 0.58, P < 0.001). A more realistic model which does not predict an unlimited delay in laying dates towards the north was obtained using logarithmic regression laying date = –179.738 + 111.635 log(PHOT) (Fig. 1; $F_{1,16}$ = 25.35, R^2 = 0.61, P < 0.001). The data from Tenerife (xerophytic scrub) and the Iberian Peninsula diverged from the main tendency as displayed by the regression line, but data from one region compensates for those of the other. Also, Kestrels bred earlier the higher the temperature (TEMP WINT and TEMP SPRI), the lower the spring rainfall (RAIN SPRI) and the higher the winter evaporation (AE WINT) (Table 4).

According to AIC_c the best models explaining clutch size are shown in Table 2; for model averaging under AIC_c selection, see Table 3b. The values of Akaike weights indicate that the models are practically interchangeable. Of these models, the best one included NEST TYPE and TEMP SPRI ($F_{2,22}$ = 32.10, R^2 = 0.75, P < 0.001; clutch size = 5.610 – 0.465 NEST TYPE– 0.005 TEMP SPRI). This finding indicates that at constant spring thermal conditions, clutch size was 0.46 ± 0.08 SE eggs lower in natural nests than in nest-boxes.

Clutch size and the AE SPRI : AE WINT ratio significantly correlated with each other (r = 0.51, P = 0.01). When using a transformed, logarithmic equation and applying AIC_c, the average model was log clutch size = 0.437 − 0.022 log AE WINT + 0.016 log AE SPRI (SE for log AE WINT = 0.009; SE for log AE SPRI = 0.011). Clutch size was not significantly related to AE SPRI (P > 0.05) but was inversely related to AE WINT (r = –0.52; P = 0.008; Fig. 2).

4. Discussion

In the Kestrel populations of the Western Palaearctic, photoperiod was the main but not sole factor associated with variation in laying dates. Kestrels bred earlier where winter and spring temperatures were higher and spring rainfall was lower. Laying date was also correlated with spring-season evaporation. Climatic factors such as rainfall, winter and spring temperature, related with laying date, probably exert a direct influence on male hunting activity (Cavé 1968, Meijer *et al.* 1990). Increased food supply for the female could trigger the onset of laying within the annual limits set by a particular endogenous system synchronized by the photoperiod (Meijer 1989, Meijer *et al.* 1992). Our

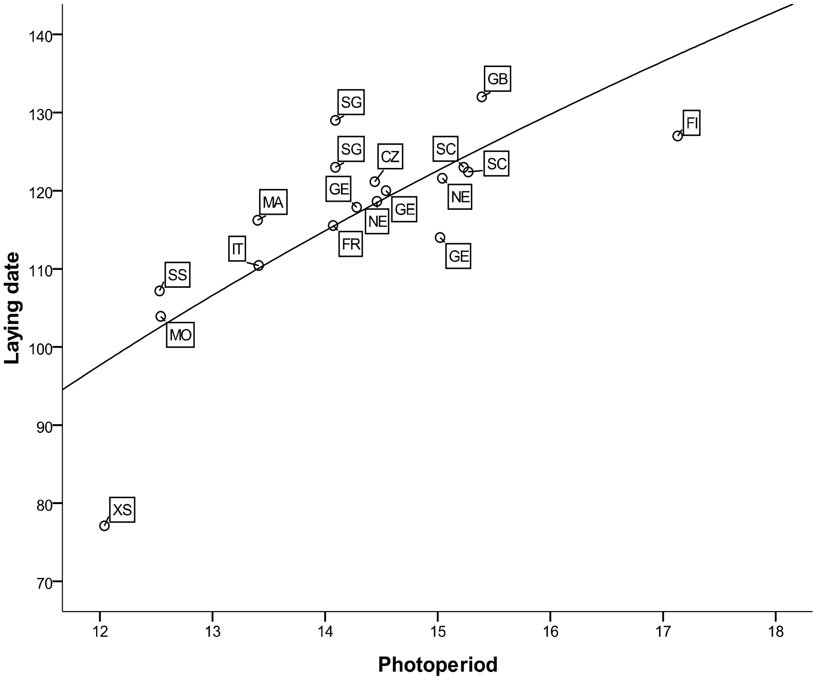

Fig. 1. Variation in mean laying date (LD, 11 March = day 70) according to photoperiod (PHOT) in Eurasian Kestrel populations of the Western Palaearctic region. Regression eq.: LD = –179.738 + 111.635 log (PHOT). Areas considered: CZ (Czech Republic); FI (Finland); FR (Auxois, France); GB (Great Britain); GE (Germany); IT (Roma, Italy); MA (Mallorca Island); MO (Morocco); NE (The Netherlands); SC (Scotland); SG (Segovia, Spain); SS (subalpine scrub and northern pine forest above 1,000 m asl of Tenerife Island); XS (xerophytic scrub below 1,000 m asl of Tenerife Island).

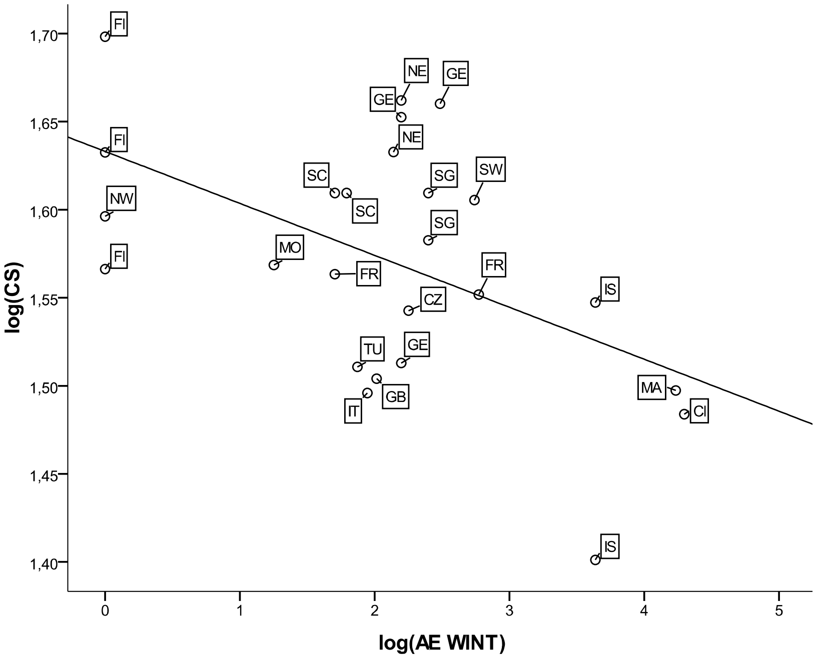

Fig. 2. Relationship between mean clutch size (CS) and winter actual evapotranspiration (AE WINT; logarithmic scale) in Eurasian Kestrel populations of the Western Palaearctic region: CI (Tenerife Island, Canary Islands); CZ (Czech Republic); FI (Finland); FR (France); GB (Great Britain); GE (Germany); IS (Israel); IT (Italy); MA (Mallorca Island); MO (Morocco); NE (The Netherlands); NW (Norway); SC (Scotland); SG (Iberian peninsula, Spain); SW (Switzerland); TU (Tunisia).

results diverge from the postulate of Lambrechts *et al.* (1997) in that differences in laying date among Kestrel populations cannot be solely explained by photoperiod; food resources and weather conditions were clearly involved too.

Laying date of Kestrels positively correlates with latitude in the Western Palaearctic region (Carrillo & González-Dávila 2009). Contrary to this general trend, however, kestrel populations in central Spain (39–40º N) breed later than more northerly European populations, for reasons that are not clear (Moreno 2004). Two main, mutually non-exclusive hypotheses may explain this. The first is the degree of migration that is higher the further north a given Kestrel population breeds. These northern Kestrels may over-winter further south than do southern breeders (e.g., Spanish Kestrels) whose populations are generally sedentary or partial migrants (Village 1990). As long-distance migrants advance their breeding phenology in response to climatic cues (Sanz 2002), these northern Kestrels may have a narrower "temporal window" for breeding and postnuptial moult before migration than their southern counterparts have. Secondly, diet differences may be important. Northern populations feed mainly on endothermic prey (i.e., microtine voles).

Maximum levels of food resources are achieved slowly further south after the onset of spring (Ricklefs 1980). The Spanish Kestrels mostly depend on ectothermic prey (i.e., insects and reptiles) during the nestling period; in early spring, they must wait for their prey to become active and abundant (Aparicio 1990, Gil-Delgado *et al.* 1995). A delay in the feeding behaviour of male courtship may in turn delay the body-reserve and egg formation in the female (Meijer *et al.* 1990). However, the differences in laying date between populations could also be explained by adaptive genetic divergence (Casagrande *et al*. 2006), the age of the pair members or their previous breeding experience (Village 1986). The data available do not allow us to support one hypothesis over another.

If seasonal fluctuation in food supply was the main determinant of the geographic tendencies in clutch size (Ricklefs 1980), the density of territorial breeding pairs would be influenced primarily by winter mortality (Village 1985, Kostrzewa & Kostrzewa 1991). Therefore, environments with greater seasonal fluctuation in resources should favour larger clutch sizes. Our findings are consistent with this idea; we observed a significant tendency towards a northward increase in clutch size to be related to the seasonality of food resources. However, we could not verify whether variation in clutch size is influenced by the breeding density of Kestrels, because most of the studies considered do not provide density data. However, another explanation is possible: mild winters in the southern Palaearctic could favour the survival of low-quality females that produce small clutches, thus reducing the mean clutch size of the population.

Southern regions, such as the Iberian Peninsula, are wintering areas for northern Kestrels (Village 1990). The reason why resource competition does not manifest in a greater-than-observed clutch size could occur because wintering Kestrels feed on different and less abundant prey (i.e., mantids and flying ants) as compared to residents who prey on mammals and crickets (Aparicio 2000). So, territory holding by residents would confer an advantage for resources of higher nutritional value and an avoidance of competition with migrant individuals (Newton 1979).

Geo-environmental variation in clutch size may be attributable to nest-box breeding (Carrillo & González-Dávila 2009, present study) because natural nests suffer higher predation rates than nest-boxes (Kostrzewa & Kostrzewa 1997, Fargallo *et al.* 2001). In addition, nest dimensions may not significantly affect clutch size (Fargallo *et al.* 2001, Carrillo & González-Dávila 2005). Without detailed information on predation for different regions, we cannot confirm if clutch size decreases with increasing predation (Martin 1992). However, a previous study suggests that predator density may not significantly influence clutch size in natural nests (Carrillo & Aparicio 2001).

A possible limitation of the present study is the migratory behaviour in Kestrels. The proportion of short- and long-distance migrants and residents varies over the Western Palaearctic region but the migratory strategy may also vary within a given population (Village 1990). In addition, winter evaporation does not reflect food resources for migrants whose wintering destination may depend on their breeding area and is not known for all individuals (Village 1990).

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Maantieteellisten ympäristötekijöiden vaikutukset tuulihaukan pesimämuuttujiin länsipalearktisella vyöhykkeellä

Maantieteellinen sijainti vaikuttaa paljon ympäristötekijöihin, kuten valojaksoisuuteen ja perustuottavuuteen. Lintujen pesimäpanostus saattaa heijastella erilaisia vasteita näihin maantieteellisistä olosuhteista riippuviin tekijöihin. Tutkimme tuulihaukan (*Falco tinnunculus*) keskimääräisen muninta-ajankohdan ja pesyekoon maantieteellistä vaihtelua suhteessa valojaksoisuuteen, resurssien vuodenaikaisuuteen, lämpötilaan sekä edellistalven ja pesimäkauden sademäärään. Oletimme, että haihtumisen (evapotranspiraation) määrä on suorassa suhteessa kasvien perustuottavuuteen ja ravintoresursseihin.

Käyttämällä julkaistuja aineistoja 23 alueelta länsipalearktisella vyöhykkeellä (28–65° N) havaitsimme, että haudonta-ajankohta riippui valojaksoisuudesta. Tuulihaukat myös pesivät aiemmin, kun talven ja kevään lämpötilat olivat korkeampia, keväällä satoi vähemmän ja talven haihdunta oli vähäisempää.

Pesyekokoon vaikuttivat voimakkaimmin pesätyyppi (pesälaatikko tai luonnonpesä), talven haihdunta ja kevään lämpötila. Pesyekoko riippui suoraan kevään ja talven haihdunnan suhteesta, ei riippunut kevään haihdunnasta mutta oli kääntäen riippuvainen talven haihdunnasta. Edellistalven resurssien niukkuuden (alhaisen haihdunnan) vaikutus pesyekokoon tukee nk. Ashmolen hypoteesiä. Käytettävissä ollut aineisto ei anna eväitä arvioida pesivien parien tiheyden vaikutusta pesyekokoon.

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