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Egg investment strategies adopted by a desertic passerine, the Saxaul Sparrow (*Passer ammodendri*)

Xinkang Bao^{1*} , Wei Zhao¹, Fangqing Liu², Jianliang Li¹ and Donghui Ma¹

Abstract

Background: As one of the reproductive strategies adopted by bird species, variation in investment in egg production and its influencing factors are important and well-studied subjects. Intraclutch changes in egg size associated with laying order may reflect a strategy of “brood survival” or “brood reduction” adopted by female birds in different situations.

Methods: We conducted field studies on the breeding parameters of the Saxaul Sparrow (*Passer ammodendri*) in Gansu Province, China from 2010 to 2017, to clarify the factors affecting the egg investment and reproductive performance of this passerine species.

Results: Our results revealed significant differences in clutch size, egg size and the fledging rate between the first and second brood of Saxaul Sparrows and suggested that this typical desert species allocates more breeding resources to the more favourable second brood period, leading to greater reproductive output. Female body size presented a positive relationship with egg size, and male body size presented positive relationships with clutch size and hatchability. The females that started their clutches later laid more eggs, and hatchability and the fledging rate also increased with a later laying date in the first brood period. With successive eggs laid within the 5-egg clutches (the most frequent clutch size), egg size increased for the first three eggs and then significantly decreased.

Conclusions: Our results indicate that female Saxaul Sparrows increased egg investment because of good quality of paired males and good environmental conditions. The intraclutch variation of egg size suggests that this species inhabiting an arid environment adopts a “brood reduction” strategy.

Keywords: Brood reduction strategy, Clutch size, Egg size, Fledging rate, Hatchability, Reproductive strategy, Saxaul Sparrow

Background

In birds, the amount and quality of resources allocated to egg production can profoundly influence the growth and survival of progeny (Williams 1994; Mousseau and Fox 1998; Krist 2011), and the allocation of resources to

different eggs is an important component of the breeding strategy of birds that may affect fitness through offspring survival (Hargitai et al. 2005; Reed et al. 2009). Clutch size and egg size are interrelated traits of reproductive investment. A larger clutch size might result in greater reproductive output, and a larger egg size means that more nutrition is deposited in an egg, which will lead to the hatching of good-quality nestlings, contributing to their survival. According to Lack (1954), birds produce a larger clutch in periods when resources are most abundant. Variation in clutch size is a strategy

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that is sometimes used by females to maximize fitness in response to environmental conditions (Dolenec et al. 2011).

Previous studies have consistently shown that females of bird species can adjust egg size in response to physiological factors (Christians 2002; Kvalnes et al. 2013). In a review of avian egg size, Christians (2002) summarized the relationships between egg size and female body characteristics (mass, size and condition), and the results often supported the hypothesis that heavier females lay larger eggs. With respect to the relationships between male body characteristics and egg investment, some studies have indicated that female birds invest more in reproduction (such as laying larger eggs) after copulating with preferred males (Møller 1994; Cunningham and Russell 2000).

Some studies have indicated that in multi-brooded passerine birds, female quality decreases over the course of the breeding season owing to the metabolic costs of egg production (Hegner and Wingfield 1986; Lindén and Møller 1989; Christians et al. 2001). Kvalnes et al. (2013) found that the egg size of House Sparrows (*Passer domesticus*) in northern Norway decreased from the first to the third brood and attributed this variation to physiological constraints on the laying female. Another research indicated that multi-brooded females reduce egg size during the breeding season because conditions during the later period are favourable, so smaller eggs are adequate for survival (Yampolsky and Scheiner 1996).

Slagsvold et al. (1984) suggested that the nestling that hatches from the last-laid egg is at a disadvantage compared with its siblings; they analysed intraclutch variation in egg size in 67 bird species and identified two strategies. Birds that lay relatively larger final eggs adopt a “brood survival” strategy, in which the last nestling can compete with its older siblings. The other strategy is “brood reduction”, which means that the last nestling hatching from the relatively smaller final eggs will be sacrificed in the event of food shortage. Previous studies have shown that altricial bird species can adjust their investment strategy and increase egg size during the laying sequence under more favourable conditions to facilitate the raising of the whole brood (Hargitai et al. 2005). For example, in a population of Tree Sparrows (*Passer montanus*) in northwestern Croatia (Dolenec et al. 2011), the female birds were found to use a “brood survival” strategy for the second clutch, while they used a “brood reduction” strategy for the first and third clutches. Furthermore, nine passerine bird species breeding in rich subalpine birch forests in southern Swedish Lapland were shown to uniformly exhibit a significant increase in egg size in the later part of the

laying sequence, in which the last egg was 2.1–6.5% larger than the mean size for the clutch (Enemar and Arheimer 1999).

The Saxaul Sparrow (*Passer ammodendri*) is a passerine species occurring in remote parts of Asia that is less studied than any other *Passer* species (Summers-Smith 1988) and is a representative species of the desert region. Our field studies were conducted in the Gansu An’xi Extremely-Arid Desert National Nature Reserve located in Guazhou County of Gansu Province in western China, which is characterized by typical central Asian weather conditions and drought-prone arid habitats. The egg investment of some *Passer* species, such as the Tree Sparrow (*P. montanus*) and House Sparrow (*P. domesticus*) living in other habitats, is well known (Murphy 1978; Summers-Smith 1988; Dolenec et al. 2011; Kvalnes et al. 2013), whereas that of the Saxaul Sparrow living in an extremely arid habitat has not been well studied. For example, what are the factors affecting the clutch size and egg size of the Saxaul Sparrow? Do environmental factors (such as ambient temperature) and the body characteristics of males and females have special influences on egg investment in this species? How does this two-brooded *Passer* species strategically invest resources in clutch size and egg size during the breeding season? Does the Saxaul Sparrow adopt the “brood reduction” strategy of laying smaller final eggs under desert environmental conditions as we predicted? This paper will discuss the reproductive strategies of a multi-brooded passerine adapted to a desert environment.

Methods

Study area and species

Field work was carried out from 2010 to 2017 in wooded area (40° 21' N, 96° 13' E) within the An’xi Extremely-Arid Desert National Nature Reserve. The annual average temperature at the study site from 2010 to 2017 was 9.57 °C (with extremes of −23.3 to 40.9 °C), and the mean annual precipitation was 41.72 mm (data from a meteorological station built in the study area in 2009). The wood is composed of *Elaeagnus angusifolia* (90%), *Populus gansuensis*, and *Salix matsudana* and is surrounded by desert with several areas of cropland. Since 2009, 110 nest boxes have been mounted on the sparrow’s natural nesting tree species (*E. angusifolia*). The sparrows show a strong preference for wooden nest boxes leading to a 100% use rate, despite having previously built tree nests. In this region, the Saxaul Sparrow is a resident species and rears two broods of young per breeding season. The breeding season lasts from early May to early August. Both sexes take part in nest building and feeding the young. The sexes of the Saxaul Sparrow are sesquimorphic; males exhibit a broad black stripe on the crown

and a black bib spreading laterally on the breast, which are easy to distinguish from females, whose colours are more muted and less contrasting.

Reproductive data

Nest boxes were inspected daily during the egg-laying period to record the date at which the first egg was laid and the exact egg laying order in each nest. Laying order was indicated by numerals marked on the egg surface with a waterproof marker. The laying date was the date of the appearance of the first egg of each clutch. Egg length and width were measured with micrometre callipers to the nearest 0.01 mm. Egg volume was calculated as follows: $\text{volume} = 0.51 LB^2$, where L is the maximum egg length, and B is the maximum egg breadth (Hoyt 1979). The egg size of each clutch was measured as the mean egg volume of all eggs in a clutch. To avoid disturbance as much as possible, all nest visits were conducted in the afternoon when the adults left the nest for a relatively long time. After the clutches were complete, the nests were not disturbed again until the predicted hatching date, at which time they were checked daily until the eggs had hatched. The nests continued to be checked every 2 days until the nestlings fledged. Unhatched eggs were defined as those still remaining as egg when the nestlings were processed at 8 days. Hatchability was calculated as the percentage of eggs surviving to the time of hatching that produced a nestling. The eggs lost to predation, accidental breakage or any other unknown factors were excluded. The fledging rate is defined here as the percentage of nestlings that survived to 8 days of age (Coe and Rotenberry 2003).

For a more detailed understanding of the variation in egg size, a within-clutch coefficient of variation of egg size (CV of egg size) was calculated (as described by Yosef and Zduniak 2004). To account for variation related to years, we standardized intraclutch egg size across years by subtracting the mean value in a particular year from the actual value and dividing the result by the standard deviation for that year (Hargitai et al. 2005). The deviation of the final egg from the mean egg size of the clutch (referred to as the %D value) was calculated as an indication of either a “brood reduction” or “brood survival” strategy as follows: $\%D = 100 (evf - evm) / evm$, where evf = volume of the final egg, and evm = mean egg volume of a clutch (Slagsvold et al. 1984; Dolenc et al. 2011).

Parental body size

Adult Saxaul Sparrows were captured during chick rearing using mist nets placed near their nests and then fitted with a unique combination of coloured bands for individual identification. General measurements of body size were obtained. After capture, a small video recorder

was hung on a tree close to the nest to identify the true parents of the nest. We used a single variable (tarsus length, ± 0.01 mm) to estimate body size for both males and females, as suggested by Rising and Somers (1989).

Environmental variables

Ambient climate data were available from a weather station constructed at the study site. The ambient temperature and ambient humidity for each clutch were calculated as the mean daily average temperature or humidity for a 9-day period extending from 4 days before until 4 days after the laying of the first egg (Hargitai et al. 2005). This period experienced by female birds during egg production corresponds to the time required for rapid follicular development and egg formation in the oviduct for small female passerines (Hargitai et al. 2005). The coefficient of variation of the daily average temperature (CV of temperature) within this 9-day period was also calculated to represent the degree of weather change during egg laying. We calculated the CV of the daily average temperature during the first brood (from 1 May to 10 June) and the second brood (from 10 June to 20 July) to compare climatic stability between these two periods.

Statistical analysis

To meet the criteria of the parameter test, all percentage data were arcsine transformed. To illustrate the mean differences between two broods, we only included the data of double brooders that were definitely identified by colour bands and applied the paired T test.

We fitted linear mixed models (LMMs) to evaluate the factors correlated with clutch size, egg size, hatchability and fledging rate. To explain the correlations, LMMs were constructed including the following putative explanatory variables (as fixed effects): laying date, ambient temperature, ambient humidity, CV of the temperature during egg laying, clutch size, egg size, the %D value of the final egg, the tarsus length of the parents (male and female) and interactions between pairs of these variables. The random effect components in all models took into consideration the repeated sampling of females in different years (fitting both female identity and years). The LMMs were fitted assuming a Gaussian error distribution in the “lme4” package of the R statistical program (Bates et al. 2014). Model selection was performed via maximum likelihood comparison of competing models using the Akaike information criterion (AIC) and Bayesian information criterion (BIC) approaches, which provided identical results. The AIC and BIC scores were compared between the models, and we identified the most parsimonious model as the best-fit model. In every breeding season, the individuals produced two broods in distinctly different stages, so we performed the model selection

and LMM analysis for the first brood and the second brood separately. We considered coefficients with $P < 0.05$ significant.

Results

The average clutch size was 5.13 ± 0.89 (965 nests), with a range of 2–8. The average egg size of a clutch was $2.59 \pm 0.21 \text{ cm}^3$ (965 nests), with a range of 2.00–3.36 cm^3 . The average hatching rate was 0.82 ± 0.19 (774 nests), and the average fledging rate was 0.84 ± 0.28 (772 nests).

Comparison between two broods

Most of the Saxaul Sparrows laid two broods each breeding season. A total of 71.7% of pairs kept the original mate and used the same nest boxes (ringed pairs $n = 53$ in 2014), and 28.3% of pairs replaced their mates in the second brood. The egg-laying date of the first brood was from 1 to 31 May, and that of the second brood was from 10 June to 9 July. The CV of temperature during the first brood was significantly higher than that during the second brood ($F = 289.08$, $df = 1$ and 522 , $P < 0.001$).

From 2010 to 2017, a total of 367 pairs (nests) were well monitored and confirmed to keep the original mate and to breed two broods in same breeding season. Within the 367 nests, there were just 248 nests with hatching data and 246 nests with fledging data. The difference between these first and second nesting attempts indicated that the mean values of clutch size, egg size, the final egg %D value, and the fledging rate of the second brood were significantly higher than those of the first brood (Table 1).

Intraclutch variation

The Saxaul Sparrows laid 2–8 eggs per clutch with the following distribution across 965 broods: 0.2% (2 eggs), 2.8% (3 eggs), 16.8% (4 eggs), 50.2% (5 eggs), 24.4% (6 eggs), 5.0% (7 eggs), and 0.7% (8 eggs). We analysed the variation of intraclutch egg size with the laying order in advance and obtained similar trends for each clutch size. Therefore, we only considered a clutch size of 5 (the most frequent clutch size, 50.2%) in the evaluation of intraclutch egg size variation with laying order. Significant

differences in egg size within a clutch were found ($F = 14.73$, $P < 0.001$). With successive eggs laid within the 5-egg clutches, egg size increased for the first three eggs and then significantly decreased (Fig. 1). The intraclutch pattern of the 5-egg clutches was independent of the ambient temperature (temperature \times laying order interaction: $F = 1.83$, $df = 4$ and 128 , $P = 0.09$) and parental body size (size \times laying order interaction: $F = 0.31$, $df = 4$ and 132 , $P = 0.78$ for females and $F = 0.13$, $df = 4$ and 176 , $P = 0.85$ for males).

A post hoc test (LSD test) indicated that the deviation of the final egg from the mean egg size of a clutch (%D value) was not significantly different between years ($P > 0.10$). Among different clutch sizes, the %D value was -1.43 ± 7.05 for three-egg clutches ($n = 14$), -1.78 ± 4.66 for four-egg clutches ($n = 78$), -2.72 ± 4.31 for five-egg clutches ($n = 252$), -1.83 ± 5.18 for six-egg clutches ($n = 106$), and -0.46 ± 4.74 for seven-egg clutches ($n = 17$). The %D value of the second brood

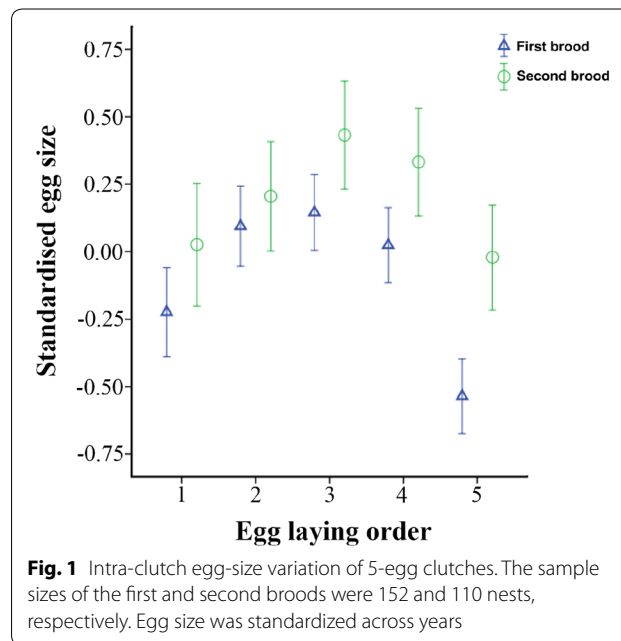


Fig. 1 Intra-clutch egg-size variation of 5-egg clutches. The sample sizes of the first and second broods were 152 and 110 nests, respectively. Egg size was standardized across years

Table 1 Comparison of breeding parameters between two broods

Brood number	Clutch size	Egg size	Final egg %D value	Coefficient of variation (CV)	Hatching rate	Fledging rate
First	4.85 ± 0.73	2.58 ± 0.20	-2.62 ± 4.31	4.36 ± 2.58	0.83 ± 0.19	0.81 ± 0.32
Second	5.42 ± 0.93	2.61 ± 0.21	-0.92 ± 4.68	4.70 ± 3.07	0.80 ± 0.20	0.86 ± 0.23
Paired <i>T</i> tes	$t = -9.648$ $df = 366$ $P < 0.001^*$	$t = -2.530$ $df = 366$ $P = 0.012^*$	$t = -5.398$ $df = 366$ $P < 0.001^*$	$t = -1.630$ $df = 366$ $P = 0.104$	$t = 1.568$ $df = 247$ $P = 0.118$	$t = -2.434$ $df = 245$ $P = 0.016^*$

*Significance at the level of 0.05

(-0.92 ± 4.68 , $n = 367$) was significantly greater than that of the first brood (-2.62 ± 4.31 , $n = 367$).

Ambient humidity, laying date and parental traits

Potential factors influencing clutch size, egg size, hatchability and fledging rate in different broods of the Saxaul Sparrow were examined in LMMs analysis. The results indicated that laying date and male body size exhibited a significant positive correlation with clutch size for both broods (Table 2) and that ambient humidity during egg laying in the first brood also presented a positive relationship with clutch size. Egg size was significantly influenced by the body size of females and by male mate body size during the second brood. As the clutch size of both broods increased and the laying date of the first brood became later, the hatchability of the nests increased

significantly. The male’s body size also exhibited a significant influence on hatchability. Regarding the fledging rate, only the laying date of the first brood had a significant effect, but for hatchability and egg size, male body size exhibited a marginally significant ($P < 0.10$) effect during the first brood.

Discussion

Seasonal declines of clutch size and other components of reproductive performance are very common in birds (Hochachka 1990). Multi-brooded passerine species show a decrease in egg size from the first to later broods because of physiological constraints on the laying female bird (i.e., the decreases in intrinsic quality and fat reserves) (Perrins 1996; Kvalnes et al. 2013) or because smaller eggs are adequate for survival under favourable environments (Yampolsky and Scheiner

Table 2 Analysis of deviance table (type II Wald Chi-square tests) for the best-fit models to explain the effect of different factors (fixed effects of model) on clutch size, egg size, hatchability and fledging rate. Female identity and year were considered as random effects in all models

Response	First brood			Second brood			
	Estimate	t value	P	Estimate	t value	P	
Clutch size							
Laying date	0.02 ± 0.01	3.498	<i>0.00***</i>	Laying date	-0.03 ± 0.01	-3.802	<i>0.00***</i>
Egg size	-0.26 ± 0.21	-1.264	0.21	Egg size	-0.12 ± 0.33	-0.359	0.72
Ambient humidity	0.02 ± 0.01	2.026	<i>0.04*</i>	Ambient humidity	0.01 ± 0.01	1.083	0.28
%D of the final egg	-0.02 ± 0.01	-1.870	0.06	Female’s body size	0.03 ± 0.09	0.315	0.75
Female’s body size	0.06 ± 0.06	1.000	0.32	Male’s body size	0.62 ± 0.10	6.240	<i>0.00***</i>
Male’s body size	0.43 ± 0.06	7.696	<i>0.00***</i>				
Egg size							
Laying date	0.00 ± 0.00	0.874	0.38	Laying date	0.00 ± 0.00	0.459	0.65
Clutch size	-0.03 ± 0.02	-1.636	0.10	Clutch size	-0.00 ± 0.02	-0.072	0.94
%D of the final egg	-0.00 ± 0.00	-1.558	0.12	Ambient humidity	-0.00 ± 0.00	-1.738	0.08
Female’s body size	0.05 ± 0.02	2.795	<i>0.01**</i>	Female’s body size	0.04 ± 0.02	2.184	<i>0.03*</i>
Male’s body size	0.02 ± 0.02	0.930	0.35	Male’s body size	0.05 ± 0.02	2.465	<i>0.01*</i>
Hatchability							
Laying date	0.00 ± 0.00	2.087	<i>0.04*</i>	Laying date	-0.00 ± 0.00	-0.748	0.45
Clutch size	-0.06 ± 0.02	-3.397	<i>0.00***</i>	Clutch size	-0.05 ± 0.02	-2.945	<i>0.00**</i>
Egg size	0.05 ± 0.06	0.759	0.45	Egg size	0.05 ± 0.07	0.644	0.52
Ambient humidity	0.00 ± 0.00	0.601	0.55	%D of the final egg	-0.00 ± 0.00	-0.198	0.84
Female’s body size	0.03 ± 0.02	1.398	0.16	Female’s body size	0.00 ± 0.02	0.030	0.98
Male’s body size	0.07 ± 0.02	3.635	<i>0.00***</i>	Male’s body size	0.05 ± 0.02	2.154	<i>0.03*</i>
Fledging rate							
Laying date	0.01 ± 0.00	2.340	<i>0.02*</i>	Laying date	-0.00 ± 0.00	-0.747	0.46
Hatchability	-0.17 ± 0.09	-1.894	0.06	Hatchability	-0.14 ± 0.07	-1.838	0.07
Clutch size	0.01 ± 0.02	0.682	0.50	Clutch size	-0.01 ± 0.02	-0.626	0.53
Egg size	0.15 ± 0.08	1.943	0.05	Egg size	0.10 ± 0.06	1.601	0.11
Female’s body size	-0.01 ± 0.01	-0.718	0.47	Female’s body size	-0.00 ± 0.02	-0.061	0.95
Male’s body size	0.01 ± 0.01	1.832	0.07	Male’s body size	0.02 ± 0.02	0.921	0.36

Italic values indicate statistically significant associations

***p < 0.001, **p < 0.01, * p < 0.05

1996). In a double-brooded Desert Finch (*Rhodospiza obsoleta*) population, Yosef and Zduniak (2004) suggested that the parents are more capable of fledging young successfully during more stable summer conditions, leading to less variable eggs and smaller clutch sizes in the second brood period. Our results indicated that contrary to common seasonal trends and physiological constraints, female Saxaul Sparrows laid significantly more eggs per clutch and did not decrease egg size during successive broods. In the study area, the early period in the breeding season (April–May) was characterized by lower temperatures, less precipitation, inconsistent and extreme weather conditions, and even sand storms (Liu and Yang 2006). The second part of the breeding season (June–July) was typically a much more stable period (the CV of temperature during the first brood was significantly higher than that during the second brood). We suggest that the Saxaul Sparrows living in this extremely arid environment allocate more breeding resources to the second brood, which is produced under relatively favourable conditions. This strategy resulted in a better reproductive output (i.e., the fledging rate of the second brood was significantly higher than that of the first brood).

Birds producing a relatively large final egg adopt a “brood survival” strategy, whereas birds adopting a “brood reduction” strategy produce a smaller final egg (particularly birds with large clutches) (Slagsvold et al. 1984). Among different bird species (Enemar and Arheimer 1999) and even within a single species (Dolenec et al. 2011), the two strategies may vary with breeding conditions. For example, in a population of Tree Sparrows in northwestern Croatia (Dolenec et al. 2011), the female birds were found to adopt a “brood survival” strategy for the second clutch (the deviation of the final egg size from the mean egg size of a clutch, %*D* value = 1.58), while they adopted a “brood reduction” strategy for the first (%*D* value = -1.58) and third clutches (%*D* value = -1.07). The common understanding is that under favourable environmental conditions, egg size within a clutch increases with egg laying order (Enemar and Arheimer 1999; Hargitai et al. 2005; Dolenec et al. 2011). According to our results regarding intraclutch variations (Fig. 1) and the relative size of the final egg, the female Saxaul Sparrow adopts a “brood reduction” strategy for both the first (%*D* value = -2.62) and second clutches (%*D* value = -0.92). This strategy is compatible with its habitat. In desert environments, where weather conditions are often mutable and extreme, birds face unpredictable abiotic conditions and cannot guarantee the survival of the last egg, which hatches asynchronously in disadvantageous circumstances. However, once conditions change in a relatively stable direction, such as

the second brood period, the Saxaul Sparrow may tend to eliminate discrimination among eggs within a clutch (the second brood exhibits a significantly higher %*D* value than the first brood).

Individuals producing larger eggs are forced to lay smaller clutches, a relationship that seems intuitively obvious (Smith and Fretwell 1974). However, a literature survey indicated that egg size is generally (in 40 of 63 studies and species) unrelated to clutch size (Christians 2002). Under favourable conditions, such as warm weather, a large clutch with large-sized eggs is the best combination for high fledging success and productivity in *Ficedula hypoleuca* (Järvinen and Väisänen 1984). In our analysis, we failed to find a negative relationship between egg size and clutch size. Our further analysis revealed that above a clutch size of four, five, or six eggs, there was also no significant correlation between clutch size and egg size, which is similar to the results obtained from a study of another passerine species, *Ficedula albicollis* (Hargitai et al. 2005).

We found that the laying date was an important factor affecting clutch size and that it also significantly affected hatchability and fledging rates, especially during the first brood period when the climate conditions were unstable. A negative relationship between laying date and clutch size is common in altricial species (Crick et al. 1993; Gil-Delgado et al. 2005). In many cavity-nesting species, it has been reported that the number of eggs per clutch often decreases as the breeding season progresses (Goodenough et al. 2009). One potential cause of the decline in clutch size observed in many avian populations is that food availability decreases as the breeding season progresses and that late breeders exhibit a lower fledging mass and lower reproductive success (Siikamäki 1998). Another interpretation is that younger females (Järvinen 1991) or lower-quality individuals (Christians et al. 2001) may lay fewer eggs and lay later in the season. However, the situation was different in our study; the number of eggs per clutch clearly increased when the laying date was late in both the first and second brood periods. We suggest that during the first brood, a breeder laying early faces a capricious climate and that breeding activities are often interrupted or their products are destroyed by unexpected sandstorms, intense cool weather or even snowfall. Environmental conditions, including food abundance, tend to become favourable as the brood progresses, so females that start clutching later will lay more eggs to achieve greater reproductive output, and the finding that the hatchability and fledging rate of the first brood increased as the season advanced supports the hypothesis that a relatively later laying date will result in a higher reproductive success.

Among environmental factors, ambient temperature is well studied and is considered to affect the availability of food resources for female birds and thermoregulatory requirements during egg formation (Haftorn 1986; Magrath 1992; Nager and Noordwijk 1992; Hargitai et al. 2005). We did not detect any effect of ambient temperature on clutch size or egg size, but ambient humidity exhibited a positive relationship with clutch size during the first brood. It is well established that precipitation is the main limiting factor affecting productivity in desert ecosystems. Higher ambient humidity during egg laying may signal to a sparrow that good precipitation conditions will occur in that season.

It is common for female body quality to present a significant positive relationship with egg size (Christians 2002). Our data did reveal a significant correlation of female body size with egg size but not with clutch size. The two sexes share the responsibility of feeding the young in this species. Our results suggested that the female birds laid more eggs in a clutch when they paired with male birds exhibiting high quality. The hatchability of the Saxaul Sparrow depends mainly on egg fertilization, and 80.2% of unhatched eggs were unfertilized (our data). It makes sense that in the Saxaul Sparrow, the male's body size presents a positive relationship with hatchability.

Conclusions

The reproductive input and output of the Saxaul Sparrow, including clutch size, egg size and fledging rate, were significantly higher in the second brood than in the first brood. Our data support the hypotheses that larger females lay larger eggs and that females increase egg investment (more eggs) due to good condition of their mates (male body size) and good environmental conditions (later laying date and higher ambient humidity). The variation in egg size within a clutch suggests that the Saxaul Sparrow adopts a brood reduction strategy. In the allocation of breeding resources between two broods and the effect of laying date and ambient weather-related factors, we detected different adaptive adjustments in egg investment in this passerine species.

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Authors' contributions

Project design was developed by XB and WZ. XB, FL, JL and DM did the field-work, collected the data. XB and WZ conducted the analysis, wrote the paper, prepared figures and tables. All authors shared in editing and revising the manuscript. All authors read and approved the final manuscript.

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Availability of data and materials

The datasets collected in this study are archived at Gansu Key Laboratory of Biomonitoring and Bioremediation for Environmental Pollution, and are available from the corresponding author on reasonable request.

Ethics approval and consent to participate

This research complies with the current laws of China, and was approved under the Ethics Committee of School of Life Sciences, Lanzhou University. Field research was conducted with permission from the Bureau of the Gansu An'xi Extremely-Arid Desert National Nature Reserve.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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