# Temporal covariation of egg volume and breeding conditions in the Common Kestrel (*Falco tinnunculus*) in the Mediterranean region

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Most studies on variation in egg size in the Common Kestrel (*Falco tinnunculus*) have been carried out in central and northern Europe, whereas less is known about populations in the Mediterranean basin. We investigated the variation in egg volume in a Mediterranean population of Common Kestrel over a six-year period in relation to clutch size, breeding time, hatching success, and weather conditions. Eggs were generally bigger in larger clutches, and egg volume tended to decrease over the breeding season, but these patterns were not consistent among breeding seasons. Egg volume did not significantly vary in relation to weather conditions and did not predict hatching or fledging success. This study showed that (a) the patterns of covariation among laying date, clutch size and egg volume varied inconsistently over multiple years, and (b) egg volume poorly predicted the probabilities of hatching and fledging in the studied population.

## 1. Introduction

Egg size is one of the most widely studied life-history traits in evolutionary ecology (Williams 1994, Bernardo 1996, Christians 2002). Although a number of factors have been proposed to explain variation in egg size among and within species (e.g., food availability, female age and genetics), the selective forces that maintain such variation remain poorly understood (Williams 1994, Bernardo 1996, Christians 2002). Nutritional or physical limitations can constrain the amount of resources deposited in the egg and hence its size (Congdon & Gibbons 1987, Christians 2002). However, supplemental food or enhanced food quality rarely increase egg size. Parental attributes may contribute to variation in egg size, but body mass, size or condition of a female generally explain less than 20% of variation in egg size (Christians 2002). Female age is another factor potentially affecting egg volume, although its effect varies among species, and likely depends on the life-history strategy evolved by the species itself. In some species, egg size increases from young to intermediate maternal ages and then decreases (Sydeman & Emslie 1992), whereas in others it tends to decline with maternal age (Reid 1988). Finally, it has also been suggested that a genetic component can constrain egg volume and explain the low intra-clutch variation, as observed in many species (Väisänen *et al.* 1972, van Noordwijk *et al.* 1981, Bernardo 1996; see also tables 1 and 2 in Christians 2002).

Table 1. Descriptive statistics (*N* or mean ± standard error) for egg length (mm), egg width (mm) and egg volume (cm$^3$), measured in a Mediterranean population of Common Kestrels during 2002–2007. Variation in egg volume among different clutch sizes, within a given year, was tested using Tukey's test. Statistically significant results are indicated with the letter a (significant difference between 4- and 5-egg clutches), b (between 4- and 6-egg clutches) or c (between 5- and 6-egg clutches).

| Year | Clutch size | *N* clutches | *N* eggs | Egg length | Egg width | Egg volume |
|---|---|---|---|---|---|---|
| 2002 | 4 | 6 | 23 | 38.50 ± 0.43 | 30.68 ± 0.26 | 18.57 ± 0.49b |
| | 5 | 25 | 122 | 38.79 ± 0.14 | 31.13 ± 0.09 | 19.20 ± 0.15c |
| | 6 | 7 | 42 | 39.78 ± 0.23 | 31.29 ± 0.15 | 19.91 ± 0.27b,c |
| Total, 2002 | | 38 | 187 | 38.97 ± 0.12 | 31.11 ± 0.08 | 19.28 ± 0.13 |
| 2003 | 4 | 15 | 60 | 38.90 ± 0.16 | 31.26 ± 0.11 | 19.42 ± 0.20a,b |
| | 5 | 35 | 173 | 39.21 ± 0.10 | 31.52 ± 0.06 | 19.89 ± 0.10a |
| | 6 | 19 | 111 | 39.53 ± 0.14 | 31.46 ± 0.09 | 19.99 ± 0.16b |
| Total, 2003 | | 69 | 344 | 39.26 ± 0.07 | 31.46 ± 0.05 | 19.84 ± 0.08 |
| 2004 | 4 | 15 | 60 | 38.78 ± 0.15 | 30.97 ± 0.10 | 18.97 ± 0.14b |
| | 5 | 34 | 159 | 39.10 ± 0.12 | 31.15 ± 0.08 | 19.39 ± 0.13c |
| | 6 | 3 | 18 | 39.39 ± 0.25 | 31.73 ± 0.20 | 20.26 ± 0.35b,c |
| Total, 2004 | | 52 | 237 | 39.04 ± 0.09 | 31.15 ± 0.06 | 19.35 ± 0.10 |
| 2005 | 4 | 9 | 36 | 39.47 ± 0.30 | 30.78 ± 0.20 | 19.10 ± 0.29 |
| | 5 | 26 | 122 | 38.92 ± 0.12 | 31.27 ± 0.09 | 19.44 ± 0.14 |
| | 6 | 15 | 90 | 39.22 ± 0.15 | 30.97 ± 0.11 | 19.23 ± 0.18 |
| Total, 2005 | | 50 | 248 | 39.11 ± 0.09 | 31.09 ± 0.07 | 19.31 ± 0.10 |
| 2006 | 4 | 3 | 12 | 39.55 ± 0.48 | 31.28 ± 0.24 | 19.76 ± 0.42 |
| | 5 | 27 | 131 | 39.03 ± 0.13 | 31.07 ± 0.09 | 19.24 ± 0.13 |
| | 6 | 9 | 54 | 39.16 ± 0.19 | 31.44 ± 0.12 | 19.76 ± 0.20 |
| Total, 2006 | | 39 | 197 | 39.09 ± 0.11 | 31.18 ± 0.07 | 19.42 ± 0.11 |
| 2007 | 4 | 5 | 20 | 38.87 ± 0.40 | 30.91 ± 0.20 | 18.97 ± 0.37b |
| | 5 | 24 | 117 | 39.21 ± 0.15 | 31.41 ± 0.10 | 19.77 ± 0.15 |
| | 6 | 3 | 18 | 39.76 ± 0.24 | 31.69 ± 0.14 | 20.37 ± 0.22b |
| Total, 2007 | | 32 | 155 | 39.23 ± 0.13 | 31.38 ± 0.08 | 19.73 ± 0.13 |

The extent that egg size may influence offspring fitness is a poorly understood topic (Williams 1994, Christians 2002), and studies report either positive or no significant associations between egg size and hatching or fledging success. For example, in some studies egg size was positively correlated with hatching success or nestling survival (Magrath 1992, Nilsson & Svensson 1993, Wiebe & Bortolotti 1996, Valkama *et al.* 2002, Wagner & Williams 2007), whereas in others such correlations were not found (Reid & Boersma 1990, Smith *et al.* 1993). The primary benefit of larger eggs might be to increase the chances of survival in the first few days after hatching (Williams 1994), but such benefits might only emerge in low-quality environments (Smith *et al.* 1995). Recent evidence suggests that specific egg components, such as hormones and antioxidants, rather than size, might affect the development of the embryo and the survival of offspring (e.g., Schwabl 1993, Mousseau & Fox 1998, Groothuis *et al.* 2005, Carere & Balthazart 2007).

Variation in egg size in Common Kestrels (*Falco tinnunculus*) has been well studied in temperate regions (central and northern Europe), while less is known about this species in other regions, such as the Mediterranean basin (Aparicio 1999). In this article, we analysed the variation in egg volume in a Mediterranean population of Common Kestrel over a six-year period in relation to clutch size, breeding time, hatching success, and weather conditions. We also explored possible covariance among traits to evaluate their consistency over multiple years.

## 2. Material and methods

### 2.1. Study species, study area and data collection

The Common Kestrel is a single-brooded, open-area associated bird of prey that is common throughout the Mediterranean basin (Village 1990). In contrast to northern populations, Kestrels in the region of the present study have a broader diet and are year-round residents with some winter dispersion mostly by juveniles (Cramp & Simmons 1980, Village 1990, Brichetti & Fracasso 2003, Costantini *et al.* 2005, 2007).

The field study was carried out from 2002 to 2007 in the countryside of Rome, Italy, within an area of about 1200 km$^2$. Data from 280 clutches (46.7 clutches/year; 118 nest boxes) for a total number of 1368 eggs were collected (Table 1). Reproductive data were collected from nest boxes attached to pylons of power lines. These nest boxes were primarily (80%) in cultivated (cereal fields) and uncultivated areas (fallow fields and pastures). The nest boxes were visited every 3–5 days from the end of March to mid-July to assess the occupation and to record laying date, clutch size, hatching success and fledging success (see also Costantini *et al.* 2010). Kestrels lay eggs in one-day intervals and incubate them for 27–29 days (Cramp & Simmons 1980, Global Raptor Information Network 2009, authors' personal observations). Thus, the laying date was estimated by recording the day of the first egg laid or by subtracting 33, 34, or 35 days from the hatching date of four, five and six-egg clutches, respectively. The hatching date was estimated by a growth curve using the wing length as a dependent variable (maximum error ± 1 day) or by observing the actual hatching event. Sample sizes may differ among reproductive variables because not all data were recorded from each nest. For each egg, the length and the width were measured, and the egg volume was calculated using Hoyt's (1976) formula:

$$\text{Egg length}^2 \times \text{Egg width} \times 0.51 \qquad (1)$$

Data on maximum daily temperatures and daily rainfall were obtained from two meteorological stations in the study area: Porta Maggiore and Tor Bella Monaca (http://www.romameteo.it)

Monthly mean maximum temperatures and total monthly rainfall were calculated and subsequently averaged for each climatic variable because the values collected from the two stations correlated strongly ($r \geq 0.90$). The period December–February was considered winter, and March–April (laying phase; Costantini *et al.* 2010) was considered early spring. For statistical purposes, variation in weather was compressed into a single variable ("weather index"; PC1) obtained from Principal Components Analysis (Grosbois *et al.* 2008). Here, higher values of PC1 indicate rainier winter and spring seasons and lower winter- and spring-season maximum temperatures.

### 2.2. Statistical analyses

Generalized Linear Mixed Models in SPSS (version 15.0) were used to determine the factors accounting for egg volume variation. Individual egg was always used as a sampling unit. A given nest box may have appeared more than once in the data because they were monitored for multiple years. Thus, some pairs could have contributed with more than one brood to the dataset. For this reason, Nest box ($n = 118$) was included as a random factor to account for inter-dependence of the sampling units (eggs). Year was included as a random factor, while Clutch size, Hatching date, and Weather index (PC1) were included as covariates. We also considered the interactions Clutch size × Year, Clutch size × Hatching date, and Hatching date × Year.

The power of egg volume in predicting hatching or fledging success was evaluated as follows. First, Generalized Linear Mixed Models were used to evaluate whether the egg volume differed between hatched and unhatched eggs, including only clutches for which both hatched and unhatched eggs were recorded (39 clutches, 191 eggs). Clutch and Year were included as random factors, Hatching success of the egg was included as a fixed factor (0 = unhatched; 1 = hatched), and Clutch size and Hatching date were treated as covariates. We also included the interactions Clutch size × Hatching success, Year × Hatching success, and Hatching date × Hatching success into the model. Second, Generalized Linear Mixed Models were used to evaluate whether the within-

clutch mean values of egg volume predicted the hatching or fledging success of the whole clutch or brood, respectively. In each model, Year was included as a random factor and Egg volume was included as a covariate. The model also included the interaction between Year and Egg volume. Hatching success (ratio between the number of hatchlings and the clutch size) or fledging success (ratio between the number of fledglings and the number of hatchlings) were included as dependent variables.

Significant ($p < 0.05$) covariation or interactions between the main factor and a covariate were evaluated using Pearson correlations to obtain the sign and magnitude of the covariation. Here, within-clutch mean values were used to avoid pseudoreplication. The intra-nest correlation coefficient was calculated according to Lessells & Boag (1987) to show the intra-nest-box repeatability of egg volume. Interactions were removed from the models when not significant, and the analyses were subsequently repeated, following Engqvist (2005). Degrees of freedom were calculated using the Satterthwaite's approximation method.

## 3. Results

Egg volume ($n = 1{,}368$; mean $\pm$ SE and range: $19.51 \pm 0.04$ cm$^3$, $12.49$–$25.38$ cm$^3$) was characterized by significant variation among nest boxes with an intra-nest-box correlation coefficient of $0.47$ ($p < 0.001$). Such variation was mainly due to differences in egg length rather than in egg width. Although the length and width of an egg were generally correlated (for within-nest mean values $r = 0.55$, $p < 0.001$), the variation in egg length (SD $1.48$, range $11.71$ mm) was higher than that of egg width (SD $0.97$, range $7.25$ mm).

Eggs were bigger in larger clutches ($F_{1,1352.5} = 22.44$, $p < 0.001$; Fig. 1), but this pattern varied among breeding seasons (Clutch size $\times$ Year: $F_{5,426.8} = 8.86$, $p < 0.001$). In 2005, bigger eggs were recorded from five-egg clutches, and in 2006 bigger eggs were recorded from four- and six-egg clutches (Table 1). Egg volume generally decreased over the breeding season ($F_{1,1351.2} = 32.17$, $p < 0.001$; $r = -0.14$), but this pattern varied among breeding seasons (Hatching date $\times$ Year: $F_{5,144.7} = 4.43$, $p < 0.001$). In 2006, a positive correlation be-
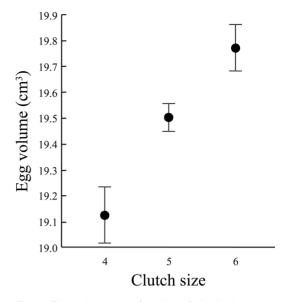


Fig. 1. Egg volume as a function of clutch size (mean ± standard error).

tween egg volume and hatching date was found ($r = 0.16$), whereas in the other years the correlation was negative and the magnitude of the correlation ($r$) varied between $-0.06$ and $-0.38$. The decrease in egg volume over the breeding season also differed among clutches (Cutch size $\times$ Hatching date: $F_{1,1353.0} = 26.16$, $p < 0.001$; Fig. 2). Finally, egg volume variation was not explained by changes in weather conditions ($F_{1,2.917} = 1.80$, $p = 0.27$).

In the full model, hatched (mean $\pm$ SE, $19.00$ cm$^3$ $\pm 0.12$, $n = 133$) and unhatched ($19.12$ cm$^3$ $\pm 0.21$, $n = 58$) eggs coming from a same clutch did not significantly differ in volume. The interactions between Hatching success and Year, Clutch size or Hatching date were non-significant. Hatched and unhatched eggs did not significantly differ in volume even after excluding interactions from the model. Similarly, egg volume did not predict hatching success of the whole clutch ($r = 0.07$) or fledging success of the brood ($r = 0.10$).

## 4. Discussion

Egg measurements of the studied Common Kestrels were similar to those reported for other European populations (see table 29 in Village 1990, Valkama *et al.* 2002). Only British Common Kestrels seem to lay slightly larger eggs (Village
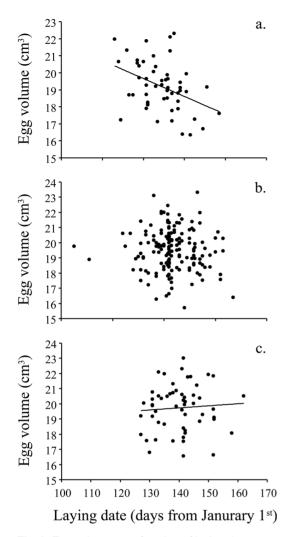
Fig. 2. Egg volume as a function of laying date (within-nest mean values). (a) In four-egg clutches, egg volume increased with laying date ($r = -0.34$). (b) In five-egg clutches, egg volume did not significantly vary with laying date ($r = 0.05$). (c) In six-egg clutches, egg volume increased with laying date ($r = 0.13$).

1990). Egg length varied more than egg width. Egg width may be constrained by the width of the female oviduct (Grant 1982, Järvinen & Väisänen 1983), which suggests that females may respond to environmental changes mainly by varying the length rather than the width of the egg.

Intra-nest-box repeatability of egg volume was significant. In the present study, adults were not trapped; hence it remains unclear whether nest boxes were occupied by the same females every

year. For this reason, whether this intra-nest repeatability mirrored a genetic component of egg volume or the effect of habitat quality (e.g., food availability) could not be evaluated. Observations of the same known females in certain nest boxes in subsequent years, confirmed by occasional ringing or using nest-box cameras (www.birdcam.it) show that females can be faithful to their nest box in the Italian study region, but the faithfulness cannot be generalized to all females. Even if the egg volume was measured for the same female for several years, it would remain impossible to determine if the repeatability observed for egg volume was due to genetic or environmental factors. This is because estimates of repeatability may be inflated due to the fact that a female that breeds in the same nest box for several years is exposed to similar environmental conditions in each breeding attempt. In a Finnish population of the Common Kestrel, Valkama et al. (2002) found that the egg volume was highly repeatable in 23 individual females that had bred twice in their study area. Valkama et al. (2002) concluded that such a high repeatability indicates a strong genetic component to egg-size determination. In the present study, however – for the above reasons – the contribution of genetics to variation in egg volume cannot be shown.

Eggs tended to be bigger in larger and earlier clutches, although these patterns were not consistent among breeding seasons. For birds of prey, food availability can affect the reproductive activity and determine breeding parameters. For example, food availability decreases as the season progresses, causing a decline in clutch/brood or egg size and/or requires an increased parental effort (Cavé 1968, Daan & Dijkstra 1982, Dijkstra et al. 1982, Beukeboom et al. 1988, Tolonen & Korpimäki 1995, Valkama et al. 2002). In the present study, the decrease in egg volume along the breeding season was most evident in four-egg clutches, whereas in six-egg clutches, egg volume increased with laying date. In the present study population, the laying phase spreads over a two-and-a-half-month period and clutch size decreases with later laying date. Within this pattern, the laying interval of six-egg clutches is lower than that of four-egg clutches (35 vs. 49 days) and is mainly restricted to the beginning of the breeding season. Given this different breeding span, it is likely that Common

Kestrels laying six-egg clutches at the beginning of the breeding season avoid the poorer environmental conditions of the later half of the season and so their investment in eggs is less constrained by prey availability. Food abundance was not quantified here; therefore, one cannot judge if food affected the breeding performance of Common Kestrels. Unlike Kestrel populations in northern Italy or in northern Europe, the trophic niche of Kestrels in central and southern Italy appears broader, including lizards, birds, voles, and insects (Rizzo *et al.* 1991, Piattella *et al.* 1999, Costantini *et al.* 2005, 2007, Costantini & Dell'Omo 2010). A correct measure of prey abundance and availability is therefore difficult to obtain, given the width of the trophic niche and the high ecological diversity of the prey species. This quantification is further complicated by differences in feeding habits between Kestrel individuals sharing a hunting area (Costantini *et al.* 2007), these differences being partly independent of prey abundance. Similarly, in a Kestrel population breeding in northern Italy, the occurrence of small mammals in the diet was significantly different from that estimated in the field by trapping, indicating that Kestrels act as selective predators (Casagrande *et al.* 2008). The reproduction of Kestrels living in areas other than the Mediterranean is affected by food availability. For example, in a Finnish kestrel population, Valkama *et al.* (2002) found that egg volume decreased with laying date in years of low vole abundance, but was unaffected by date in years of abundant voles. However, they could not find a significant correlation between egg volume and the abundance of *Microtus* voles after controlling for laying date. In the American Kestrel (*Falco sparverius*), Bird & Laguë (1982) found a negative correlation between laying date and egg size in captive individuals fed *ad libitum*. Wiebe & Bortolotti (1995, 1996) found that food supplementation to free-living American Kestrels increased egg size, but did not affect the coefficient of variation of egg size within clutches. They also found that egg size was correlated with small mammal abundance in their study area, females in good body condition tended to lay larger eggs, and egg size declined throughout the breeding season but only in the years with poorest food conditions.

It is difficult to extrapolate the above-summarized results to the present study area due to the life-history variation between the two species or among the study regions. Given the wider trophic niche and the occurrence of individual feeding habits in Mediterranean Common Kestrels, compared to northern Common Kestrels, the Kestrels studied here are probably less limited by the availability of a specific prey than are more northern populations which mainly prey upon voles. However, the importance of diet in determining variation in egg volume and other breeding parameters should be evaluated by more detailed studies, such as experimental manipulation of food availability. For example, Aparicio (1999) found that supplementation of food before egg laying did not significantly affect egg volume in a Spanish population. However, he also found that food supplementation increased the volume of first- but not last-laid eggs. Clearly, food availability could affect the parental investment in individual eggs across the laying sequence, rather than in the clutch as a whole.

Parental traits, such as body condition, body size and individual age, can also affect egg volume in birds (e.g., Williams 1994, Wiebe & Bortolotti 1995, Christians 2002, Michel *et al.* 2003). However, the specific maternal traits that affect egg size are still unclear (Christians 2002). For example, age, body mass and female size generally explain less than 20% of the variation in egg size within species (Christians 2002). Given that data on parents were not collected here, the quantification of the effect of parental quality to variation in egg volume could not be done. Future studies are therefore needed to quantify the extent to which parental attributes (e.g., nutritional status, body size, stress level, hormonal status or territory quality) influence egg-size variation.

Variation in winter and spring weather did not significantly explain egg volume variation although in a previous study weather affected the reproductive decisions and reproductive success in our Kestrel population (Costantini *et al.* 2010). In the current study, environmental variation may have been masked by genetic influences, or the analytical approach was unable to detect significant environmental effects. Significant effects of weather on egg volume have sometimes not been found (Christians 2002; Golawski 2008), whereas some studies have reported strong correlations (Jàrvinen 1991; Christians 2002; Mills *et al.* 2008). Statistical non-significance should not be

interpreted as indicating a zero effect (McGarvey 2007), but the differences among the cited papers could depend on the capacity of populations to synchronize the reproductive phenology to changes in the environment, e.g., food availability may be related to weather conditions. Alternatively, but not mutually exclusively, the differences could result from geographic variation in life-history parameters in the focal species. Given the variation in results described above, experimental studies are needed to evaluate (i) to what extent weather conditions affect egg volume variation, (ii) through which mechanisms weather can affect egg volume, and (iii) to assess if species or conspecific populations differ in the capacity of withstanding changes in weather.

Hatched and unhatched eggs within a given clutch did not differ in volume, and the mean egg volume of a clutch did not predict the hatching success of the clutch itself nor the fledging success of the brood. Hence, at least in Kestrels breeding in the present study region, egg volume was not a good predictor of reproductive success. Conversely to what was reported here, the probability of eggs to successfully hatch increased with egg volume in the American Kestrel (Wiebe & Bortolotti 1995) and in a Finnish population of the Common Kestrel (Valkama *et al.* 2002).

In conclusion, this study showed that the patterns of covariation among laying date, clutch size and egg volume were not consistently statistically significant (i.e., they varied remarkably) among breeding seasons. The fact that females laying later in the season can lay eggs of volume similar to those laid by females earlier in the season supports the hypothesis that in the present study region the "nesting early in the season is better" paradigm is not the only plausible theory to explain life-history variation in populations of Common Kestrel (Casagrande *et al.* 2006, Costantini *et al.* 2009).

## Munatilavuuden ja pesimäolosuhteiden yhteisvaihtelu tuulihaukalla Välimeren seudulla

Tuulihaukan (*Falco tinnunculus*) munakoon vaihtelua on tutkittu paljon Keski- ja Pohjois-Euroopassa, mutta vähän Välimeren seudulla. Tutkimme lajin munakoon vaihtelua Välimeren seudulla kuuden vuoden aikana suhteessa pesyekokoon, pesimäajankohtaan, kuoriutumisprosenttiin ja sääoloihin. Yleisesti ottaen munat olivat suurempia suuremmissa pesyeissä, ja munakoko pieneni pesimäkauden edetessä, mutta nämä tulokset vaihtelivat vuodesta toiseen. Munatilavuus ei riippunut sääoloista. Tutkimus osoitti, että (a) muninta-ajankohdan, pesyekoon ja munatilavuuden yhteisvaihtelu oli erilaista eri vuosina, ja (b) munatilavuus oli huono kuoriutumis- ja lentopoikasprosentin ennakoija tutkitussa populaatiossa.

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