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# The allocation between egg size and clutch size depends on local nest survival rate in a mean of bet-hedging in a shorebird

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## Abstract

**Background:** The allocation of resources between offspring size and number is a central question of life-history theory. Although several studies have tested the existence of this trade-off, few studies have investigated how environmental variation influences the allocation of resources to offspring size and offspring number. Additionally, the relationship between population dynamics and the offspring size and number allocation is far less understood.

**Methods:** We investigate whether resource allocation between egg size and clutch size is influenced by the ambient temperature and whether it may be related to apparent nest survival rate. We measured 1548 eggs from 541 nests of two closely related shorebird species, the Kentish Plover (*Charadrius alexandrinus*) and the White-faced Plover (*C. dealbatus*) in China, in four populations that exhibit contrasting ambient environments. We weighed females, monitored nest survival, and calculated the variance of ambient temperature.

**Results:** Although we found that egg size and clutch size were all different between the four breeding populations, the reproductive investment (i.e. total clutch volume) was similar between populations. We also found that populations with a high survival rate had relatively larger eggs and a smaller clutch than populations with a low nest survival rate. The latter result is in line with a conservative/diversified bet-hedging strategy.

**Conclusions:** Our findings suggest that plovers may increasing fitness by investing fewer, larger or many, small according local nest survival rate to make a similar investment in reproduction, and thereby may have an impact on population demography.

**Keywords:** Ambient temperature, Bet-hedging strategy, Nest survival rate, Resource allocation, Shorebirds

## Background

Understanding the relationship between the size and number of progeny is a central question of life-history theory (Clutton-Brock 1991; Stearns 1992). Indeed, egg and yolk mass can strongly affect the quality of offspring across a variety of taxa (Krist 2011). Larger eggs have a higher hatching rate (Saino et al. 2004) and higher

nestling survival rate than smaller eggs (Williams 1994; Arnold et al. 2006), and nestlings from heavier eggs are also more likely to have higher fitness after fledging (Smith and Bruun 1998; Krist 2011). However, given finite resources for breeding females, life-history theory predicts that larger eggs or larger offspring are expected to be produced at the expense of fewer progeny (Clutton-Brock 1991; Stearns 1992). Several interspecies (Blackburn 1991; Christians 2000; Charnov et al. 2006) and intraspecies (Fleming and Gross 1990; Williams 2001) studies have shown negative relationships between clutch

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size and egg size, which means females will allocate resources between the number and quality of offspring. However, the existence of the number-size trade-off should not only be tested (Lessells et al. 1989; Hein et al. 2018), but should also be explored under the impacts of different environment and/or maternal conditions, and their consequences on resource allocation strategy.

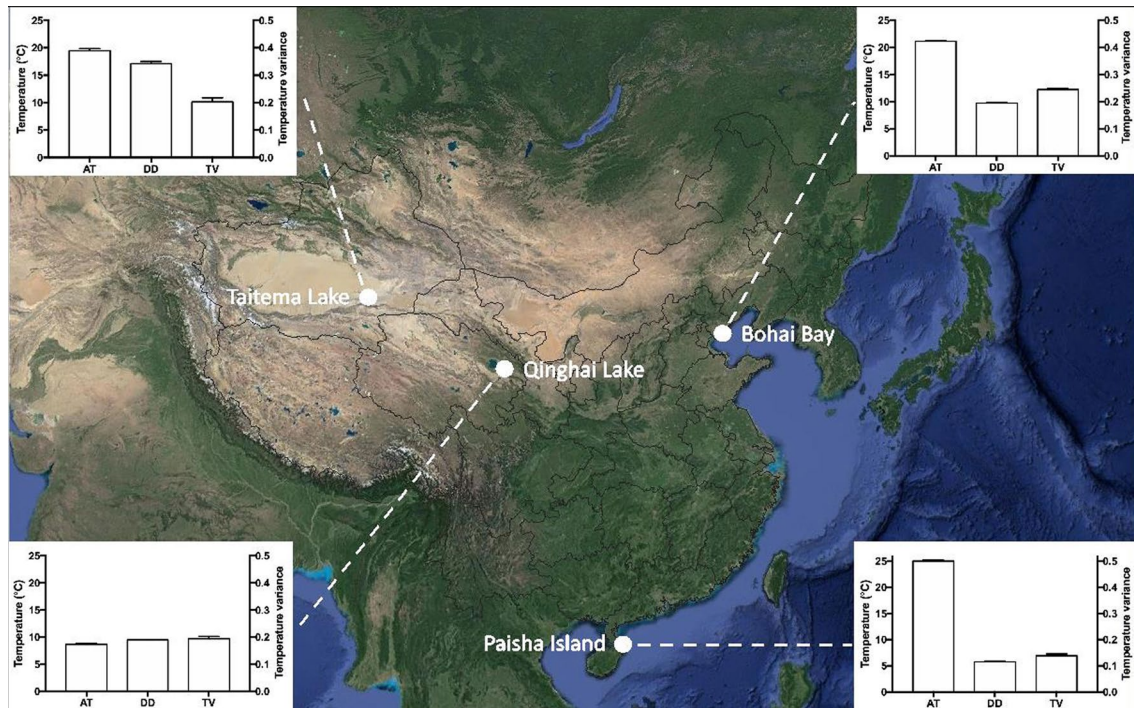
In any given reproduction attempt, life-history theory suggests that parents should make a fundamental decision about how to allocate resources between egg size and clutch size (Stearns 1992). A handful of studies show that this size-number trade-off strategy may vary with environmental conditions and may interact by maternal effects (Crean and Marshall 2009). Individual breeding in the lower latitudes produces fewer larger offspring than high latitudes (Fleming and Gross 1990) or drought year (Abell 1999). However, there has been no attempt to explain the relationship between the offspring size-number trade-off and population dynamics, such as nest survival rate.

The nest survival rate in many species highly depends on the predation risk and anthropogenic disturbance of both adults and the nest. Predator effects on prey demography have traditionally been ascribed to direct killing (Preisser et al. 2005; Que et al. 2015), but predators and human may also have indirect effects on the breeding decisions of prey species (Creel et al. 2007; Travers et al. 2010). Clutch size may decrease under a low nest survival rate as a low investment in reproduction could provide parents with the opportunity of surviving until the next reproductive event or re-laying a new nest (Doligez et al. 2003). Because of the optimal investment theory which suggests that females with more resources should produce offspring of a uniform size but in higher numbers (Smith and Fretwell 1974; Hendry et al. 2001), variation in clutch size is considered as a primary adaptation strategy to local nest survival rate (Slagsvold 1982). However, small clutch size cannot explain the adaptation of individuals who live under high nest predation risk over the long term. Despite the strong support for the existence of a size-number trade-off in both model and empirical data in birds (Williams 2001; Plaistow et al. 2007), studies on nest predation risk and its influence on breeding performance usually ignore the variation in resource allocation trade-off between egg size and clutch size.

Recent research indicates that the resource allocation between egg size and clutch size should vary according to the theory of bet-hedging (Olofsson et al. 2009). The idea behind a bet-hedging strategy is that an individual has to lower its variance in fitness between years to maximize its long-term fitness (Einum et al. 2004; Olofsson et al. 2009). There are two fundamentally different forms of bet-hedging strategy: diversified and

conservative. Diversified bet-hedging involves managing risk by increasing variation and spreading the risk. For example, to adapt to the harsh and unpredictable environment, individuals tend to produce more offspring so that potential adaptive phenotypic variation can increase the opportunity that at least some offspring can survive (Simons 2007). In contrast, a conservative bet-hedging strategy, in a stable environment, manages risk by investing more in fewer offspring (Einum and Fleming 2004; White et al. 2013). For instance, some individuals produce fewer offspring but invest more in each individual to increase the probability that each offspring will be well-equipped to handle a range of conditions. Theoretical studies indicate that individuals would develop a diversified bet-hedging breeding strategy to spread the risk under unpredictable environment (Einum and Fleming 2004; Marshall et al. 2008; Olofsson et al. 2009), but direct evidence for an adaptive origin of this behaviour is lacking (Beaumont et al. 2009).

Here, we test the bet-hedging theory on variation in egg size and number using four *Charadrius* populations breeding in different environments (Paisha Island: a tropical coast population, Bohai Bay: a temperate coast population, Taitema Lake: a desert inland lake population, and Qinghai Lake: a plateau endorheic alkaline lake population, Fig. 1). Compared with altricial species, the relationship between chick fitness and egg size seems to be clearer in precocial species (Williams 1994). Due to the lack of intensive parental care, yolk mass may be the primary parental investment in precocial species (Einum et al. 2004; Jetz et al. 2008). Hence, the resource allocation between egg size and number should be more important and closely associated with reproductive success (Balasubramaniam et al. 2016). The climate in Paisha Island is typical of a tropical monsoon, and it has the highest daily temperature among the four study sites, with an average temperature of 26.98 during breeding season (April–August) (Fig. 1). On the other three sites, Bohai Bay with a temperate climate, which has the highest unpredictability in the daily temperature of the four sites (Fig. 1), Qinghai Lake is an endorheic alkaline lake at 3200 m above sea level, and has the lowest temperature among the four study (Fig. 1) and Taitema Lake is located in the south-east of the Taklimakan Desert, and has the highest daily temperature difference during the breeding season (Fig. 1). Hence, we predicted if plovers allocate their resource between egg size and clutch size depend on ambient temperature, plovers breeding in Paisha Island have developed a conservative bet-hedging strategy which produce larger eggs of relatively small clutch size, and population breeding in the other three sites will produce a larger clutch comprising of relatively small



**Fig. 1** Ambient environment in four populations (GLMM, average temperature (AT):  $\chi^2 = 8309.706$ ,  $P < 0.001$ ; daily temperature difference (DD):  $\chi^2 = 2291.756$ ,  $P < 0.001$ ; temperature variance (TV):  $\chi^2 = 368.019$ ,  $P < 0.001$ ) in Bohai Bay, Qinghai Lake, Taitema Lake and Paisha Island. Left Y axis shows the Celsius of average temperature and daily temperature difference, right Y axis shows the variance of daily temperature within 10 days (higher means variance)

eggs, which presents a diversified bet-hedging strategy in order to spread the risk.

## Methods

### Study species and working sites

We used four populations of two related shorebird species, the Kentish Plover (*Charadrius alexandrinus*) and the White-faced Plover (*C. dealbatus*), to test variation in the resource allocation between egg size and clutch size in different temperatures. The latter species was originally described as a subspecies of *C. alexandrinus*. However, recent studies show that *C. dealbatus* is an incipient species of *C. alexandrinus*, which shows local adaptation to subtropical coastlines (Sadanandan et al. 2019; Wang et al. 2019a, b). Breeding records of *C. dealbatus* have been reported along the coast of China from Fujian Province to Hainan Island, and in south-central Vietnam (IUCN 2017), and the Kentish Plover, *C. alexandrinus* breeds in coastal areas and inland lakes in Europe, Asia and North Africa (Wiersma et al. 2016), and it is one of the common summer breeders along the northern coastline of China and some inland lakes (Que et al. 2019; Wang et al. 2019b). The Kentish Plover complex has long been an ecological model species to understand parental care and breeding system evolution in birds (Vincze et al.

2017; Székely 2019). These two precocial plovers usually produce 2 or 3 eggs, with the egg volume of a clutch being about 49.5% (unpublished data) of the female's body mass. In China, as the White-faced Plover is restricted in its range to subtropical climates (Paisha Island), comparing it with three populations of the closely related Kentish Plovers, in north temperate coastal (Bohai Bay), desert inland lake (Taitema Lake) and alpine inland lake habitats (Qinghai Lake), provides a good study system to understand local adaptation and breeding strategies.

We conducted fieldwork from April to June each year from 2016 to 2019 at Paisha Island (20° 54' N, 110° 29' E, PI), Bohai Bay (39° 14' N, 118° 52' E, BB), and Qinghai Lake (36° 48' N, 100° 45' E, QL), and we only conducted fieldwork in Taitema Lake (39° 26' N 88° 12' E, TL) in 2019.

### Field data collection

#### Egg measured

At each study sites, we measured the length and breadth ( $\pm 0.01$  mm) of each egg after we found a nest. We calculated egg size using the formulas by  $V = 0.51 \times \text{length} \times \text{breadth}^2$  (Hoyt 1979), and we used the average egg size of each nest in analyses. Then we captured breeding female with a walk-in funnel trap

placed over the nests that had been incubated for at least seven days, and we measured female body mass. We estimated the egg-laying date by floating the eggs in lukewarm water (Székely et al. 2008). We checked nests at 4–5 day intervals to estimate nest survival, and near the estimated hatching date, which was approximately after the 22nd day of incubation, we checked nests daily.

In total, we measured 1548 eggs from 541 nests: 301 nests from Bohai Bay, 83 nests from Qinghai Lake, and 139 nests from Paisha Island during 2016–2019, and 18 nests from Taitema Lake in 2019.

#### **Nest survival rate**

We measured the nest survival rate in two ways: first, we calculated the number of nests that had been destroyed or had been hatched and still hatching one day before each nest was laid, then we used the percentage of nest which not been destroyed to represent the apparent nest survival rate of each nest, and second, we used nest monitoring data for each year to estimate the nest survival rate of each population per year. The nest usually lost complete of their eggs, and we classified a ‘failure’ nest if it lost the entire full clutch. In total we monitored the fate of 1204 nests of four populations.

#### **Ambient temperature**

We collected meteorological data, including daily mean temperature, daily highest and lowest temperature, from the National Meteorological Information Center (<https://www.nmic.gov.cn/en/>) of the China Meteorological Administration. As most of the effects of temperature on egg size occur during the period of rapid yolk development (RYD) (Saino et al. 2004; Ardia et al. 2006), and it usually took ten days after Kentish Plover courtship for females to lay their first eggs (Székely et al. 1999), we calculated the average value, average daily difference and variance of temperature in the ten days before each nest’s laying date. We used the average difference between the highest and lowest temperatures of each day in the ten days as the daily difference in temperature. We calculated the variance of temperature by fitting a linear model between the average temperature of each day and the number of days before the laying date, and we used the standard error of the regression as an index of the temperature variance of each plover’s experience (Simerly et al. 2000).

#### **Statistical analyses**

To control for seasonal changes, we used the Julian day, which we calculated as the number of days between the 1st March, as the egg-laying date. We established the laying date data by monitoring hatching or making an estimation using egg flotation within 11 days of hatching,

which is supposed to be accurate (Székely et al. 2008). The different of egg size among the four populations were tested by fitting GLMMs, in which laying date was entered as a fixed index and the parameter years was entered as a random effect. One of the study species, the White-faced Plover (*C. dealbatus*) was formerly treated as subspecies of Kentish Plover (Swinhoe 1870; Hartert and Jackson 1915). Some earlier studies suggested it might be a full species based on its unique morphology and ecology (Kennerley et al. 2008; Rheindt et al. 2011). And this hypothesis has been lately supported by genetic works (Sadanandan et al. 2019; Wang et al. 2019b). Even though, *C. dealbatus* shows a low level of genome-wide divergence with *C. alexandrinus*, indicating the two taxa being a pair of incipient species (Wang et al. 2019a). In order allow comparisons of life-history traits and breeding parameters, we firstly obtained genetic relatedness of the four populations of the two species by calculating genome-wide pairwise population differentiation ( $F_{ST}$ ) using the dataset and the method in Wang et al. (2019a). Then we incorporated pairwise  $F_{ST}$  values as a covariance matrix (Additional file 1: Table S1) representing the amount of shared evolutionary history between four populations and performed phylogenetic generalized linear mixed models (PGLMM). We first fit a PGLMM to estimate the influence of apparent nest survival rate and ambient environment on eggs size, as the mean of eggs size within a clutch was used as dependent variable, and nest survival rate, average temperature, daily temperature difference, temperature variance, clutch size, laying date and female body mass was entered as fixed indexes, and the parameter years was entered as a random effect.

We then estimated the influence of apparent nest survival rate, average temperature, daily temperature difference, temperature variance on clutch size. As the variable of plover clutch size is count data with a range from one to four and often under-dispersed, we fitted a generalized linear mixed-effect model (GLMM) with Conway-Maxwell-Poisson distribution (Sellers et al. 2010) to analyse the influence of apparent nest survival rate, laying date, average temperature, daily temperature difference, temperature variance and female body mass on clutch size. To control the interpopulation phylogenetic relatedness, we include populations as a fixed index, and the parameter years was entered as a random effect.

We test the difference of total egg size (summation of total eggs size within a clutch) between four populations by fitting a GLMM in which laying date and female body mass enter as a fixed index, and the parameter years was entered as a random effect.

Female can allocate finite resources between egg size and clutch size (Smith and Fretwell 1974). We estimate the resource allocation variance between egg size and

clutch size by calculating the relative egg size for clutch size by regressing the mean egg size and clutch size taking the residuals across all nests (Martin 2008). We applied a PGLMM to analysis effects of apparent nest survival rate, average temperature, daily temperature difference, temperature variance, laying date and female body mass on this size-number allocation strategy, and the parameter years was entered as a random effect.

We fitted the PGLMM analyses using “phyr” package (Li et al. 2020) and we performed GLMM analyses using the “glmmTMB” package (Magnusson et al. 2017). We conducted all statistical analyses using R version 3.4.1 (R Development Core Team; <https://cran.r-project.org/>).

## Results

### Breeding performance and ambient environment between populations

Egg size and clutch size was significantly different among the four populations (egg size: GLMM,  $\chi^2=60.739$ ,  $P<0.001$ ,  $n=541$ ; clutch size: GLMM,  $\chi^2=29.019$ ,  $P<0.001$ ,  $n=541$ ). In Bohai Bay, females produce the smallest egg and the largest clutch size comparing with the other three populations (Fig. 2a). Additionally, female breeding in Qinghai Lake and Taitema Lake produced relative larger egg size and smaller clutch size among the four populations (Fig. 2a).

The egg size was not statistically correlated with any environmental factors, such as ambient temperature, daily temperature difference and temperature variance, however, egg size increased with female body mass (Table 1). Additionally, clutch size decreased with laying date processing and increased with average

**Table 1 Relationships between egg size and clutch size, female body mass, laying date, apparent nest survival rate and temperature variables in four populations of two congeneric plovers (PGLMM)**

Parameter	Estimate	SE	Z	P
Egg size (n = 541)				
Intercept	6.983	0.598	11.669	<0.001***
Clutch size	-0.037	0.062	-0.587	0.557
Female body mass	0.047	0.008	6.078	<0.001***
Laying date	0.003	0.003	1.294	0.196
Ambient temperature	-0.003	0.014	-0.227	0.820
Daily temperature difference	-0.022	0.020	-1.079	0.280
Temperature variance	-0.420	0.335	-1.255	0.210
Apparent nest survival rate	0.371	0.176	2.107	0.035*

The parameter Years was entered as a random factor

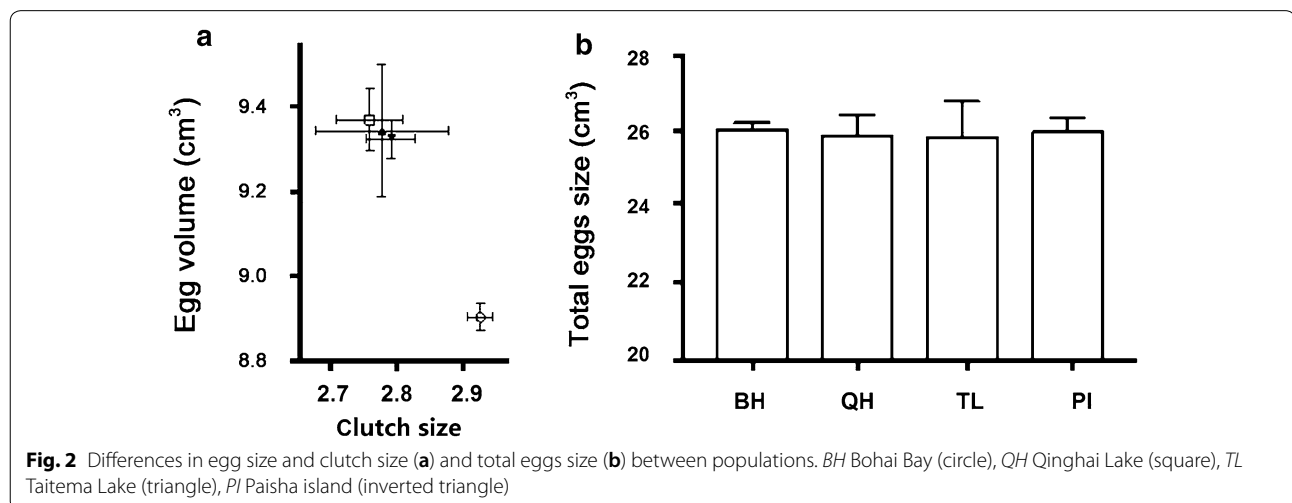
Significant relationships are indicated as \*  $P<0.05$ , \*\*  $P<0.01$ , and \*\*\*  $P<0.001$

temperature increasing (Table 2). Additionally, the total egg size within a clutch has no difference between four populations (GLMM:  $\chi^2=1.870$ ,  $P=0.600$ ,  $n=541$ , Fig. 2b).

### Resource allocation between egg size and clutch size relates to nest survival

Nest survival rates were different between populations: plovers breeding in Taitema Lake had the highest nest survival rate (0.702,  $n=47$  nests), followed by the population in Qinghai Lake ( $0.458 \pm 0.161$ ,  $n=106$  nests), Bohai Bay ( $0.287 \pm 0.082$ ,  $n=741$  nests) and Paisha Island ( $0.359 \pm 0.058$ ,  $n=310$  nests).

We found egg size increased with elevated level of local nest survival rate (Table 1; Fig. 3a), and clutch



**Table 2 Relationships between clutch sizes and female body mass, laying date, apparent nest survival rate and temperature variables in four populations of two congeneric plovers (GLMM): white-faced plover at Paisha Island (PI), and Kentish plover at Bohai Bay (BH), Qinghai Lake (QH), and Taitema Lake (TL)**

Parameter	Estimate	SE	$\chi^2$	P
Clutch size (n = 541)				
Intercept	1.197	0.114		
Populations (BH as baseline)			29.019	<0.001***
QH	0.101	2.888		
TL	-0.008	0.053		
PI	-0.175	0.038		
Female body mass	-0.000	0.002	0.002	0.965
Laying date	-0.003	0.001	24.375	<0.001***
Ambient temperature	0.011	0.004	8.544	0.003**
Daily temperature difference	-0.004	0.006	0.431	0.512
Temperature variance	0.060	0.077	0.612	0.434
Apparent nest survival rate	-0.077	0.038	4.078	0.043*

The parameter Years was entered as a random factor

Significant relationships are indicated as \*  $P < 0.05$ , \*\*  $P < 0.01$ , and \*\*\*  $P < 0.001$

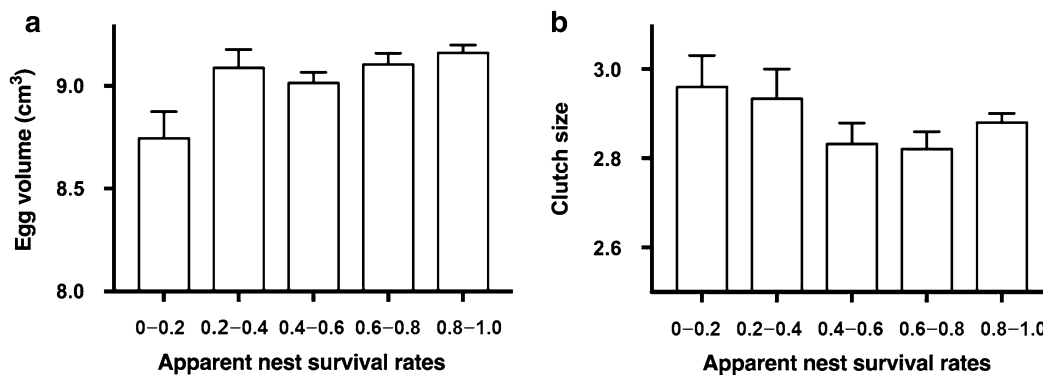
size also decreased with elevated level of nest survival rate (Table 2; Fig. 3b). Additionally, the egg size-clutch size allocation strategy was positively correlated with nest survival rate, meaning that plovers produce many small eggs within a clutch at a low nest survival rate and produce fewer larger eggs when local nest survival rate is high (Table 3; Fig. 4).

However, neither the ambient environment parameters (i.e. average temperature, daily temperature difference and temperature variance) nor the laying date have influence on the egg size-clutch size allocation strategy (Table 3).

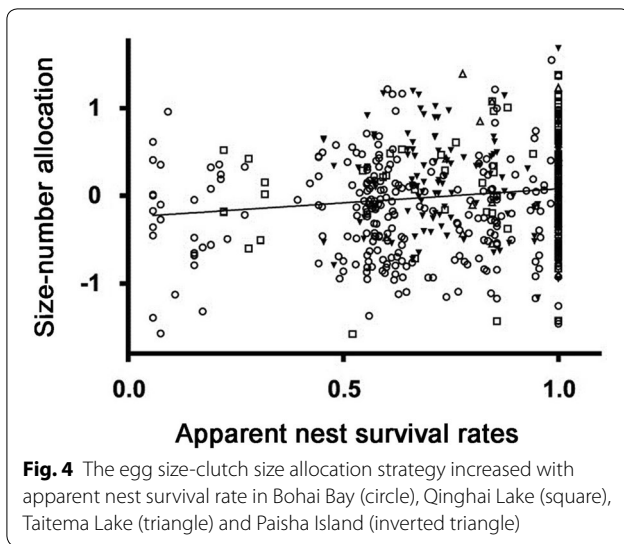
### Discussion

In this study, we found that four plover populations adopted different patterns of resource allocation between egg size and clutch size. However, inconsistent with our prediction, the egg size and clutch size did not show tight correlation with ambient temperature. In the Paisha Island with predictable environment, the population did not show a conservative bet-hedging strategy on egg size and clutch size. We found the plover population at Bohai Bay showed a diversified bet-hedging strategy with the smallest egg size but the largest clutch size of the study populations. In contrast, the Qinghai Lake and Taitema Lake populations produced larger eggs but smaller clutches, which is consistent with a conservative bet-hedging strategy. Additionally, we found that the different allocations between egg size and clutch size seemed to be affected by apparent nest survival in that: plovers will produce fewer but large eggs under a high local nest survival rate, and produce many but small eggs under a low local nest survival rate. In addition, clutch size decreased with the advancement of laying date and decrease in ambient average temperature.

The finding that clutch size declined with progressed breeding season is consistent with several other studies that have also found a seasonal decline in clutch size (Rowe et al. 1994; Decker et al. 2012). It has been suggested that individuals that breed early in the season may have greater experience than late breeders (Nol et al. 1987), and eggs that are laid earlier give offspring more time before winter and migration (Winkler and Allen 1996). Hence, plovers that breed early in the season may invest more in current reproduction. Additionally, we found a positive correlation between clutch size and ambient temperature. Possible reasons for this are that less energy is required for thermoregulation in warmer temperatures, so more energy can be allocated toward reproduction (Meijer et al. 1999), and warmer



**Fig. 3** The egg size (a) and clutch size (b) correlated with apparent nest survival rate in four populations



**Fig. 4** The egg size-clutch size allocation strategy increased with apparent nest survival rate in Bohai Bay (circle), Qinghai Lake (square), Taitema Lake (triangle) and Paisha Island (inverted triangle)

**Table 3 Relationships between the egg size-clutch size allocation strategy (higher value means larger egg size with small clutch size) and laying date, apparent nest survival rate and temperature variables in four populations of two congeneric plovers (PGLMM)**

Parameter	Estimate	SE	Z	P
Egg size-clutch size allocation strategy (n = 541)				
Intercept	-2.177	0.562	-3.876	<0.001***
Female body mass	0.047	0.008	6.037	<0.001***
Laying date	0.003	0.003	1.063	0.288
Ambient temperature	-0.002	0.014	-0.117	0.907
Daily temperature difference	-0.022	0.020	-1.075	0.282
Temperature variance	0.403	0.335	-1.201	0.230
Apparent nest survival rate	0.348	0.176	1.983	0.047*

The parameter Years was entered as a random factor

Significant relationships are indicated as \*  $P < 0.05$ , \*\*  $P < 0.01$ , and \*\*\*  $P < 0.001$

temperatures increase avian food availability (Winkler et al. 2013).

The allocation of resources between egg size and clutch size was different between the four populations: the Bohai Bay population produced many small eggs, and plovers breeding in Qinghai Lake and Taitema Lake tended to produce fewer larger eggs, and Paisha Island was in the middle of these two diversified and conservative bet-hedging strategies.

The bet-hedging strategies, which suggest to manage risk by spread or pull together, are expected to evolve under conditions of unpredictable environmental variance (Einum and Fleming 2004; Simons 2011). Although there was substantial variation in the ambient

temperature between the four populations, the allocation between egg size and number was not influenced by ambient temperature, daily temperature difference or temperature consistency. Bohai Bay has the highest variance of temperature and Taitema Lake has the highest daily temperature different which suggest to be environmental unpredictable, and plover breeding here should spread the risk according a diversified bet-hedging strategy. In our study, Bohai Bay population produced the largest clutch size and smallest egg size which show a diversified bet-hedging strategy. However, inconsistent with the prediction, plover breeding in Taitema Lake show a relative conservative bet-hedging strategy which produce larger eggs but smaller clutches. Additionally, the predictable tropical environment in Paisha Island is a favorable condition for reproduction, and bet-hedging strategy according to ambient environment suggests that parents breeding here are risk averse and should produce egg larger than those unstable environment (Einum and Fleming 2004). However, Paisha Island population is between those two bet-hedging strategies, which show the second smaller egg size and second larger clutch size among these four populations.

In our study, resource allocation between egg size and clutch size involved a bet-hedging strategy that was dependent on the apparent nest survival rate. Bohai Bay has the lowest nest survival rate reported worldwide for this species (Que et al. 2015), which shows a diversified bet-hedging strategy. On the other hand, populations breeding along Qinghai Lake and Taitema Lake have relatively higher nest survival rates showing a conservative bet-hedging strategy. Despite the extremely low average temperature in Qinghai Lake and highest daily temperature different in Taitema Lake, these two populations have a relatively high nest survival rate. This may be because of limited human habitation in these two populations: Qinghai Lake is in the Qinghai-Tibetan plateau, which is the world's highest plateau, and Taitema Lake is no man's land. For Kentish Plover, since anthropogenic disturbance seem to be critical for nest survival (Que et al. 2015), the absence of anthropogenic disturbance may lead to a higher nest survival rate in Qinghai Lake and Taitema Lake.

Reproductive failure caused by nest predation and anthropogenic disturbance represents an important source of natural selection (Chalfoun et al. 2010; Smith et al. 2012; Que et al. 2015; Halimubieke et al. 2020), and it significantly influences reproductive strategies (Lack 1947; Mönkkönen et al. 2009). The egg mortality rate may decrease the optimal clutch size for many reasons. Skutch (1949) suggested that there is a brood-size dependent predation rate, and a smaller-sized nest is

more difficult for a predator to discover (Perrins 1977; Snow 1978). Additionally, a smaller clutch size is likely to be a strategy to allow rapid re-mating and re-laying if a nest was destroyed (Eggers et al. 2005; Dillon et al. 2017; Zanette et al. 2011). Nevertheless, study reported increasing reproductive investment with increasing nest predation rate and that parents should increase their clutch size to compensate for the decreased number of successful broods because of predation (Griebeler et al. 2010). Despite the inconsistency, these studies all focus on the relationship between clutch size and nest survival rate but not the allocation between egg size and clutch size. In our study, plovers increased investment in egg size at the expense of lower numbers of eggs when the nest survival rate was high, which suggests plover could use different bet-hedging strategies between egg size and clutch size to achieve similar reproductive success.

Under higher nest survival rates, the plovers produced a small clutch of larger eggs. Under a guaranteed hatching environment, this strategy might have benefits for the long-term survival of the population. Individuals hatching from larger eggs are more likely to have greater reproductive success during their lifetime (Smith and Bruun 1998; Krist 2011) than lower quality offspring from smaller eggs (Song et al. 2018) and therefore represent higher reproductive fitness for their parents. Additionally, we found that there was no difference of total eggs size, which represent an equal investment of female at one breeding attempt among populations. Despite the significant variation in egg size and clutch size between the four populations, plovers may use different resource allocation strategies between each egg size and clutch size to make a similar investment in one breeding attempt.

## Conclusions

We found that plovers allocate resources between egg size and clutch size following the diversified and conservative bet-hedging strategies. Plovers breeding in a temperate environment in Bohai Bay produced a larger clutch of relatively small eggs, which presents a diversified bet-hedging strategy. Additionally, the ambient temperature did not influence resource allocation between egg size and clutch size, apparent nest survival rate did. We suggest that nest survival rate, which determines the fate of an egg, could substantial influence the potential benefit of investing in a given egg than other environmental factors that indirectly influence the egg's fitness. This might also suggest variation in ambient temperature did not influence investment of parental resource at an early stage of breeding attempts, i.e. egg-laying, yet indeed affects investment of time allocation, such parental care behaviour at incubation stage under different environments (Vincze et al. 2017). Overall, our findings highlight nest survival is a critical factor that have

shaped life-history characters in ground-nesting birds, and further promote understanding of the drivers of geographical variations of life-history traits.

## Supplementary information

**Supplementary information** accompanies this paper at <https://doi.org/10.1186/s40657-020-00225-6>.

**Additional file 1: Table S1.** The genome-wide pairwise population differentiation ( $F_{ST}$ ) shows low divergence among four plover populations.

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## Authors' contributions

ZS, LX, and YL conceived the research ideas, conducted the analyses, and wrote the manuscript; PQ, NH, and QH contributed to data collection and result interpretation; TS participated in project design, advised on data analyses and manuscript writing, and reviewed drafts of the paper; YL and ZZ coordinated the study system of the plovers in China. All authors read and approved the final manuscript.

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## Availability of data and materials

The datasets generated and analysed during the current study are available from the corresponding author upon reasonable request.

## Ethical approval and consent to participate

This study was conducted with standard protocol (Székely et al. 2008) which in accordance with the ethical standards of the Sun Yat-sen university and university of Bath. Birds were ringed and handled by trained people aiming to cause as little disturbance to birds as possible.

## Consent for publication

Not applicable.

## Competing interests

The authors declare that they have no competing interests.

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