

Tibetan Birds Lay Larger Eggs at the Cost of Egg Number

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Abstract

Life history theory predicts that when breeding in harsh environments, selection favors organisms to allocate more energy into fewer offspring at the expense of offspring number. However, it is unclear whether such a trade-off remains evident in the presence of parental care, which might compromise the maternal investment to offspring quality. We address this question using a comparative approach for phylogenetically-paired passerines breeding in the Tibet Plateau vs. adjacent lowlands, the two systems that sharply differ in environmental hardness. While total biomass of eggs within a clutch became lighter towards Tibet, clutch size decreased and egg size increased. Tibetan birds were more time-constrained in breeding duration but had longer incubation and nestling periods than their lowland counterparts. Despite so, nestlings reared in Tibet were of similar body mass at fledging to those reared in lowlands. Therefore, more investment in fewer eggs as well as in incubation and provisioning young suggests that Tibetan birds are making the best of a bad job to ensure offspring survival under the hard conditions. This research supports a role of adaptive reproductive allocation by animals with parental care in the evolution of life history strategy along elevational gradients.

Introduction

Size and number of offspring are two major forms of investment that organisms make in reproduction. Corresponding to the quality and quantity of offspring, the two traits can give organisms different fitness rewards according to environments. Mild environments allow more, smaller offspring to survive, whereas stressful environments select for breeders that prioritize offspring quality at the expense of offspring quantity (Roff 2002; Czesak and Fox 2003; Rollinson and Hutchings 2013). Therefore, life history theory predicts that organisms should adaptively budget their investment in reproduction through trading-off between offspring size and number in a specific environment to maximize fitness (Smith and Fretwell 1974).

While ecological conditions drive the co-variation in offspring size and number, parental care might alter the strategy of maternal investment in the two traits. Taxa giving no parental care are expected to make the trade-off of quality vs. quantity more. In contrast, high levels of parental care may mitigate the influence of offspring quality on fitness and thus permit a reduced investment in individual offspring, potentially constraining the trade-off (Figuerola and Green 2006).

Elevation presents an environmental gradient along which climates tend to be cold and seasonable, and food resources become poor, making the growth and survivorship of offspring increasingly challengeable (Keller et al. 2013; Boyle et al. 2016). As expected, a reproductive strategy in favor of offspring size against offspring number towards high elevations has been seen in a variety of ectothermic organisms where parental care is generally absent (e.g., crustaceans: Wilhelm and Schindler 2000; insects: Blanckenhorn 1997; amphibians: Liao and Lu 2011; Chen et al. 2013; Liao et al. 2014). A similar strategy of life history is expected to be taken by precocial birds where parental care levels are relatively low (Badyaev 1997; Badyaev and Ghalambor 2001). There is evidence showing that the positive relationship

between egg size (a quality indicator, see below) and offspring performance characterized by growth and survival is more obvious in precocial than altricial species (Williams 1994, but see Krist 2011). The trade-off between clutch size and egg size along elevational gradients has been demonstrated across precocial galliform species that breed in temperate regions (Balasubramaniam and Rotenberry 2016).

In contrast, altricial birds might compromise investment to offspring quality with more developed parental care in the form of incubation and offspring provisioning. This could particularly be the case for high-elevation passerines. Empirical studies have found that compared to their lowland congeners, high-elevation passerines lay fewer and smaller clutches but pay greater per capita provisioning efforts, spend longer time in incubation and rearing young with male parents being engaged more (Badyaev 1997; Badyaev and Ghalambor 2001). Typically, prolonged incubation and nestling periods may improve immunity of nestlings (Ricklefs 1992) and allow nestlings to reach a relatively large size at fledging (Björklund 1996).

However, a few altricial species in higher-elevation regions have been found to produce larger eggs when they produce smaller clutches at the same time (Lu 2005; 2008; Lu et al. 2007, 2008, 2010; Li and Lu 2012). Egg size is an indicator of offspring quality and larger eggs have fitness advantages over smaller ones (Christians 2002; Krist 2011). Empirical work has shown that larger eggs contain more yolk so that hatchlings from larger eggs carry more nutrient reserves (Williams 2005), which may facilitate nestling growth. Larger nestlings may alleviate thermoregulatory stresses or water loss through the enlarged surface area to volume ratio (Carey et al. 1994), and enjoy a great survival advantage when developing under oxygen-poor conditions (Einum et al. 2002). These empirical studies on individual species imply that high-elevation altricial birds take a maternal investment strategy in favor of egg size over egg number even though they have made more investment in other components of parental care which may enhance offspring quality.

It is surprising that although an elevational decline in clutch size of altricial species has been demonstrated to be the norm (Hille and Cooper 2015; Boyle et al. 2016), whether this trend causes a corresponding increase in egg size has received little systematic evaluation. Two intraspecific studies, which concluded that high-elevation breeders pursue strategies of prioritizing offspring quality over offspring quantity, used body mass, growth rate or survival probability of nestlings rather than egg size to measure offspring quality (Bears et al. 2009; Lundblad and Conway 2020). These estimators make it difficult to distinguish the investment to egg size from that to nestling care or nest predation.

With an average elevation of more than 4000 m and a territory of 2,500,000 km², the Tibet Plateau is the world's highest and largest highland. Organisms inhabiting the plateau are at the limit of their elevational distribution. Abiotic factors in the Tibet plateau such as climate, seasonality and air oxygen availability are usually at their extremes (Fig. 1). Also, plant productivity and the resultant insect abundance as a major food resource for many birds are poor in the high-elevation habitats. The unique environments offer a good opportunity to see the evolution of avian life history across elevations. Although data from several separate studies on individual species indicate a trade-off between egg size and number towards

the Tibet Plateau (Lu 2005, 2008; Lu et al. 2007, 2008, 2010; Li and Lu 2012), yet no synthetic analysis has been made to conclude generality of the pattern.

Here, we used the data from Tibetan passerine species vs. their lowland counterparts to test the prediction that Tibetan birds value more upon offspring quality over offspring quantity through producing larger but fewer eggs. Maternal investment strategy in egg size and number can be related to elevational variation in breeding season duration and parental investment in incubation and nestling care. We thus also evaluated the variation in these parameters across elevations.

Materials And Methods

Data collection

We compiled the dataset using pairs of closely related taxa with one breeding in the Tibet plateau and the other in the lowland China to allow for pairwise comparison. Such an approach depends little on phylogenetic history among clades (Møller and Birkhead 1992) and excludes variables like developmental mode, migration status, diet and nest type that might affect life history traits (Böhning-Gaese et al. 2000). Therefore, it provides a powerful test for the concordance between life history traits and elevation.

Nevertheless, treating elevation as a binominal variable, the pairwise comparison cannot capture the cline of life history traits, given that the differences in breeding elevation vary greatly between the sister taxa. Therefore, we also made regression analyses with species as independent data points. In the analyses, data based on paired taxa may minimize the influence of phylogenetic context on the relationship between life history traits and elevations, and avoid the unbalancedness of samples because much few Tibetan species have been studied.

We first choose a Tibetan passerine species and then matched it with a closely related taxon in lowlands. A pair of species was included only when the information on clutch size and egg size both is available for two paired counterparts from published reports or our own unpublished records. In choosing lowland taxa, we gave populations or subspecies of the same species a priority, which would make the results more conservative. If such a taxon is unavailable, a member within the same genus was considered. Most low-elevation counterparts were restricted to lowland China, but a few occurring in other regions were chosen because of unavailability for the counterparts in lowland China. We also included several Tibetan endemics (10 pairs) which breed in two different elevations within the Tibet plateau.

In addition to mean clutch size and egg size, we recorded breeding season length, incubation period, nestling period and relative fledging mass (nestling mass at fledging divided by adult female mass). We also extracted the following traits for these matched pairs of species: elevation and latitude at which the field studies were conducted, and mean adult female body mass from published ornithological handbooks, using the values from the sites adjacent to those at which the breeding data were reported. A taxon was included only when its breeding information was based on more than five nests. When several

estimates are available for a species from different studies, we used their mean value taking sample sizes into account.

Finally, our dataset contains 31 pairs of passerine birds known clutch size and egg size, which involve 26 genera and 15 families (Appendix 1). Of these, 24 pairs are available for breeding season length, 22 pairs for incubation period, 22 pairs for nestling period and 10 pairs for relative mass of fledglings. As a consequence, the number of pairs differs among analyses. We are confident that our dataset reflects the information currently available for Tibetan birds. Additionally, egg size is comparable across species because sex difference in this trait is usually absent despite the existence of sexual size dimorphism of adult birds in some species (Rutkowska et al. 2014).

Data analyses

A repeated-measures one-way ANOVA was performed to make pairwise comparisons, where breeding elevation of sister taxa were ranked as high or low and treated as a fix factor. For conventional regression analyses in which species are independent data points, a general linear mixed model was run letting 'species pair' nest within the family as a random term to control for phylogenetic dependency (Harvey and Pagel 1991; Covas 2012).

We assessed how clutch size and egg size responded to elevational gradients, respectively. Selection might act on total investment in egg production (investment in both egg size and egg number together) and this would mask the trade-off between these two traits (Czesak and Fox 2003). Therefore, we investigated whether total egg production, measures as the mean clutch size multiplying egg size, depended on elevation. A trade-off between egg size and number would be plausible if the former increased and the latter decreased along elevational gradients, and meanwhile the total clutch mass exhibited no altitudinal trend.

Considering that seasonal time constraint can exert selection on life history traits such as offspring growth which in turn affects the trade-off between offspring quality and quantity (Sniegula et al. 2016), we analyzed the breeding season length in relation elevations, with an assumption that relative to their lowland counterparts, high-elevation birds are more time-constrained. Selection for more investment in offspring quality might also be expressed through increasing parental efforts in terms of incubation and young rearing, which might allow a compromise on investment to egg size (Badyaev and Ghalambor 2001). To see whether this occurs, we compared duration of incubation and nestling periods across elevations. Moreover, we evaluated the relationship between fledgling mass relative to adult female mass and elevation, aiming to see whether the expected reproductive strategies taken by higher-elevation birds facilitate nestlings to fledge at a heavier body mass.

In these analyses, we included latitude and female body mass as the covariates to control for their potential effect on the response variables. The former as a geographic gradient have been known to be responsible for variation in life history traits (Böhning-Gaese et al. 2000), and the latter itself is a life

history trait that may involve in the trade-off of resource allocation (Kozłowski et al. 2020). A stepwise backward method was used to determine which of elevation, latitude and female body mass may significantly predict a life history trait. To do so, we first fitted a full model that included the three potential predictor variables, and then individually removed those with $P > 0.10$ until all predictor variables had $P < 0.10$ in the final model. This P -value criterion for one variable to be remained in the model allowed us to see the tendency of elevational effect on life history traits, although the significance level throughout the analyses was set at 0.05.

Prior to the analyses, all continuous variables were \log_{10} -transformed to correct for heterocedasticity and allometric effects. We also used z-score to standardize the \log_{10} -transformed data (mean = 0, $SD = 1$) so that the partial regression coefficients as effect size can be compared among explanatory variables and among different studies.

Results

The repeated-measures one-way ANOVA for pairwise comparisons revealed that Tibetan birds laid significantly smaller clutches than their lowland counterparts, accounting for latitude (Table 1, Fig. 2a). Accordingly, higher-elevation taxa also tended to lay larger eggs compared to lower-elevation birds (Table 1, Fig. 2b). The total biomass of eggs within a single clutch significantly declined towards highland Tibet (Table 1, Fig. 2c). Similar patterns were detected when the analyses excluded the 10 species that only breed in the Tibet plateau (Table S1).

Table 1

A summary of the repeated-measures one-way ANOVA for pairwise comparisons between Tibetan birds and their lowland counterparts to determine whether variation in several critical parameters of reproduction depended on breeding elevation, controlling for latitude and female body size of several critical parameters of reproduction. Covariate variables were selected following a stepwise backward regression method, with those whose *P* value was more than 0.10 are presented

	<i>df</i>	<i>F</i>	<i>P</i>
Clutch size			
Elevation	1, 29	10.95	0.003
Latitude	1, 29	3.04	0.092
Egg size			
Elevation	1, 29	7.56	0.010
Female body mass	1, 29	3.58	0.068
Total clutch volume			
Elevation	1, 29	9.88	0.004
Female body mass	1, 29	4.48	0.043
Breeding season length			
Elevation	1, 22	55.60	< 0.001
Incubation period			
Elevation	1, 20	16.21	0.001
Nestling period			
Elevation	1, 19	9.64	0.006
Female body mass	1, 19	5.35	0.032
Relative mass of fledglings			
Elevation	1, 9	0.19	0.673

General linear mixed models with specie as independent data points also found a significant increase in egg size with elevation (Table 2). However, elevation failed to enter the model and predicted variation in clutch size. In addition, the total egg volume did not change as elevations increased. After removing the 10 species endemic to the Tibet plateau, the relationship between clutch size and elevation ($\beta \pm SE = -0.44 \pm 0.09$, $df = 23.03$, $t = 4.81$, $P < 0.001$) and that between total egg volume and elevation ($\beta \pm SE = -0.09 \pm 0.04$, $df = 22.44$, $t = 2.54$, $P = 0.019$) became same as those obtained through pairwise comparisons

(Table S2). This result suggests that the elevational tendency for clutch size decline no longer continued towards highland Tibet where elevations are extremely high. Therefore, according to the fact that total egg biomass tended to decrease elevationally, it can be concluded that the opposite elevational changes in egg number and egg size was the consequence of a trade-off of parental investment between the two traits.

Table 2

A summary of the general linear mixed models to determine whether variation in several critical parameters of reproduction depended on breeding elevation, controlling for latitude and female body size in Tibetan passerines and their lowland counterparts. Possible phylogenetic effects were corrected for through nesting 'species pair' within the family as a random term. Predictor variables were selected following a stepwise backward regression method, with those whose *P* value was more than 0.10 are presented

	$\beta \pm SE$	<i>df</i>	<i>t</i>	<i>P</i>
Clutch size				
Latitude	0.43 ± 0.08	39.10	5.02	< 0.001
Egg size				
Elevation	0.10 ± 0.03	45.65	3.42	0.001
Female body size	0.96 ± 0.04	29.57	25.14	< 0.001
Total clutch volume				
Latitude	0.12 ± 0.04	38.32	3.22	0.003
Female body size	0.90 ± 0.07	21.55	13.27	< 0.001
Breeding season length				
Elevation	-0.59 ± 0.14	41.15	4.29	< 0.001
Incubation period				
Elevation	0.19 ± 0.10	48.00	1.84	0.071
Female body size	0.71 ± 0.11	48.00	6.37	< 0.001
Nestling period				
Elevation	0.17 ± 0.10	25.50	1.76	0.090
Female body size	0.52 ± 0.16	30.60	3.17	0.003
Relative mass of fledglings				
Female body size	-0.69 ± 0.14	26.97	4.83	< 0.001

Both repeated-measures one-way ANOVA and general linear mixed model analyses showed that towards the Tibet plateau, the breeding season duration of birds decreased significantly (Tables 1 and 2, Fig. 2d). There was a strong elevational increase in the length of both incubation and nestling periods when holding latitude and female body mass constant (Fig. 2e, f). Despite having received an extended parental care, fledglings reared by higher-elevation birds were of similar mass to those reared by their lowland counterparts (Fig. 2g). The results did not change qualitatively when the Tibetan endemic species were removed from the analyses (Tables S1 and 2).

Discussion

The current research confirms that passerine birds breeding in highland Tibet have smaller clutches than their lowland counterparts. Such an elevational cline in clutch size is consistent with that reported across populations of the same species or different species in other regions of the world (Badyaev 1997; Badyaev and Ghalambor 2001; Hille and Cooper 2015; Boyle et al. 2016). Importantly, our data further show that in accompany with the elevational decline in clutch size, Tibetan birds increase their egg size. Since total clutch mass is lighter for Tibetan birds and there is a strong negative correlation between clutch size and egg size, the larger eggs laid by high-elevation birds should be a consequence of trading-off against egg numbers within a single clutch. Variation in life history traits along environmental gradients can be due to either phenotypic plasticity or adaptive genetic divergences among populations. The results of pairwise comparison between sister taxa suggest a relatively recent macroevolutionary divergence of life history traits in association with local adaptation (Freckleton et al. 2002). A similar pattern of elevational covariation in clutch size vs. egg size has been observed in temperate galliformes (Balasubramaniam and Rotenberry 2016). However, in a meta-analysis with 13 species, Boyle et al. (2016) failed to detect an elevational increase in egg size, more likely because their study species occur within a limited range of elevations and the analyses did not control for egg number.

Tibetan birds have a shorter duration of breeding activity than their lowland counterparts. Similar findings have been reported across species (Boyle et al. 2016) or within a species (Bears et al. 2009; Lundblad and Conway 2020). This implies higher-elevation birds to be more and low-elevation ones to be less, time-constrained when performing breeding activities. The seasonal time limitation should be a selective pressure that promotes higher-elevation mothers to invest more energy in individual eggs, and the added energy would sustain the resultant nestlings to attain a fledging size necessary for post-fledging survival (Lundblad and Conway 2020). One might argue that this could not be the case because lowland birds also face a limitation of seasonal time when they raise more than a clutch per season. In fact, many lowland avian breeders are single-brooded species, or multiple-broodedness is performed facultatively in that only partial individuals within a population laying more than a brood during a breeding season (Bańbura and Zieliński 1998; Böehning-Gaese et al. 2000).

Tibetan birds spend longer time in incubation and provisioning offspring. The pattern is present for passerines breeding in other high-elevation regions (Badyaev 1997; Badyaev and Ghalambor 2001; Boyle et al. 2016). Prolonged development may allow offspring to establish a more effective immune system

which in turn may improve survival (Ricklefs 1992). In addition, previous studies have shown that males of higher-elevation birds share more parental care than males of lower-elevation birds (Badyaev and Ghalambor 2001). Therefore, while Tibetan birds increase their parental investment to improve offspring quality in terms of prolonging the time of offspring care, they do not compromise to investment in egg size even at the cost of egg number.

However, despite the larger investment in individual eggs and extended parental care and less sibling competition as a result of small clutches, nestlings of Tibetan breeders do not achieve a greater fledging size compared to lowland nestlings. Thus, larger eggs should be, along with the extended parental care, selected for to compensate the slow growth of embryos and nestlings at higher elevations, where offspring growth and metabolic rate are limited by cold climates, poor food supply (Gebhart-Henrich and Richner 1998) and low oxygen availability (Dillon et al. 2006). Small clutches and accordingly large eggs may be favored by high nest predation rates (Martin 1995). Low levels of both diversity and density of predators on the Tibet plateau suggest nest predation not to be the driver of the trade-off between egg size vs. egg number. Therefore, we conclude that when extended parental care by Tibetan breeders may not be sufficient to overcome the constraints on offspring development, increasing egg size should be a strategy of making the best of a bad job to cope with the extremely harsh environments.

An interesting finding of the current research is the inclusion of species endemic to the Tibet plateau altered the tendency of clutch size. Clutch size no longer continued to decline towards extremely high elevations, although the elevational tendency of other reproductive parameters still remained. These results suggest that relative to lowland birds, Tibetan birds can effectively trade off energy allocation between egg size and egg number. Within extremely harsh environments on the Tibet plateau, further decrease in clutch size as elevations increase would reduce individual fitness and limit population productivity. It is likely that Tibetan birds breeding at much high elevations cut down the investment in future reproduction to avoid the risk of current fitness reduction from small clutches.

There is an environmentally dependent optimal balance of energy allocation between offspring quality and quantity. According to the standardized coefficients of partial regression, the elevational decline in clutch size is slower for our dataset consisting mostly of mid-latitude species (-0.44) than that of temperate birds across species (-0.56 , Badyaev 1997) and within species (-0.75 , Badyaev and Ghalambor 2001), but faster than that across tropical species (0.24 , Boyce et al. 2015). The difference shows that the intensity of selection for variation in clutch size along elevational gradients may interact with latitude along which clutch size regularly varies (Boyle et al. 2016; Pincheira-Donoso and Hunt 2016). Whether the rate at which egg size increases with elevation becomes correspondingly fast towards high latitudes remains to be evaluated. A comparative analysis for galliformes revealed that while temperate higher-elevation species produce smaller clutches of larger eggs, tropical higher-elevation species produce both larger clutches and larger eggs (Balasubramaniam and Rotenberry 2016). It is possible that the good conditions such as those in tropical high elevations, compared to those in temperate or Tibetan high elevations, allow birds to relax the trade-off between competing life history traits.

We acknowledge that despite clear evidence for the trade-off between clutch size and egg size across elevational gradients, there is a need to evaluate the adaptive values of egg size using other fitness indicators, such as hatching success, nestling growth rate and their survival probability at or after fledging. To further estimate the proximate mechanisms behind this, physiological advantages of large eggs should be measured, especially under a hypoxic condition (Dillon et al. 2006). It has been reported that males of high-elevation birds contribute more to parental care than males of low-elevation birds (Badyaev and Ghalambor 2001), high-elevation birds also have extended parental care of post fledging (Potapov 2004). Such comparisons remain to be made when analyzing the evolution of life history towards the Tibet plateau. These studies will be particularly useful for answering a controversial question of whether high-elevation birds survive better than low-elevation ones (Bears et al. 2009; Lundblad and Conway 2020).

Declarations

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Electronic supplementary material

The online version of this article contains supplementary material, which is available to authorized users.

Compliance with ethical standards

Conflict of interest

The authors declare that they have no conflict of interest.

Statement of animal rights

This article does not involve any manipulation of animals.

Author contribution statement

XL conceived the idea. XL and YG collected data, performed statistical analyses, and wrote the manuscript. Both authors read and approved the final manuscript.

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Figures

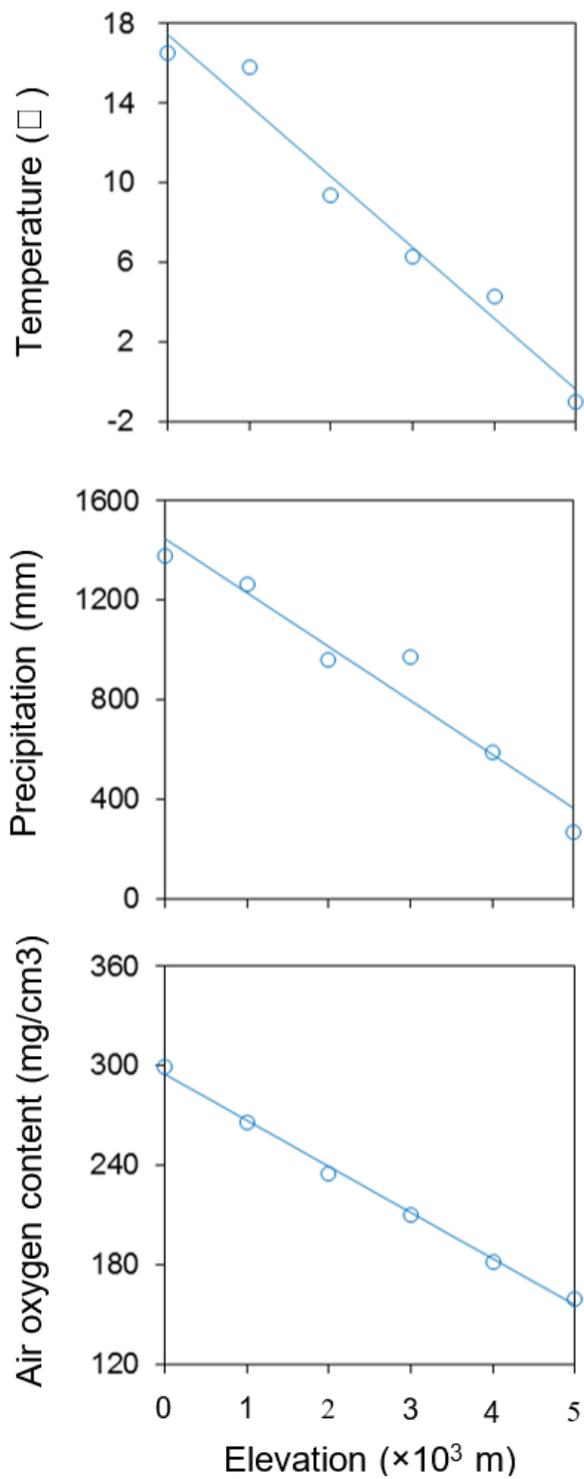


Figure 1

Elevational clines of annual mean air temperature, annual total precipitation and air oxygen content from lowland China to the Tibet Plateau at 30°N . The information came from records of 6 weather stations over 30 years. Lines are least-squares regression slopes

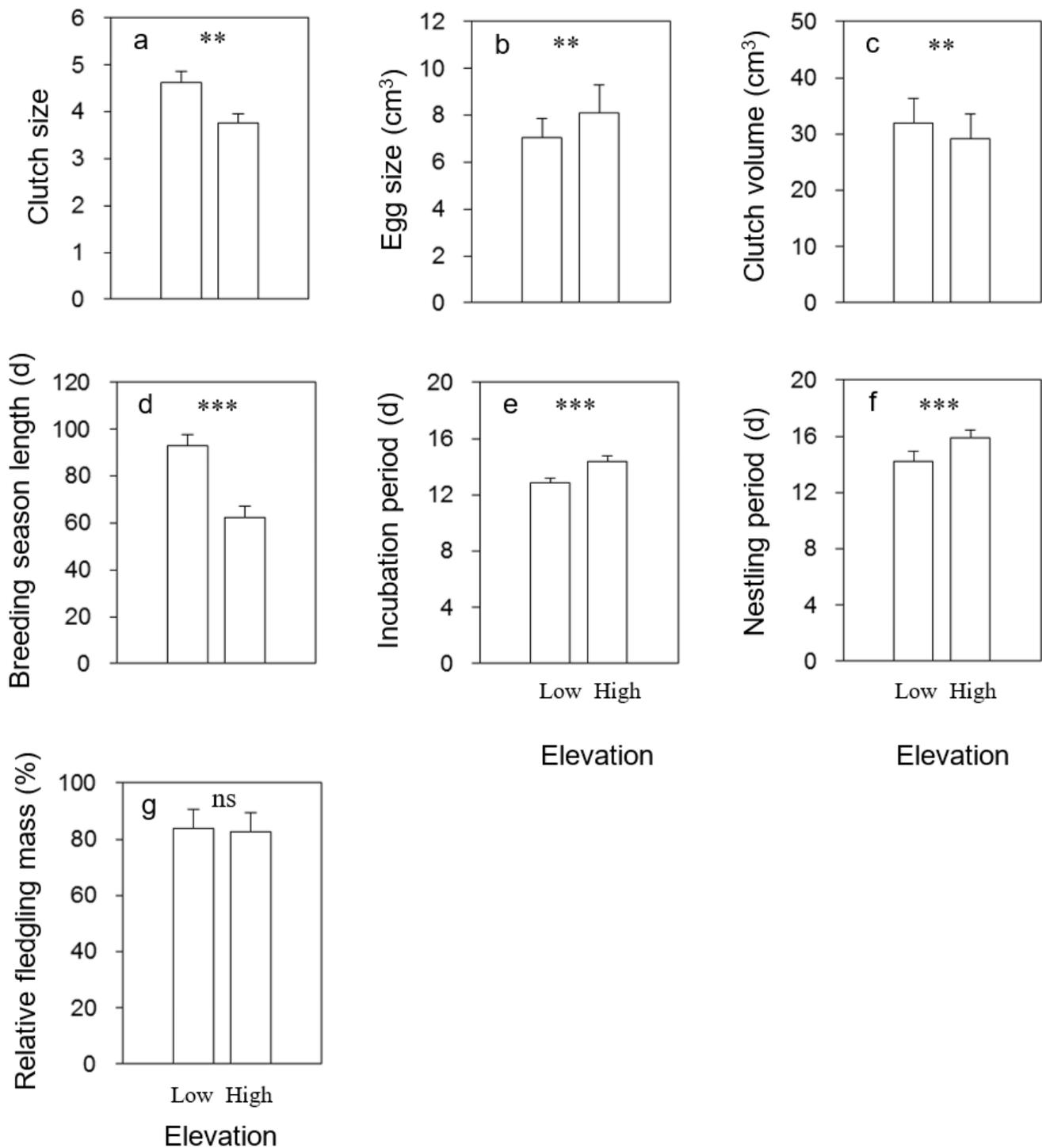


Figure 2

A comparison of breeding parameters between paired Tibetan birds and their lowland counterparts. Values are presented as mean + SE, with sample size and the significance level of repeated measure one-way ANOVA (Table 1). * P < 0.05, ** P < 0.01, *** P < 0.001

Supplementary Files

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- [Appendix1.docx](#)
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