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ORIGINAL ARTICLE

Patterns in egg size variability of island-dwelling kestrels

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Abstract

Island-dwelling birds may maximize their reproductive output by investing more in larger and fewer eggs than their close mainland counterparts (Lack's predictions). Less predictable environments could lead to increased intra- and inter-clutch egg size variability (environmental predictability hypothesis, EPH). Because these predictions have only seldom been tested, especially in raptors, we analysed egg size variability of the Common Kestrel (*Falco tinnunculus*) inhabiting a xeric scrub on Tenerife Island (Spain) over a twelve-year period. We also examined patterns of geographical variations in egg volume within the Western Palaearctic. In Tenerife, clutches of three, four, and five eggs had a higher volume than the six-egg clutches. Although egg volume decreased throughout the breeding season, this pattern was not constant over the years. Egg volume was positively correlated with hatching success, but not so with fledging success; it was inversely associated with rainfall in the previous autumn and temperature in March. Tenerife kestrels had a smaller mean egg volume in comparison to continental counterparts. However, after controlling for the effect of female body mass, the eggs were significantly larger, which seems to support Lack's predictions. Also, egg volume in the Western Palaearctic kestrel populations increased with latitude. Tenerife kestrels had low intra-clutch and high inter-clutch egg volume variability, supporting only the predictions on inter-clutch variability of the EPH. Breeding strategies of Tenerife kestrels seem to be adapted to unpredictable rainfall fluctuations over the years. The effects of environmental factors on life-history traits provide support for changes in breeding strategies of island-dwelling birds, highlighting a great investment per egg/offspring produced.

Keywords Egg characteristics · Environmental predictability hypothesis · Lack's predictions · Latitudinal variations · Western Palaearctic · Xeric-oceanic island environments

Zusammenfassung

Muster in der Variabilität der Eigröße inselbewohnender Turmfalken

Inselbewohnende Vögel können ihre Fortpflanzungsleistung maximieren, indem sie mehr in größere und weniger Eier investieren als ihre nahen Artgenossen auf dem Festland (Lack'sche Vorhersage). Weniger vorhersehbare Umweltbedingungen

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könnten zu einer größeren Variabilität der Eigrößen innerhalb und zwischen den Gelegen führen (Hypothese der ökologischen Vorhersagbarkeit, EPH). Da diese Vorhersagen, insbesondere bei Greifvögeln, nur selten getestet wurden, haben wir die Variabilität der Eigröße des Turmfalken (*Falco tinnunculus*), der trockenes Buschland auf der Insel Teneriffas (Spanien) bewohnt, über einen Zeitraum von zwölf Jahren untersucht. Außerdem untersuchten wir die geografischen Schwankungen des Eiervolumens in der westlichen Paläarktis. Auf Teneriffa hatten Gelege mit drei, vier und fünf Eiern ein höheres Volumen als Gelege mit sechs Eiern. Obwohl das Eivolumen während der Brutsaison abnahm, war dieses Muster über die Jahre hinweg nicht konstant. Das Eivolumen war positiv mit dem Schlupferfolg korreliert, nicht aber mit dem erfolgreichen Flüggewerden; es stand in umgekehrtem Zusammenhang mit den Niederschlägen im vorangegangenen Herbst und der Temperatur im März. Turmfalken von Teneriffa hatten ein geringeres durchschnittliches Eivolumen im Vergleich zu ihren kontinentalen Artgenossen. Nach Kontrolle der Auswirkungen der weiblichen Körpermasse waren die Eier jedoch deutlich größer, was die Lack'schen Vorhersagen zu bestätigen scheint. Außerdem nahm das Eivolumen in den westpaläarktischen Turmfalkenpopulationen mit dem Breitengrad zu. Bei den Turmfalken auf Teneriffa war die Variabilität des Eivolumens innerhalb des Geleges gering und zwischen den Gelegen hoch, was nur die Vorhersagen zur Variabilität zwischen den Gelegen der EPH unterstützt. Die Brutstrategien der Turmfalken von Teneriffa scheinen an die unvorhersehbaren Niederschlagsschwankungen im Laufe der Jahre angepasst zu sein. Die Auswirkungen von Umweltfaktoren auf lebensgeschichtliche Merkmale ("life-history traits") unterstützen Veränderungen in den Brutstrategien von Inselvögeln, wobei eine große Investition pro produziertem Ei/Nachwuchs deutlich wird.

Introduction

Natural selection through different evolutionary forces can influence intra and inter-clutch egg size variability. Several competent hypotheses at different scales have been proposed in order to explain the adaptive significance of intraspecific egg size variability associated with environmental conditions. The spatial patterns in the life-history traits (e.g., clutch and egg size) exhibited within species reflect their covariation with environmental conditions (e.g., rainfall, temperature) and geographical variation (e.g., latitude, longitude) (Gaston et al. 2008). Moreover, hatching success, chick growth rate and survival, as well as juvenile survival (reviewed by Krist 2011), are influenced by egg size. The environmental predictability hypothesis postulates that, as the availability of resources in the environment becomes less predictable, intra-clutch (within-female) and inter-clutch (between-females) egg size variability increases (Koops et al. 2003). About 70% of the variation in egg size is because of differences between clutches, i.e. between individual females; not within clutches, i.e. within individual females. This highlights the fact that egg size reflects an inherent characteristic of an individual female's phenotype (Christians 2002; Williams 2012). For many birds, several constraints, such as female body condition, weather, habitat quality, and insularity associated with latitude has been related with bird egg size variability (e.g. Hõrak et al. 1995; Covas 2012). However, there are few studies describing geographical variations on bird egg size variability (Heming and Marini 2015), including island-dwelling birds (Covas 2012).

In environments with low seasonal variations of resources and milder climate, such as subtropical islands, population densities of birds would remain near to carrying capacity. According to Ashmole's hypothesis (Ashmole 1963; Ricklefs 1980), in systems with limited and low seasonal variability of resources, the population density is expected to remain somewhat constantly near the maximum. Also, without fluctuations in resource availability caused by seasonal extremes (winter), there are no seasonal peaks in mortality that would free up those resources to be allocated in producing large clutches during the following breeding season. In such populations, individuals with small clutches eventually end up with more offspring than those that produce large clutches without the sufficient resources to support them. So, island-dwelling birds faced with these conditions can maximize their reproductive output by investing more in egg size and less in clutch size; therefore, raising higher quality offspring with a greater chance of survival (Lack 1970). Island-dwelling birds and their mainland counterparts may often differ in their life-history traits, such as egg size (Covas 2012). Breeding strategies of island-dwelling birds have evolved according to island features through behavioural (Stamps and Buechner 1985; Griffith 2000), morphological (Carrascal et al. 1994; Donázar et al. 2002), and physiological changes (Blanco et al. 2014; Sayol et al. 2018), as a response to evolutionary processes. These adjustments (i.e. insular syndrome) include, for instance, a tendency to follow the 'island rule' (i.e., smaller species evolve towards larger size in their insular forms; Clegg and Owens 2002), smaller clutch size and larger and fewer eggs than their close mainland counterparts (Lack 1970; Covas 2012). Ecological requirements, biotic interactions and environmental stress in island ecosystems can be efficient evolutionary forces (Whittaker and Fernández-Palacios 2007). Especially, environments affected by unpredictable rainfall, strongly condition the breeding biology of island birds inhabiting arid ecosystems (Illera and Díaz 2006). Despite the outstanding bio-ecological island features with regards to breeding strategies of island-dwelling birds, egg size variability and broad-scale patterns of breeding adaptations are poorly documented, especially for raptors.

Island-dwelling raptors exhibit a suite of breeding adaptations, such as smaller clutches, or delay in timing of breeding, than their close mainland counterparts (Thibault et al. 1992; Carrillo and González-Dávila 2009). However, it seems that this is not a widespread trend neither in diurnal (Thibault et al. 1992) nor in nocturnal raptors (Vidal et al. 1984). A geographical trend for clutch size in raptors is an increase with latitude, especially for those laying clutches larger than two eggs (Newton 1979; Carrillo and González-Dávila 2009). The Common Kestrel (*Falco tinnunculus*, hereafter kestrel) has continental and island forms throughout the Palaearctic. The kestrel is a small-sized monogamous diurnal raptor and, generally, single-brooded. They breed in rocky cavities, tree holes, other birds' disused nests, human buildings and in nest boxes; their usual clutch size being four to six eggs (Costantini and Dell´Omo 2020). Observational and experimental studies on breeding traits performed on Palaearctic continental kestrels have revealed some ecological aspects about their egg size. For instance, hatching asynchrony may be conditioned by intra-clutch egg size variability (Aparicio 1999); inter-clutch egg size variability within the season are influenced by the abundance of their main prey (Valkama et al. 2002); patterns of egg size vary among breeding seasons (Costantini et al. 2010). Although fitness-related traits and kestrel breeding strategies have been widely studied in scattered areas over the Western Palaearctic (Costantini and Dell´Omo 2020), there have been scarce investigations for island populations (Carrillo and González-Dávila 2005; Carrillo-Hidalgo et al. 2020).

The primary aim of this study was to analyse egg size variability in a kestrel population inhabiting an arid environment in a milder oceanic island with long-term data throughout a twelve-year period. For this, we examined whether egg size correlates with any fitness-related parameters (i.e., laying date, clutch size, hatching and fledging success), in relation to female phenotype, weather and the physiographic characteristics of kestrel territories. Second, on considering the environmental unpredictability in the study area due to irregular rainfall, and the postulates of the environmental predictability hypothesis (Koops et al. 2003), we expect island kestrels to have a great intra- and inter-clutch egg size variability. Third, taking into account that the specific characteristics of the island environments lead to convergent adaptations in organisms, often called 'island syndrome' (Whittaker and Fernández-Palacios 2007), as well as the postulates by Lack (1970), we predicted that the Tenerife kestrels (*Falco tinnunculus canariensis*) would have larger and fewer eggs than their close mainland counterparts (*F. t. tinnunculus*). Finally, despite the diverse ecological studies on latitudinal gradient in clutch size for birds, there is an insufficient number of attempts to investigate the geographical variation in egg size (Heming and Marini 2015). Widespread geographical range and a relatively high diversity of life-history traits (Village 1990; Körpimaki and Wiehn 1998; Fargallo et al. 2001; Costantini and Dell´Omo 2020; Kujala et al. 2024) make the kestrel an interesting model for evaluating patterns of geographical variations in egg size. Specifically, to our knowledge, egg size variability in island-dwelling kestrels has not been studied, and neither have the patterns of geographical variations in this trait. Thus, we evaluated patterns of geographical variations in egg size for the Western Palaearctic kestrel populations.

Material and methods

Study area

Tenerife (27.59°N-28.40°N, 16.5°W-16.55°W) is a volcanic island located in the Atlantic Ocean, about 292 km off the west coast of Morocco. It is the largest (2034 km^2) and highest (max. alt. 3715 m a.s.l.) island of the Canary Islands. Its climate is modulated by the influence of the North Atlantic Oscillation (García-Herrera et al. 2001). The study area (south-east slopes 0–275 m a.s.l.) is a southern xerophytic scrub of about 100 km^2 in Granadilla de Abona, predominantly composed of *Euphorbia balsamifera*, *E. obtusifolia, E. canariensis*, *Plocama pendula*, *Ceropegia fusca* and *Launaea arborescens*. The area is part of the arid desertic Inframediterranean bioclimatic belt of Tenerife with *Ceropegio fuscae-Euphorbio balsamiferae sigmetum* as a climatophilous vegetation series (del Arco et al. 2006). The climate is arid, with annual rainfall <200 mm, generally distributed during the first and the last quarter of the year; mean monthly temperatures between 18 °C and 25 °C, frequent strong winds and high solar radiation (García-Herrera et al. 2001). The area includes some agricultural greenhouses, open air tomato plots, an industrial zone, an airport, four villages and goat enclosures.

Study species

In the study area, kestrels (*Falco tinnunculus canariensis*) are single-brooded and breed as solitary pairs in rocky cavities, generally in weathered pyroclastic and basaltic deposits. They start laying from within the second fortnight of February up until the first fortnight of April (mean = 15 th March, SD = 12.3, range = 11 th February–25 th April, $n =$ 159 clutches). Of the clutches, 79% take place in March (mean clutch size = 4.41, SD = 0.72, range = 3–6, n = 159 clutches). Weather conditions influence breeding parameters; specifically, earlier laying date is associated with increased rainfall during the previous autumn, and mean clutch size shows positive correlation with rainfall during the month prior to laying (Carrillo and González-Dávila 2010a).

General methods

The field study was conducted throughout twelve breeding seasons (February–June 2007–2019, except 2017). Nest-sites were found before the onset of laying by observing courtship behaviour. We carried out regular visits to determine laying date, clutch size, hatching date, brood size, and number of fledglings. We calculated the mean laying date for each year with the mean date of laying of the first egg of all pairs studied. When laying date was unknown, we estimated clutch initiation dating back 30 days (the median incubation period) from the date of the first hatched egg, considering that the laying interval of each egg occurs every two days (Village 1990; J. C.-H. personal observation).

The mean clutch size of each year was calculated as the mean number of eggs of all clutches. We considered a clutch complete when incubation had begun and no new eggs were laid for five days (Aparicio 1994). When possible, we determined the laying order of eggs within clutches. Data from 159 clutches (13.3 clutches/year, SD = 5.4) of a total number of 701 eggs were recorded (n = 701). We excluded the only two-egg clutch we found from all statistical analyses. In Tenerife, the same observer (J.C.-H.) measured and marked the eggs with a waterproof felt-tip pen and measured its maximum length (L) and width (W) with a digital calliper (AMIG, Spain) to the nearest 0.01 mm. We calculated the mean egg volume according to Hoyt (1979; $V = 0.51\ LW^2$) and Douglas (1990; $V = K_v\ LW^2$, where K_v corrects for variation in shape and is calculated as $0.5236 - [0.5236 \times 2(L/W)/100]$). Because the results of both equations showed no differences ($r = 0.999$, $p < 0.001$), we decided to use Hoyt's (1979). We calculated the egg mass (M) by applying the Hoyt´s (1979) equation ($M = K_m\ LW^2$ with $K_m = 0.548\ g/cm^3$). We always refer to egg volume in this study given that egg volume and mass are dependent on one another, according to Hoyt's equations. We measured the sphericity by means of egg shape index (SPH = 100 W/L) according to Winkel (1970). In terms of intra-clutch egg size, we considered the degree of similarity that each egg has with the other eggs in the same clutch, according to Amat et al. (2001). That is, for every pair of eggs within the clutch, the volume of the smaller egg was divided by the volume of the larger one, which was then averaged.

Chicks were individually marked with metal and colour PVC rings when 15–20 days old. We trapped 33 adult breeding females, using the bal-chatri method (Berger and Mueller 1959), during the late nestling period (chicks > 15 days old), and we measured them according to Svensson (1984) and Hardey et al. (2013). See Table S1.

We analysed the main climatic variables, which can influence kestrel breeding success in the study area (i.e., mean temperature and total rainfall, from the previous autumn to breeding season; total rainfall in winter, mean temperature for February and mean temperature for March; Carrillo and González-Dávila 2010b). We considered climatic instability, when Pearson's coefficient of variation (CV), taken from the information of the months included in the evaluated period, is greater than 30% (Brown 1998). We described territory (home range) in terms of physiographic characteristics (i.e., plant cover and biomass, length of stone walls and density of rocks, stones and litter on the ground) which were measured in circular buffers of 500 m radius around each nest site. These physiographic characteristics are the most influential in the kestrel breeding success for the study area (Carrillo-Hidalgo et al. 2020). We used the three principal components (C_1: plant cover, C_2: density of rocks on the ground and C_3: length of stone walls), which explained 80.2% of the sampled information in the study area. The physiographic characteristics of each territory were measured once, as a constant data over the years, due to the unchangeability of the study area (see methodology, Carrillo-Hidalgo et al. 2020).

Data on rainfall and temperature 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. We considered the period October to December as autumn and January to March as winter.

Geographical variations

For the purpose of comparing our results with those of previous studies all over the Western Palaearctic, we analysed data from Finland, Scotland, Belarus, England, Germany, Poland, Czech Republic, Ukraine, France, Italy, and mainland Spain (Table 1). In order to compare egg size variability between Tenerife kestrel population and that of the nearest continental population, we considered mainland Spain because we had no data from Morocco. We excluded those data compiled in general publications (i.e. atlases) from the comparative analysis because the probable unsystematic methodology may influence the results. We calculated the sphericity index and the mean egg volume if not given in the original source. We considered the central point of the region as a latitudinal reference point when exact location of the population studied was not provided (i.e. Belarus, Czech Republic, Ukraine).

Table 1 Country, latitude, longitude and egg characteristics of the Common Kestrel populations in the Western Palaearctic. The exact areas of Czech Republic and Ukraine have not been specified in their respective references

Country	Area	Latitude	Longitude	Number of eggs	Length	Width	Volume	Sphericity	References
Finland	Kauhava	62°59'N	22°50'E	655	38.8	31.3	19.5	80.8	Körpimaki and Wiehn (1998); Valkama et al. (2002)
Scotland	Eskdalemuir	55°16'N	3°10'W	73	41.0	32.0	21.4	78.0	Village (1990)
Belarus		53°29'N	28°25'E	64	39.3	30.8	19.0	78.4	Nikiforov et al. (1989) *in* Rejt and Raczyńska (2003)
England	Leicertershire	52°38'N	1°08'W	133	40.0	32.0	20.9	80.0	Village (1990)
Germany	Westfalen	52°14'N	8°43'E	1054	39.6	31.9	20.6	80.6	Hasenclever et al. (1989)
Poland	Warsaw	52°13'N	21°00'E	60	39.5	31.9	20.5	80.8	Rejt and Raczyńska (2003)
Czech Republic		49°44'N	15°24'E	566	39.6	31.8	20.4	80.1	Pikula et al. (1984) *in* Rejt and Raczyńska (2003)
Ukraine		48°26'N	32°06'E	389	39.0	31.5	19.7	80.8	Zubarovskiy (1977)*in* Rejt and Raczyńska (2003)
France	Charente-Maritime	45°54'N	1°03'W	159	39.8	31.3	19.9	78.7	Boileau and Hoede (2009)
Italy	Roma	41°53'N	12°29'E	187	39.1	31.2	19.5	79.8	Costantini et al. (2010)
Spain (mainland)	Segovia	40°40'N	4°20'W	536	39.3	31.2	19.6	79.4	Present study
Spain (Canary Islands)	Tenerife Island	28°17'N	16°37'W	701	38.2	31.1	18.9	81.7	Present study

To examine the relationship between female phenotype and egg volume at different latitudes, we considered those populations of which we knew female body dimensions and eggs they laid (i.e., Tenerife island, 33 females; Segovia, mainland Spain, 70 females; Kauhava region, Finland, 106 females).

Statistical analysis

Intra-population variability in egg size

To corroborate whether the egg dimensions have an approximately normal distribution, the Wilk-Shapiro test was used. The distributions of egg dimensions (i.e., length, width, mass, volume, sphericity) complied with normality. The mean measure of the eggs of each clutch was used as the sample unit. We used the variance-stabilizing transformations (arcsine square root transformed) for normality and homoscedasticity of the similarity degree (skewness $= -2.636$, see electronic supplementary material Fig. S1). We calculated the intra-nest (referred to as intra-clutch because we did not know whether the same females occupy the same nest-cavities every year), and also intra-territories correlation coefficient according to Lessells and Boag (1987) to show the repeatability of egg volume. These calculations consider repeatability to be a measure of "the proportion of variance in a character that occurs among, rather than within individuals" (p. 116, Lessells and Boag 1987).

In order to investigate the environmental predictability hypothesis, we used linear mixed models (LMMs) to relate the egg volume with breeding parameters (i.e., laying date and clutch size), and with the climatic and physiographic variables above mentioned. We added year as random factor. Potential multicollinearity between these predictors was checked with the variance inflation factors (VIF) in a model that contains all the predictors. VIF obtained ranged between 1.022 and 3.238, all with a value <5, that is, a low or acceptable multicollinearity (Montgomery et al. 2012).

We ranked all possible candidate models which were then compared to Akaike's Information Criterion (Akaike 1973) and corrected for small sample sizes (AIC$_c$). ΔAIC$_c$ values and their relative normalized weights (w$_j$) were used in order to provide evidence of the relative support for each model. We considered the first fifteen models and calculated the partial standard deviation for the i-th of p predictors in model j as $s_{ij}^* = s_i VIF_{ij}^{-0.5}((n-1)/(n-p))^{0.5}$, with s_i being the sample standard deviation of the i-th predictor and VIF_{ij} the VIF for the i-th predictor in model j. The standardised estimates coefficient was obtained as $\hat{\beta}_{ij}^* = \hat{\beta}_{ij} s_{ij}^*$ where $\hat{\beta}_{ij}$ is the estimated regression coefficient of i-th predictor in model j. The model-averaged standardised parameter estimate ($\hat{\beta}_i^*$) and its standard error ($\widehat{s.e.}(\hat{\beta}_i^*)$) is provided by using the w_j (Cade 2015).

In addition, to evaluate the egg volume pattern in function of laying date, according to breeding season, we included the interaction year x laying date considering year as a fixed factor.

We estimated the breeding success in two ways: hatching success rate was the number of eggs hatched against the number of eggs laid; fledging success rate was the number of chicks fledged against the number of eggs hatched (Carrillo and González-Dávila 2005). To analyse these two rates, we used a logistic regression with binomial data (events/tests), i.e., number of eggs hatched *vs* the number of eggs laid; number of chicks fledged *vs* number of eggs hatched. For this, we included year, egg volume, laying date, and territory as covariates.

We used Pearson's correlation coefficients to examine the relationship between female phenotype and egg size ($n = 33$). We measured body mass, and also bill, tail, wing, and tarsus length, as well as their principal components (we extracted two principal components, which explained 90% of the variance: PC_1 correlated strongly with tail and wing lengths and PC_2 with bill and tarsus lengths). We used body mass because bill, tail, wing and tarsus length were not significantly related to the mean egg volume; neither individually nor as principal components (bill, $r = 0.29$, $p = 0.098$; tarsus, $r = -0.23$, $p = 0.196$; wing, $r = 0.15$, $p = 0.391$; tail, $r = 0.04$, $p = 0.815$; PC_1, $r = 0.11$, $p = 0.550$; PC_2, $r = 0.25$, $p = 0.160$). In order to examine female body condition, we used the scaled mass index in relation to tarsus length (Peig and Green 2009). In addition, we calculated this index using bill, tail and wing length as scaled variables, but it was dismissed because these parameters had fewer correlations with body mass on a log–log scale.

Geographical variations

Published studies show mean egg volume from all clutches and no exact measurements for each individual egg. Therefore, we used a lineal regression weighting the data in function of the number of eggs in the area so as to relate egg volume to latitude, quadratic latitude, longitude, quadratic longitude and the island effect (categoric variable), and applying stepwise method to variables selection. The egg dimension comparison of different countries was carried out using Student´s *t*-test, adjusted by the Bonferroni method.

We used a multivariate analysis of variance (MANOVA) to compare female phenotype (i.e., tail, wing and tarsus length, and body mass) for Tenerife Island, mainland Spain and Finland. We used LMM to study the relation between egg dimensions (width, length, volume) and the female phenotype. The female identifier has been specified as the subject, the egg dimension as dependent variable, the location (Tenerife, mainland Spain and Finland) as a factor; and female phenotype as covariate. In order to inspect whether eggs were larger on islands (i.e., Lack's predictions), we used LMM with a log–log allometric relationship for egg volume and female body mass, including the insular effect and latitude (Covas 2012). We used the scaled mass index (Peig and Green 2009) in order to examine female body condition in Tenerife, and among other populations (i.e., mainland Spain and Finland).

All tests are two tailed and a *p*-value of < 0.05 was considered as statistically significant. All values are presented as means ± 1 SD or 1 SE. Data were analysed using *SPSS* 25.0 (IBM SPSS, Armonk, NY).

Results

Intra-population variability in egg size

The mean egg length and width of kestrels in Tenerife (± SE) was 38.17 ± 0.06 mm (range: 43.43–33.42) and 31.14 ± 0.03 mm (range 34.02–27.66), respectively (Table 2). Although the length and width of an egg was correlated ($r = 0.327$, $p < 0.001$), the variability in egg length tended to be higher than that of the egg width (CV 4.4% vs CV 2.9%, respectively). The overall mean egg volume was 18.90 ± 0.06 cm^3 (range: 23.89–13.14 cm^3); the sphericity was 81.72 ± 0.14 (range: 94.34–67.74) and the similarity degree was 0.96 ± 0.002 (range: 0.99–0.82). The eggs within the different clutches were similar, with 80.5% of them having a similarity degree > 0.95. Intra-clutch repeatability of egg volume was significant with an intra-clutch correlation coefficient of $r_i = 0.74$ ($F_{158;542} = 13.80$, $p < 0.001$). Taking all the eggs into account, the smallest one was 55.0% of the volume of the largest one. Egg size (volume: $F_{3;653} = 6.60$, $p < 0.001$; sphericity: $F_{3;653} = 6.61$, $p < 0.001$) differed according to clutch size (on considering the clutch as a random factor). Intra-territory repeatability of egg volume was significant with a coefficient of $r_i = 0.24$ ($F_{44;114} = 2.12$, $p < 0.001$). We found no significant differences in volume between the clutches of three, four and five eggs, with a slight tendency to increase; these clutches had a significantly higher volume than the six-egg ones (Fig. 1, Table 2). Clutches of four eggs were less spherical than those of five eggs; although we did not find such differences in clutches of three and six eggs. Egg volume and sphericity were negatively correlated ($r = -0.133$, $p < 0.001$); smaller eggs tended to be relatively more spherical. Egg similarity degree showed no significant differences regarding clutch size ($F_{3;155} = 0.63$, $p = 0.599$).

Table 2 Egg characteristics as a function of clutch size in Tenerife kestrels. The homogeneous subsets with Tukey tests for $\alpha = 0.05$ are indicated with the same letter (a, b or c), and arcsine-square root-transformed are marked with *. *N* or mean ± SE

Clutch size	Number of clutches	Number of eggs	Length (mm)	Width (mm)	Mass (g)	Volume (cm^3)	Sphericity	Similarity degree
3	14	42	37.97 ± 0.26^b	30.97 ± 0.12^b	19.97 ± 0.20^b	18.59 ± 0.18^b	81.73 ± 0.62^{ab}	0.96 ± 0.004
4	74	296	38.31 ± 0.09^b	31.04 ± 0.05^b	20.25 ± 0.09^b	18.85 ± 0.08^b	81.15 ± 0.21^a	0.96 ± 0.003
5	63	315	38.20 ± 0.09^b	31.34 ± 0.05^c	20.59 ± 0.09^b	19.16 ± 0.08^b	82.17 ± 0.22^b	0.96 ± 0.003
6	8	48	37.24 ± 0.28^a	30.56 ± 0.15^a	19.10 ± 0.28^a	17.78 ± 0.26^a	82.22 ± 0.61^{ab}	0.95 ± 0.011
Total	159	701	38.17 ± 0.06	31.14 ± 0.03	20.31 ± 0.06	18.90 ± 0.06	81.72 ± 0.14	0.96 ± 0.002
General linear model			$F_{3;\,653} = 4.546$	$F_{3;\,653} = 8.915$	$F_{3;\,653} = 6.600$	$F_{3;\,653} = 6.600$	$F_{3;\,653} = 6.614$	$F_{3;\,111} = 0.761$*
(Random factor: clutch)			$p = 0.004$	$p < 0.001$	$p < 0.001$	$p < 0.001$	$p < 0.001$	$p = 0.518$
Wilk-Shapiro (p)			0.255	0.156	0.200	0.200	0.088	< 0.001

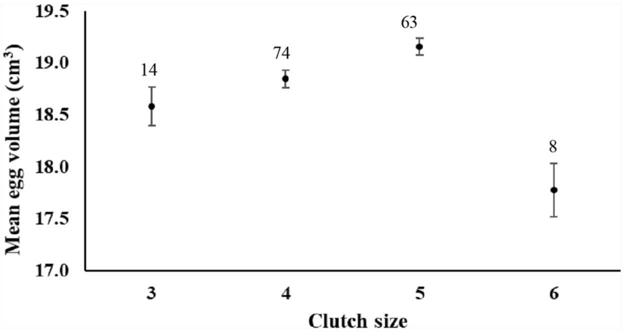

Fig. 1 Relationship between egg volume and clutch size (mean ± SE) of Tenerife kestrels. Sample sizes (number of clutches) are above the bars

The CV of the sphericity remained more stable (in relation to their average) than that of the volume throughout the study-period years (Table 3). Volume, sphericity and similarity had the highest CV in 2010, coinciding with the winter which saw the most rainfall (electronic supplementary material Fig. S2). On the other hand, the volume CV in 2012 was the lowest, coinciding with the driest winter. We found an unstable climate due to a high variability in autumn and winter rainfall (CV = 52.3% and 52.9%, respectively) over the years, although temperature remained stable (electronic supplementary material Table S2).

Egg volume decreased with later laying date ($F_{1;101} = 4.48$, $p < 0.037$). Each day that passed after laying date egg volume decreased by 0.019 cm^3 (95% CI: 0.008, 0.030) on average, independently from clutch size (Fig. 2). However, this pattern varied from one year to another (laying date × year: $F_{11;101} = 2.59$, $p = 0.006$), especially due to the influence of the year 2010 (electronic supplementary material Fig. S2).

Egg volume was neither affected by the physiographic characteristics of territories (all $p > 0.4$) nor by breeding season ($F_{11;134} = 1.35$, $p = 0.203$). Egg volume was inversely associated with rainfall in the previous autumn (coefficient $= -0.009$, $p = 0.002$) and temperature in March (coefficient $= -0.691$, $p = 0.005$; Table 4).

Hatching success rate was positively associated with egg volume ($\chi^2_1 = 7.953$, $p = 0.005$), but was not associated with laying date ($\chi^2_1 = 3.526$, $p = 0.060$), territory (C_1, C_2, C_3; all $p > 0.183$), nor year ($\chi^2_1 = 2.931$, $p = 0.087$). Fledging success rate was not associated with egg volume ($\chi^2_1 = 0.022$, $p = 0.883$), territory (C_1, C_2, C_3; all $p > 0.062$), nor laying date ($\chi^2_1 = 1.731$, $p = 0.188$).

Females with best body condition laid eggs with greater volume, length and width ($r = 0.46$, $p = 0.008$; $r = 0.33$, $p = 0.060$; $r = 0.41$, $p = 0.018$, respectively), but with no significant relation to clutch size ($r = -0.22$, $p = 0.229$), sphericity ($r = -0.05$, $p = 0.770$), nor similarity degree ($r = 0.13$, $p = 0.488$).

Geographical variations

Egg volume in Tenerife and Belarus did not differ and was lower to that of the rest of the populations ($p < 0.001$). Egg length in Tenerife was significantly shorter to that of the other eleven reference populations (all $p < 0.001$, Table 1). On considering the width, there were no significant differences between Tenerife, Italy and mainland Spain ($p > 0.115$); egg width in these populations was significantly less than that of other countries ($p < 0.001$), except for that in Belarus ($p = 0.012$). Tenerife kestrel eggs had the highest sphericity of any other continental populations ($p < 0.001$). Egg sphericity decreased with increasing latitude ($r = -0.297$, $p < 0.001$) thus leading to the increase of egg length ($r = 0.485$, $p < 0.001$).

Egg volume increased significantly with latitude (Fig. 3; estimated mean egg volume = 7.170 + 0.511 Latitude—0.005 Latitude^2—0.022 Longitude + 0.805 island [$r^2 = 0.859$, SE = 0.243, $p < 0.001$]), although less so at high latitudes. Egg volume increased significantly as longitude

Table 3 Kestrel yearly breeding success and egg characteristics in Tenerife (*SD* standard deviation, *CV* coefficient of variation, laying dates are shown as ordinal dates, *1* 1 st January)

	N° of clutches	Laying date		N° of eggs	Hatching success	Fledging success	Volume			Sphericity			Similarity degree		
		Mean	SD		%	%	Mean	SD	CV	Mean	SD	CV	Mean	SD	CV
2007	16	70.5	6.5	75	85.3	92.2	19.40	1.41	7.3	82.71	3.74	4.5	0.97	0.02	1.9
2008	15	75.7	12.8	62	82.3	84.3	19.67	1.37	7.0	81.87	3.32	4.1	0.96	0.01	1.4
2009	20	71.1	6.5	88	88.6	79.5	18.68	1.17	6.2	80.63	3.36	4.2	0.96	0.02	1.8
2010	9	61.3	9.0	45	95.6	88.4	18.32	1.93	10.5	80.58	4.53	5.6	0.92	0.04	4.4
2011	20	69.7	15.1	97	84.5	84.1	19.17	1.53	8.0	82.64	3.37	4.1	0.96	0.02	1.7
2012	8	91.6	9.7	30	90.0	96.3	18.94	1.07	5.7	81.89	3.80	4.6	0.97	0.01	1.5
2013	17	75.5	7.6	77	88.3	76.5	18.52	1.62	8.8	82.06	4.33	5.3	0.95	0.04	4.2
2014	20	70.9	12.1	91	92.3	66.7	18.23	1.58	8.7	81.54	4.35	5.3	0.96	0.01	1.5
2015	11	81.2	9.8	45	88.9	95.0	18.83	1.21	6.4	82.12	3.08	3.8	0.97	0.01	1.4
2016	10	83.4	9.9	39	82.1	53.1	19.22	1.36	7.1	80.46	3.25	4.0	0.97	0.02	1.6
2018	4	85.0	10.4	18	77.8	78.6	19.07	1.22	6.4	80.05	2.68	3.3	0.96	0.01	1.0
2019	9	76.1	15.3	34	82.4	78.6	19.20	1.46	7.6	82.25	3.18	3.9	0.96	0.02	1.8
Statistic*		$F_{11,645} = 40.94$			$F_{11,95} = 0.71$	$F_{11,86} = 1.45$	$F_{11,645} = 9.58$			$F_{11,645} = 3.72$			$F_{11,103} = 2.09$		
p-value		< 0.001			0.726	0.165	< 0.001			< 0.001			0.028		

*Controlling by clutch (random factor)

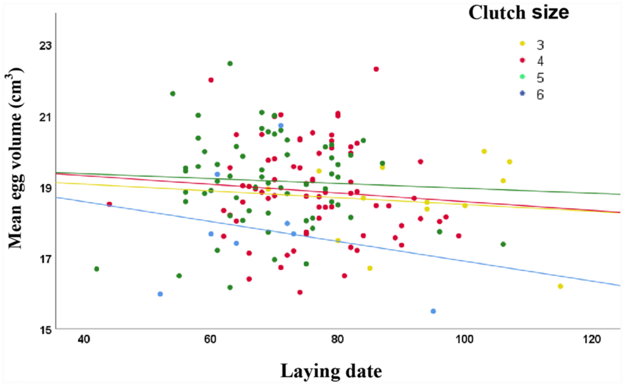

Fig. 2 Mean egg volume (cm^3) as a function of laying date (ordinal dates, 1 = 1 st January) in accordance to clutch size in Tenerife kestrel population

trended westward. However, longitude weight in the model is tenfold less than latitude (standardized coefficient − 0.489 *vs* 8.089). Therefore, the island effect leads to a reduction in volume in mainland eggs of 0.805 cm^3 (SE $=0.016$, $p < 0.001$), in the event of equal latitude and longitude.

Egg volume of Tenerife kestrels, after controlling for the female body mass, was larger than the mainland Spain and Finland ($p = 0.030$), but we found no differences between the latter two ($p = 0.537$). Female body dimensions between Tenerife, mainland Spain and Finland populations showed significant differences (body mass, wing and tarsus length, $p < 0.001$; tail length, $p = 0.013$; see electronic supplementary material Table S3).

Regarding those populations in which females were measured, the mean clutch size was 4.41 (SD $=0.72$) for Tenerife island, 4.87 (SD $=0.90$) for mainland Spain and 5.16 (SD $=1.27$) for Finland. The mean clutch size in Tenerife was smaller to that in mainland Spain (95% CI: − 0.76, − 0.17) and Finland (95% CI:– 1.03, − 0.46), with no differences between the populations of the latter two ($p = 0.082$). Egg volume, on considering the three populations, was positively correlated with the female body mass (slope $=0.025$, SE $=0.006$, $p < 0.001$), and had no relation with the tail, wing and tarsus length.

Discussion

Intra-population variability in egg size

Egg size (i.e., volume and sphericity) of Tenerife kestrels differed according to clutch size, showing a slight tendency to increase in the majority of clutches, from three to five eggs. We found that the length and width of an egg was correlated, but the variability in egg length tended to be higher than that of the egg width. Although differences between egg length and width could have an anatomical explanation, seeing as the width of the oviduct primarily shapes egg width (Joyner 1994), experimental (Martínez-Padilla 2006) and observational studies (Valkama et al. 2002) on kestrels found no evidence correlating egg size and female body mass or condition. In fact, it has been suggested that female body mass or condition explains less than 20% of the bird egg size variability, and physiological characteristics of each female could be determinant factors which influence egg size (Christians 2002; Williams 2012).

We found a high value of intra-clutch repeatability of egg volume (0.74) which is similar to northern continental kestrel populations (0.88, Finland; Valkama et al. 2002) but greater than southern continental populations (0.47, Italy; Costantini et al. 2010). In accordance with the majority of studies on bird egg size (Christians 2002; Williams 2012), 74% of the total variability in egg volume is explained by the differences between clutches (i.e., between individual females) rather than within clutches in our study. High intra-clutch repeatability found in Tenerife population would indicate a strong genetic component in egg size determination, unrelated to female size, as has been explained for continental kestrels (Valkama et al. 2002). Female body condition could explain for high inter-clutch egg volume variability we found. Females with a better body condition laid eggs of a greater volume, length and width. In addition, egg volume and shape were negatively correlated in this island population. This suggests that egg size adjustment of female kestrels under fluctuating environmental conditions (weather, food) could be constrained by a genetic component. This would also be in agreement with the finding that egg volume was neither affected by physiographic characteristics of territories nor did it vary over the study period.

Intra-nest repeatability data, referred to as intra-clutch in this study, must be observed with caution because we did not know whether the same females occupy the same nest-cavities each year. For this reason, it is uncertain whether the intra-nest repeatability of Tenerife populations reflected a genetic component of egg volume, or whether it was the effect of environmental conditions (e.g., food availability) and physiological characteristics of each female. Environmental predictability hypothesis postulates that as the environment becomes less predictable, intra and inter-clutch egg size variability will increase (Koops et al. 2003). Our findings support the prediction on inter-clutch but not that of intra-clutch egg size variability of this hypothesis. However, it is likely that the predictions on intra-clutch may not meet the criteria because of the study area being thermally stable.

Table 4 **a** Fifteen best models explaining egg volume using generalised linear models with quasi-Akaike's Information Criterion (AIC$_c$) and **b** model-averaged standardised parameter estimate ($\hat{\hat{\beta}}_i^*$) and its standard error ($\widehat{s.e.}(\hat{\hat{\beta}}_i^*)$). df = degrees of freedom, $\Delta_j = (\mathrm{AIC_c})_j - \min \mathrm{AIC_c}$, $w_{ij} = \exp(-\Delta_j/2)/\Sigma\exp(-\Delta_r/2)$

(A)	Variables										d.f	AIC$_c$	Δ_j	W$_j$
Model	Laying date	Clutch size	Plant cover (C$_1$)	Density of rocks (C$_2$)	Length of stone walls (C$_3$)	Previous Autumn		Winter						
						Mean Temperature	Rainfall	Temperature		Rainfall				
								February	March					
1		x					x		x		3	542.011	0.000	0.0326
2	x	x					x		x		4	542.463	0.452	0.0260
3		x					x	x	x		4	543.113	1.102	0.0188
4		x		x			x		x		3	543.611	1.600	0.0146
5		x				x	x		x		4	543.703	1.692	0.0140
6		x	x				x		x		4	543.711	1.700	0.0139
7	x	x				x	x		x		5	543.775	1.764	0.0135
8	x	x					x	x	x		5	543.937	1.926	0.0124
9		x			x		x		x		3	544.043	2.032	0.0118
10	x	x	x				x		x		5	544.115	2.103	0.0114
11	x	x		x			x		x		4	544.153	2.142	0.0112
12		x					x		x	x	4	544.232	2.221	0.0107
13	x						x		x		3	544.334	2.322	0.0102
14	x	x			x		x		x		4	544.606	2.595	0.0089
15	x	x					x		x	x	5	544.735	2.724	0.0083

(B) Model-averaged standardised parameter estimate and its standard error

	Laying date	Clutch size			Plant cover (C$_1$)	Density of rocks (C$_2$)	Length of stone walls (C$_3$)	Previous autumn		Winter		
		Equal to						Mean temperature	Rainfall	Temperature		Rainfall
		3	4	5						February	March	
$\hat{\hat{\beta}}_i^*$	− 0.0130	0.8430	1.2322	1.5049	− 0.0751	− 0.0757	− 0.0436	0.1206	− 0.0088	0.1327	− 0.6905	0.00002
$\widehat{s.e.}(\hat{\hat{\beta}}_i^*)$	0.0094	0.5804	0.4775	0.4764	0.0983	0.0959	0.1030	0.1396	0.0031	0.1323	0.2715	0.0041
p	0.083	0.073	0.005	0.001	0.222	0.215	0.336	0.194	0.002	0.158	0.005	0.477

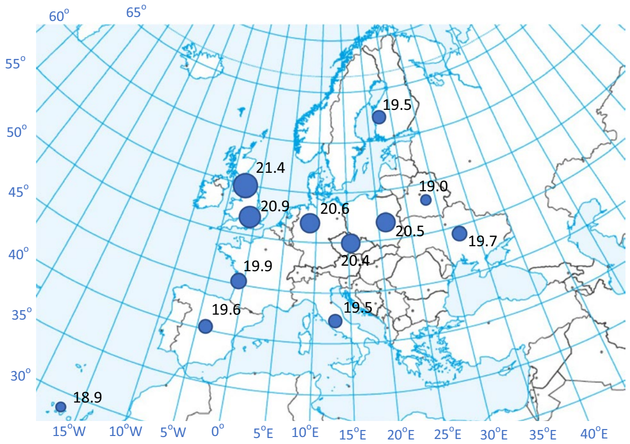

Fig. 3 Geographic variations in mean egg volume (cm^3) of the Common Kestrel populations in the Western Palaearctic. Areas considered: Belarus, Czech Republic, England, Finland, France, Germany, Italy, Poland, Scotland, mainland Spain, Tenerife island, Ukraine. The size of the dots represents the egg volume at each location. See also Table 1

So, if we also consider temperature stability, both predictions would meet the criteria of the hypothesis.

Rainfall during the previous autumn was negatively correlated with egg volume in the study population. Volume, sphericity and similarity degree had the highest CV in 2010, which was the year with earliest laying dates, also coinciding with a rainy year, as was in autumn the year before. In contrast, the CV in volume in 2012 was the lowest, coinciding with the first term (winter) of this driest year. The unpredictable weather fluctuations in the study area, modulated by the influence of the North Atlantic Oscillation (García-Herrera et al. 2001), suggest breeding adaptations associated with fluctuations in scarce rainfall periods (Carrillo and González-Dávila 2010a). That is, for the island population we studied, rainfall during the previous autumn notably influences laying date of the next breeding season, but not clutch size. Specifically, it is winter rainfall that is affecting clutch size the most. In addition, high prey availability during egg formation period is associated with clutch size; but this does not result in higher overall breeding success (Carrillo and González-Dávila 2010a). Indeed, egg volume was positively correlated with hatching success, but was not associated with fledging success. Temperatures in March were negatively correlated with egg volume in the study population. Unfortunately, we cannot confirm whether the temperature only limits the amount of nutrients needed for egg formation, or whether it is related to a disturbance in the energy balance of females during laying. However, the influence of temperature explains less than 15% of egg size variability in birds (Christians 2002).

Geographical variations

Egg volume in Tenerife kestrels was significantly larger, after controlling for the effect of female body mass, than it was for those in Finland, and the nearest continental counterparts from mainland Spain (there are no egg size data from neighbouring continental Moroccan populations). Our findings that Tenerife kestrel eggs had higher sphericity than any of the continental populations can be explained by the fact that, in warm environments, more rounded eggs would increase the surface/volume ratio, preventing metabolic rate increase of the embryo and egg overheating if the ambient temperature were high (Brulez et al. 2015).

The clutch size in Tenerife was not related with female body condition (present study) and is smaller than that of Moroccan populations (Carrillo and González-Dávila 2009). The correlation between smaller clutch size and larger size of eggs in insular bird populations (Covas 2012) may be explained by different interconnected mechanisms, not mutually exclusive. Firstly, ecological insular constraints, through natural selection, would determine clutch and egg size. Such constraints may be, for example, fluctuations of prey availability in the xeric environment associated with fluctuations in rainfall (Carrillo and González-Dávila 2010a); high kestrel population density in this environment (Carrascal and Palomino 2005) and, consequently, high intraspecific competitive pressure (Carrillo and González-Dávila 2013).

Secondly, reduced fecundity has long been assumed as one of the main life-history adaptive changes on islands. Lack (1970) indicates that insular birds may maximize their reproductive success investing more in egg size and less in egg number; thus, raising higher quality offspring with greater chance of survival. In accordance to this, the breeding success and fitness of Tenerife kestrels, in comparison to their mainland counterparts, is based on laying larger eggs and smaller clutches, as well as keeping a stable number and quality of fledglings over the years (Carrillo-Hidalgo et al. 2020, present study). The production of larger eggs and smaller clutches may represent a trade-off between conflicting selection pressures affecting reproduction and survival, especially on islands where improved survival favours reduced fecundity (Whittaker and Fernández-Palacios 2007). Probably, the island-dwelling kestrels in Tenerife exhibit a slow pace of life strategy, investing more in survival than in reproduction (Hille and Cooper 2015).

Finally, egg and clutch size increase may be matched patterns, largely due to latitudinal effect. Both patterns have been described in Western Palaearctic kestrel populations (Carrillo and González-Dávila 2009, present study), and might be explained taking into account body size dimensions of kestrels. Egg volume, on considering the three populations (i.e., Tenerife island, mainland Spain, Finland), was positively correlated with the female body mass, in such a way that female Tenerife kestrels were smaller (body mass, wing and tarsus length) than females in mainland Spain and also females in Finland (body mass and wing length). If northern individuals have larger body size ('Bergmann's rule'; Fröhlich et al. 2023), and also clutch size increases the further north, then the simultaneous increase of egg and clutch size would result in an additional outcome of geographic trends in body size and clutch size (Hõrak et al. 1995).

Ashmole's hypothesis has received support from studies matching clutch size variations and seasonality of actual evapotranspiration, which varies in direct proportion to primary plant production and food resources (Ricklefs 1980). Many birds, e.g. diurnal raptors, in the northern hemisphere tend to lay larger clutches, and their clutch size fluctuates more, than their counterparts at southern latitudes, because of a greater seasonality in the northern hemisphere in comparison to the southern one (e.g., Newton 1979; Sanz 1998). Previous studies indicate a linear relationship between clutch size and latitude in the Western Palaearctic kestrel populations (Carrillo and González-Dávila 2009). However, the inherent difficulties when testing the seasonality of resources for the different migratory patterns of kestrel populations (e.g., migrating at northern latitudes; non-migrating or residents at southern latitudes) cause a serious obstacle for putting Ashmole's hypothesis to test (Carrillo and González-Dávila 2010b).

In short, this study confirmed the effects of environmental factors (e.g., rainfall fluctuations, temperature in March), possibly influencing the female body mass, on life-history traits (e.g., clutch size/egg size) in Tenerife island kestrels, providing support for changes in breeding strategies of island-dwelling birds. Future detailed studies considering other factors such as environmental (e.g., territory quality, habitat characteristics, predation rates, weather), body condition and senescence (e.g., male and female age and quality, the geometric mean mass of both parents, parasitic load, adult survival), and behavioural factors (e.g., intra and inter-specific competition, population density, recruitment patterns) could elucidate the life-history traits (e.g., clutch size/egg size) of kestrels in different island environments and latitudes (e.g., Olsen and Cockburn 1993; Christians 2002; Williams 2012).

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Author contributions JC-H conceived the idea and performed the field work in Tenerife. JM-P and EK performed the field work in mainland Spain and Finland, respectively. EG-D and JC-H analysed the data. JC-H wrote the manuscript with help from EG-D. All authors revised the paper critically and gave final approval for publication.

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Data availability The data that support the findings of this study are available from the corresponding author upon reasonable request. Fig. S1, Fig. S2, Table S1, Table S2 and Table S3 are included as electronic supplementary material.

Declarations

Conflict of interest The authors declare no competing interests.

Ethical approval Field work was performed with the permission of the Canary Government (Cabildo de Tenerife) yearly. Although Common Kestrels in the study area are rather habituated to human presence, we remained there the least time possible on our nest visits. This research was conducted in compliance with the Guidelines to the Use of Wild Birds in Research.

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