

Colder ambient temperatures constrain female mate preference for ornamental traits

Zitan Song¹, Pinjia Que², William Jones³, Chenjing Huang⁴, NAERHULAN HALIMUBIEKE⁵, Peng Ding⁶, Zhengwang Zhang⁴, and Yang Liu¹

¹Sun Yat-Sen University

²Chengdu Research Base of Giant Panda Breeding, Sichuan Key Laboratory of Conservation Biology for Endangered Wildlife

³University of Debrecen

⁴Beijing Normal University

⁵University of Bath

⁶Xinjiang Agricultural University

September 6, 2023

Abstract

Male ornamentation is usually costly and may show trades-offs with other life-history traits such as paternal care, which can subsequently affect female preference. Studies on female mate choice have mostly examined how mate-choice cues differ in their expression or ability to be detected in different environmental contexts. However, less focus has been placed on examining how external forces affect female preferences. The purpose of this study was to explore how parental investment strategy and mate choice were mediated by ambient temperature. Specifically, we examined how male ornamentation characteristics and subsequent female incubation investment were impacted by ambient temperature in four plover populations that were breeding across an environmental gradient. We discovered that larger males had more ornamented plumage in warmer conditions, and they were favored by larger females who invested an elevated time into incubation. In contrast, in cooler conditions, males' body size and the color of their ornaments were inversely associated, and females showed weak preference for males with more colorful ornaments. These results imply that female preference for male ornament can change in response to ambient temperature and demonstrate that female preference for male ornamentation may be limited in harsher conditions with higher parental care expenses.

Colder ambient temperatures constrain female mate preference for ornamental traits.

Zitan Song^{1,2}, Pinjia Que^{3,4}, William Jones⁵, Chenjing Huang³, Naerhulan Halimubieke⁶, Peng Ding⁷, Zhengwang Zhang³, Yang Liu^{1*}

¹ State Key Laboratory of Biocontrol, School of Ecology, Sun Yat-sen University, Shenzhen, Guangdong 518107, China

² Comparative Socioecology group, Max Planck Institute of Animal Behavior, Konstanz, 78467, Germany

³ Ministry of Education Key Laboratory for Biodiversity Science and Ecological Engineering, College of Life Sciences, Beijing Normal University, Beijing 100875, China

⁴ Chengdu Research Base of Giant Panda Breeding, Chengdu, China

⁵ Department of Evolutionary Zoology and Human Biology, University of Debrecen, H-4032 Debrecen, Hungary

⁶ Milner Center for Evolution, Department of Biology and Biochemistry, University of Bath, Bath BA1 7AY, UK

⁷ College of Animal Science, Xinjiang Agricultural University, Urumqi, 830052, China

* Corresponding author: Dr. Yang Liu

Address.: State Key Laboratory of Biocontrol, School of Ecology, Sun Yat-sen University, Shenzhen, Guangdong 518107, China

Tel: +86 84114063

Fax: +86 84111587

E-mail: liuy353@mail.sysu.edu.cn

Abstract

Male ornamentation is usually costly and may show trades-offs with other life-history traits such as paternal care, which can subsequently affect female preference. Studies on female mate choice have mostly examined how mate-choice cues differ in their expression or ability to be detected in different environmental contexts. However, less focus has been placed on examining how external forces affect female preferences. The purpose of this study was to explore how parental investment strategy and mate choice were mediated by ambient temperature. Specifically, we examined how male ornamentation characteristics and subsequent female incubation investment were impacted by ambient temperature in four plover populations that were breeding across an environmental gradient. We discovered that larger males had more ornamented plumage in warmer conditions, and they were favored by larger females who invested an elevated time into incubation. In contrast, in cooler conditions, males' body size and the color of their ornaments were inversely associated, and females showed weak preference for males with more colorful ornaments. These results imply that female preference for male ornament can change in response to ambient temperature and demonstrate that female preference for male ornamentation may be limited in harsher conditions with higher parental care expenses.

Keywords: parental care, mate choice preference, ambient temperature, incubation, plover

1 INTRODUCTION

The impact of ambient temperature on animal physiology, behavior, and life history traits, is well-established. However, the underlying mechanisms of how ambient temperature influences sexual selection, which is a key evolutionary force shaping reproductive traits and behaviors, remain unclear. The cost-benefit balance of sexual selection could be influenced by ambient temperature, which can impact the growth and maintenance of sexual weapons or ornaments, alter intrasexual competition and intersexual selection, influence the variance in reproductive success, and even impact mating systems. Furthermore, the cost-benefit balance of bearing ornamentation may be more significant than that of possessing weapons, as ornamentations often have limited direct benefits. Thus, understanding how ambient temperature influences preference for secondary sexually selected traits could have significant implications for understanding of animal behavior evolution and species adaptation to changing environmental conditions.

Due to the restricted resource expenditure and predation risks, male ornament characteristics are known to be costly to develop and maintain. Reduced sexual dimorphism has been linked to lower ambient temperatures, which may restrict the aesthetic expression of male ornamentation. Additionally, it has been demonstrated that the trade-off between immunological function and plumage expression for carotenoid-based decorations acts as a sexual cue for the quality of a particular bird. Additionally, according to experimental data, male zebra finches (*Taeniopygia guttata*) tend to circulate more carotenoids in cooler climates rather than expressing them as carotenoid-based decorations. This points to a potential problem with the use of carotenoid-based decorations as accurate indicators of an individual's character in colder climates.

Ambient temperature can impact animal courtship behavior in addition to influencing the display of sexual characteristics. Several studies have shown that male courting efforts are positively correlated with temperature. This suggests that males with low resource investment engage in intensive courting behavior. This might be because they have more energy to devote to mating displays or are more driven to locate partners. Additionally, ectothermic and endothermic animals' metabolism and activity levels are greatly influenced by ambient temperature. These factors can also affect how much time these animals devote to mating and intrasexual competition.

Furthermore, ambient temperature can affect a female's post-copulatory mate preference and even a species' mating system. Parental care efforts needed significant inputs by parents as the environmental conditions became harsher, requiring longer incubation durations and intensive nest provisioning. Females in colder environments may be unable to compensate for these shortages, and instead pursue less-ornamented males with higher levels of direct parental investment because males with extravagant ornaments often provide limited parental care. Additionally, the increased necessity for parental care by both parents in colder environments may promote stable pair-bond and thus the evolution of biparental care. This transition to monogamy can be viewed as an adaptive strategy to better manage balanced parental investment and assure the survival of offspring in challenging environmental circumstances.

Shorebirds provide an ideal system within which to test the impacts of ambient temperature on mate choice. This is because shorebirds can be found breeding in a wide variety of wetland habitats across large temperature gradients, even on the intraspecific level. Specifically, we used four *Charadrius* plover populations from the Kentish plover (*C. alexandrinus*) species complex which breed in locations with significant changes in ambient temperature throughout the mating season (Figure 1 and Song et al. 2020). Our study included three populations of Kentish plovers (*C. alexandrinus* sensu stricto) and one population of white-faced plovers (*C. dealbatus*), a former subspecies of *Charadrius alexandrinus* that has recently been proven to be a full species that diverged from the former less than 600 000 years ago.

The goal of this study was to look at the effect of ambient temperature on male ornamentation, female mate choice, and parental investment across diverse populations. We specifically investigated if male ornamentation expression and its relationship to body size change with ambient temperature. Furthermore, we investigated how female mate choice at different temperatures responds to male ornamentation by assessing the connection between morphometric and ornament characteristics of males and females in mating pairings. Finally, we investigated whether female incubation investment is related to male ornamentation and if it varies with temperature. Our prediction is that under colder conditions, the trade-off between color expression and immune function on melanin and/or carotenoid may lead to a lower correlation between ornament and body size. Females may also prefer larger males with direct parental care over ornamented males with lower parental care, due to the increased need for parental investment in colder environments.

2 MATERIALS AND METHODS

2.1 Study species and working sites

The Kentish plover breeds in the northeast coast and inland saline lakes in Eurasia, while the white-faced plover is confined to the southeast coast and islands in China. We selected a white-faced plover population on Paisha Island (20° 54' N, 110° 29' E, PI) in a subtropical climate. We also used three Kentish plover populations: one in a north temperate coastal area at Bohai Bay (39° 14' N, 118° 52' E, BB), another in a desert inland lake at Taitema Lake (39° 26' N, 88° 12' E, TL), and the last one in an alpine inland lake habitat at Qinghai Lake (36° 48' N, 100° 45' E, QL). Ambient temperature was highest in the PI population, followed by BB and TL, and was lowest in the QL population (Figure 1). The distribution of these populations provides a good study system for understanding how ambient environment variance modulates local sexual selection. Both species exhibit biparental care, and extra-pair paternity rates are typically low (0-4.1%), suggesting potentially post-copulatory mate choice based on male incubation behavior. Fieldwork was conducted during the breeding seasons in 2018 and 2019, with work on Paisha Island and Bohai Bay conducted from May to June, work at Qinghai Lake from May to July, and work at Taitema Lake conducted

from May to July in 2019.

2.2 Field methods

During the incubation period, we captured and measured the body size (body mass and tarsus length) of breeding males and females using standard protocols . To observe the parents' incubation behavior, we set up a nest camera (Bushnell 119776C) anchored to the ground and positioned 1.5 m away from the nest. The camera recorded for 72 hours at one-minute intervals. In total, we captured and measured the body size and ornament traits of 131 male and 145 female adults. We were able to obtain data from 111 nests in which both parents were captured.

2.3 Ornament measurements

Both Kentish plovers and white-faced plovers exhibit sexually dimorphic plumage, with males displaying a black horizontal head stripe, two dark breast bands on each side of their breast, black eye stripes, and a rufous crown (Figure S1). Females, on the other hand, are paler and do not have dark markings (Figure S1).

To examine these plumage ornaments, we photographed each adult in three postures (dorsal and both profiles) in direct sunshine with a digital camera (SONY ILCE-6400). We photographed a scale, a white balance card (Kodak Gray Card 18% R-27), and a color checker (X-Rite ColorChecker Passport Photo). We concentrated on three different plumage ornaments: the male forehead stripe, the mask and crown, and the breast band. We used Adobe Photoshop CC (v.17.0.0) to measure the color and size of each ornament and adjusted each image for ambient light using the white-balancing tool and a white balance card as a reference. As detailed in the supplementary material, we used the relative difference of R in the RGB (red, green, blue) values to estimate the carotenoid-based red coloration (positively correlated), and the lightness ('L') axis in the CIE (Commission Internationale de l'Eclairage) LAB color space to estimate the melanin-based plumage ornaments (negatively correlated). We discovered that this approach of quantifying plover ornaments was highly repeatable (for details, see Table S1 in the supplemental material, assessed using the rptR package (Stoffel et al. 2017)).

2.4 Ambient environment data collection

For our investigation, we collected two types of ambient temperature data. We assessed the average temperature of the 10 days preceding each nest's initial egg laying date to explore the ambient temperature that may impact female partner choice during the courtship period. This is due to the 10-day gap that plovers normally have between the start of courting and the completion of the first egg . The China Meteorological Administration's National Meteorological Information Centre (<http://data.cma.cn/en>) provided the daily ambient temperature data.

To explore the ambient temperature that may influence parental incubation behaviors, we collected temperature data using nest cameras at one-minute intervals for each nest. The average temperature was calculated every three hours, and the statistical analyses section provides further information on why we chose this interval.

2.5 Statistical analyses

To investigate variations in the color and size of plover ornamental traits, we conducted a principal component analysis (PCA) to reduce the number of variables. For male plovers, the color and size of the breast band, eye stripe, and crown were subjected to a PCA. We also included the color of the head stripe since males have a stripe on their forehead (see Figure S1 and Tables S2). A negative value for "lightness" and a positive value for "redness" indicated greater color saturation, resulting in a more colorful appearance (Tables S2). MPC1 captured the variation in color and was characterized by negative values for the lightness of the breast band, eye stripe, and head stripe, combined with a positive value for the redness of the crown. MPC2 captured the variation in size and was characterized by positive values for the size of the breast band, eye stripe, and head stripe. Together, MPC1 and MPC2 explained 71.0% of the total variance in male ornament traits (Table S2). For female plovers, we conducted a PCA on the color and size of the breast band, eye stripe, and crown

(Figure S1). FPC1 captured the variation in color and was characterized by positive values for the redness of the breast band, eye stripe, and head stripe. FPC2 captured the variation in area and was characterized by positive values for the size of the breast band, eye stripe, and head stripe. Together, FPC1 and FPC2 explained 65.7% of the total variance in female ornament traits (Table S3). Finally, we tested the difference in ornamental traits between male and female plovers in four populations using one-way ANOVA.

To allow comparisons between Kentish and white-faced plovers, we first obtained the genetic relatedness among the four populations by calculating a genome-wide pairwise population differentiation (F_{st}) using the dataset and methods of . Then, we incorporated the pairwise F_{st} values in a covariance matrix representing the amount of shared evolutionary history between the four populations and performed phylogenetic generalized linear mixed models (PGLMM).

To account for sampling uncertainty in our estimates, we performed a bootstrapping procedure for all analyses. This involved randomly resampling the data with replacements for each bootstrap iteration (i), running 1,000 PGLMM analyses, and reporting the 95% confidence interval of the estimate. The PGLMM results, including the estimate, z value, and p value, as well as the 95% CI of the estimate based on the bootstrapping procedure, are presented throughout the results section.

2.6 Modelling the relationships between male body size, ornamental traits, and temperature

To examine the impact of temperature on the correlation between male body size and ornamental traits, we employed phylogenetic generalized linear mixed models (PGLMMs). The models had male body mass as the dependent variable, and the independent variables were the ornament PCA values (coloration: MPC1; size: MPC2) and ambient temperature. By incorporating the interaction between males PCA values and ambient temperature, we aimed to investigate the potential moderating role of temperature in the relationship between male body size and ornamental traits. Moreover, we included both the breeding season and incubation duration as fixed effects in the models to control for possible variation in male body condition. Additionally, population and year were considered as random effects to account for any unobserved heterogeneity across different populations and years.

2.7 Modelling the relationships between male ornamental traits, female body size, and temperature

As female body size is correlated with female fecundity, larger females of both Kentish plover and white-faced plover tended to have larger egg sizes , which suggested a positive effect on offspring survival rate and fitness . In accordance with sexual selection theory, which suggests that more fecund females should mate with males with more elaborate ornaments, we investigated the effects of male ornament PC1 and PC2 values, male body size, ambient temperature, and their interactions on female body size using phylogenetic generalized linear mixed models (PGLMMs). In addition, we included laying date and incubation period as fixed effects, while population and year were included as random effects.

2.8 Modelling the effect of male ornamental traits and temperature on parental investment during incubation

We classified incubation behavior as either female attendance, male attendance, or absence of both parents at the nest. Due to instances of nest predation, abandonment, or camera malfunctions, we only analyzed data from 71 nests with continuous recordings exceeding 24 hours. We first tested the effect of ambient temperature on total incubation time for each nest using a PGLMM. To control for the effect of ambient temperature on total incubation time (see results), we calculated the average daily incubation attendance of both parents and used the ratio of an individual parent's attendance to the total incubation time as a measure of their investment. To investigate the effect of male and female ornamental traits, body size, and temperature on parental investment, we employed PGLMMs. Fixed factors included temperature and the interaction between temperature and individual traits (if significant).

2.9 Path analysis of the effects of male ornamental traits and female body size on parental

investment during incubation

To investigate whether an individual’s investment in incubation depended on its or its mate’s body size or ornamentation, we conducted a series of path analyses. We recorded incubation behavior at 3-hour intervals, as parents typically alternate incubation every 46.725 ± 3.383 minute (mean \pm SE). Using data from 80 nests (also including the nest with less than 24 hours of records), we employed GLMMs in the ‘nlme’ package, with nest ID and population ID as random effects for each model structure. We tested whether female tarsus length, male body mass, female ornament color (FPC1), and male ornament color (MPC1) had directional effects on male and female incubation investment within a 3-hour period. As female plovers typically dominate diurnal incubation and males usually incubate at night, we transformed the time for each scan from a 24-hour clock to a continuous time variable that spans across midnight using a cosine transformation.

We constructed a series of alternative path models to examine the effects of ambient temperature, parents’ body size, and ornament traits on their incubation behavior. Since the total amount of time required for incubation varies with time of day and ambient temperature, we included the time that the nest was empty also as a dependent variable in our path models. To account for correlations among parents’ body size and ornamentation (FPC1 and MPC1), we used the *piecewiseSEM* package to construct models in which these four variables were intercorrelated. We also included correlations between female and male incubation time.

To investigate the factors affecting male and female incubation time, we initially developed a full path model that included ambient temperature, time of day, female ornament (FPC1), male ornament (MPC1), female tarsus length (according to Table 3), and male body mass as predictor variables. Subsequently, we built 85 candidate path models by removing one to four predictor variables among parents’ body size and ornamentation from the original model while keeping ambient temperature and time of day as fixed predictors. We then evaluated the candidate models based on their Fisher C-test and AICc values and selected the best-supported path model. The final model provides insights into the parental incubation investment strategy (for more details, please refer to the supplementary material).

To investigate the impact of ambient temperature on parental incubation investment strategy, we partitioned the data based on mean ambient temperature (mean \pm SE: 23.782 ± 0.160 , with a range from 3.97 to 40.54) and implemented a bootstrapping procedure to minimize the impact of sampling error on female incubation data. We utilized the ‘phyr’ package to construct PGLMM models and the ‘piecewiseSEM’ package in R version 3.6.3 to conduct the path analysis.

3 RESULTS

3.1 The relationships between male body size, ornamental traits, and temperature

Our analysis revealed that male body mass decreased with increasing ambient temperature (Table 1). Furthermore, we discovered a significant interaction effect between male ornament coloration and ambient temperature, as evident from both Table 1 and Figure 2a. Our findings indicate that the relationship between male body mass and ornament coloration was temperature dependent. Specifically, at higher ambient temperatures, there was a positive association between male body mass and ornament coloration, while in colder environments, this relationship became negative (Figure 2b, S2).

3.2 The relationships between male ornamental traits, female body size, and temperature

We investigated the relationship between female body size and ambient temperature, and found no significant correlation (Table 2, Table S4). Moreover, we did not observe any consistent correlation between female body size and male body size (Table 2, Table S4). However, we did find an interesting interaction between ambient temperature and male ornament color (MPC1) in relation to female tarsus length (Table 2, Figure 2a, c, Figure S3). Our results suggest that larger females tend to mate with males possessing more colorful ornaments in warmer environments (Figure 2c).

Furthermore, our analysis revealed a positive correlation between female ornament coloration (FPC1) and

size (FPC2) with male ornamentation (Table S4). Additionally, we observed that ambient temperature acted as a modulator in the assortative mating based on male and female ornamentation (Table S4, Figure 2a). Specifically, we found a positive relationship between male and female ornamentation in warmer environments (Figure S4a, b).

3.3 The effect of male ornamental traits and temperature on parental investment during incubation.

We observed a high degree of consistency in both female and male incubation behavior across days (female: $R = 0.621$, confidence interval [CI]: 0.463, 0.741; male: $R = 0.468$, CI: 0.274, 0.626; Figure S5). This finding suggests that individual birds have a consistent incubation investment strategy.

Our results showed that the combined total incubation investment from both parents decreased with increasing ambient temperature (Estimate (95% CI) = -0.327 (-0.620, -0.047), $z = -2.967$, $p = 0.003$). This finding suggests that temperature is an important environmental factor that increases the overall incubation investment of plovers.

We observed that larger females invested more time in incubation compared to smaller females, as shown by a positive correlation between female incubation investment and individual tarsus length (Table 3). On the other hand, male ornamentation was found to play a role in their incubation strategy, as indicated by a significant interaction between male ornamentation and ambient temperature (Table 3, Figures 2a). Specifically, we found that more ornamented males decreased their incubation investment at warmer temperatures but increased it in colder temperatures (Table 3, Figures 2a, d, S6), suggesting that the effect of ornamentation on male incubation investment varies depending on the ambient temperature.

3.4 Path analyses

We conducted a rigorous pathway analysis to explore how ornament traits and morphometric traits influenced female and male incubation parental care investment under different temperature regimes (above or below the mean temperature). We evaluated a large set of 85 candidate models (see supplementary material for details, Table S5-S8) and identified the best-supported models for temperatures above and below the mean (Figure 3) based on the lowest AICc values that passed the Fisher's C test (Table S5, S7).

Below the mean temperature, we found that females spent less time incubating than males (t test: $t = -13.492$, $p < 0.001$, Figure 3a), and the incubation investment of both males and females was primarily influenced by ambient temperature rather than male or female ornament color and body size (Figure 3a, Table S5, S6). In contrast, above the mean temperature, females spent more time incubating than males (t test: $t = 6.163$, $p < 0.001$, Figure 3b). Interestingly, we observed that male ornament color was positively correlated with female incubation investment and negatively correlated with male incubation investment (Figure 3b, Table S7, S8), while neither female body size nor male body mass had a significant effect on parental incubation investment.

4 DISCUSSION

We conducted a comprehensive analysis of the relationship between reproductive traits (body size and ornamentation) and female investment in incubation to demonstrate how ambient temperature modulates female pre- and post-copulatory mate choice preference in plover populations. The observed phenomenon could be attributed to the trade-off between ornamentation and body size in males in colder environments. Our findings revealed a positive association between male body mass and ornamentation in warmer regions and a negative correlation in colder habitats. Larger and more colorful females preferred more colorful males in warmer habitats, but this tendency was missing in colder conditions. Furthermore, in warmer conditions, colorful males engaged less in incubation, and path studies revealed that females compensated for the reduced degree of male parental care.

However, in colder environments, parental incubation only depended on ambient temperature. Our data consistently imply that ambient temperature influences plover mate selection.

4.1 Trade-off between ornaments and morphological traits varies with ambient temperatures

Body size and mass are often employed as measurements of energy reserves and can somewhat reflect an individual's condition or quality . Previous research has found a positive correlation between sexual signals and condition indices such as body size and body condition , with some exceptions . Condition indices are projected to trade-off against other life-history features, including sexual signals, as a life-history trait . We found evidence of a trade-off between colorful ornaments and body size in males in colder environments, suggesting that under harsh environmental conditions, male traits related to self-maintenance may be favored by natural selection . In contrast, under warmer environmental conditions where the total incubation requirement is lower and suggests a mild environment, males exhibited a positive relationship between body size and ornamental traits. The relationship between body size and ornaments with ambient temperature suggests that under harsher environments, individuals may need to allocate resources to body size due to life-history trade-offs.

4.2 Phenotypic traits association between parents varies with ambient temperatures

Our findings suggest that the correlation between female body size and male ornamental coloration is influenced by temperature, indicating that temperature is an important factor in the mate choice of plovers. It is unlikely that this pattern is caused by the timing of when larger and/or more colorful males and females arrive, as we controlled for breeding start time in our analysis. Additionally, Kentish plovers typically have multiple broods during a single breeding season and often change mates between broods , making assortative mating driven by arrival time less likely to have a significant effect.

The condition-dependent mate preference hypothesis suggests that females in good condition are more selective in their choice of mates and exert stronger preferences . In addition, higher quality males tend to mate with higher quality females, and larger body size often predicts female fecundity . For instance, in a previous study, larger females of both Kentish plover and white-faced plover had larger egg sizes , which suggests a positive effect on offspring survival rate and fitness . Our findings show that the condition-dependent mate preference hypothesis applies only to warmer environments, as evidenced by the positive correlation between female body size and male ornamentation. However, this pattern was not observed in colder environments. In such conditions, male plover ornaments exhibited a trade-off with body mass, indicating that ornamentation is not a priority trait for self-maintenance. This deceptive signal of self-condition may decrease the attractiveness of males to fecund females, leading to a loss of ornament quality and potential mate status. Therefore, in colder environments, the reduced occurrence of ornamental traits on males' quality can potentially limit the impact of local sexual selection, subsequently affecting mating systems. This could be suggestive a global pattern that sexual dimorphism and polygamy are higher in birds in tropical environments .

4.3 Post-copulatory investment

Males with showy ornamentation typically invest less in direct paternal care for the nest in order to pursue other mating opportunities. This explains why females usually prefer males with elaborate ornaments for their indirect genetic benefits rather than direct investment benefits. However, our results indicate that male incubation investment is not solely determined by its ornament quality, but rather varies depending on the interaction with ambient temperature. The decrease in total incubation investment with temperature suggests that in warmer environments, the incubation investment requirement is lower compared to colder environments. In harsh environments, male ornamentation provides fewer fitness benefits to females , and direct benefits such as male parental care are more valued by females. Thus, the negative correlation between male incubation investment and ornamentation only occurs in warmer environments where male ornamentation remains attractive to females, driving females to compensate and provide more care.

Previous studies have revealed that female investment in reproduction may be influenced by the attractiveness of their mate . Our path analysis shows that in warmer environments, females that mate with more ornamented males would increase their own incubation investment to compensate for males' declining

commitment in parental care. Furthermore, we discovered that females devoted more time in incubation at higher temperatures, but males invested more in cooler temperatures. This shows that in colder climates, male investment in incubation may be more significant than ornamentation. In harsh environments, parental care is crucial for offspring survival, which may lead to biparental care, showing a greater necessity for direct investment in such situations. Overall, our path analysis suggests that temperature influences male and female investment strategies in response to mating attractiveness and parental care demands.

The impact of environmental variables on mate choice has primarily been investigated in the context of the preference switch by females between sexual traits when their ability to sense each cue is compromised. Our study contributes to this understanding by revealing that female preference for indirect benefit signals, such as male ornamentation, may be influenced by the environment. These findings might provide light on how male sexually chosen traits are retained under female selection, a phenomenon known as the 'lek paradox'. Previous studies have investigated how environmental heterogeneity can lead to variation in female mate choice, potentially explaining the lek paradox. However, they have primarily focused on mate choice intensity or thresholds for a specific male trait (reviewed by). In contrast, our work demonstrates how abiotic variables such as ambient temperature can alter female preference for male ornaments. Our findings show that natural selection pressure constrains male ornamentation preferences, whereas females display a direct preference for ornamentation in stable habitats, such as those with warmer temperatures.

AUTHOR CONTRIBUTIONS

ZS and YL conceived the study, ZS conducted the analyses, and wrote the manuscript; ZS, PQ, CH, NH and PD collected the data, ZZ and WJ contributed to data analyses and manuscript writing, and reviewed drafts of the paper. All authors reviewed the manuscript and gave final approval for publication.

ACKNOWLEDGEMENTS

We thank Tamas Szekely for his advice regarding data collection and manuscript writing. We thank Mallory Eckstut (www.liwenbianji.cn/) for linguistics comments. Thanks to Li Xu, Zihao Song, Xiao Huang and Xin Lin for their assistance at fieldwork. This research was funded by the China Postdoctoral Science Foundation (No. 2019M663221) and the British Ornithologists' Union's Career Development Bursary to ZS; the Open Fund of Key Laboratory of Biodiversity Science and Ecological Engineering, Ministry of Education to YL.

CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

Data are publicly available via the online Dryad repository: xxxx/xxxx.xxx (This data is currently uploaded as supporting information for reviewers, and will be available once the manuscript is accepted).

REFERENCES

Tables

Table 1 Relationships between male body mass with male ornament coloration (MPC1) and ornament size (MPC2), ambient temperature and laying date of two congeneric plovers (PGLMM, n = 131 individuals)

Fixed effects

Intercept

Male ornament coloration (MPC1)

Male ornament size (MPC2)

Temperature (Temp.)

Laying date

Incubation period
MPC1 × Temp.

MPC2 × Temp.

Random effects

1| Population location

1| Population phylogeny

1| Year

Residual

All data were standardised and centred. Bold items indicate statistical significance at a level of $p = 0.05$. 95% CI of estimat

Table 2 Correlation between female tarsus length and male body size vs. ornament quality of two congeneric plovers (PGLMM, $n = 111$ nests)

Fixed effects

Intercept

Male ornament coloration (MPC1)

Male ornament size (MPC2)

Male tarsus length (MTs)

Temperature (Temp.)

Laying date

Incubation period

MPC1 × Temp.

MPC2 × Temp.

MTs × Temp.

Random effects

1| Population location

1| Population phylogeny

1| Year

Residual

All data were standardised and centred. Bold items indicate statistical significance at a level of $p = 0.05$. 95% CI of estimat

Table 3 Male and female incubation investment ratio influenced by individual ornament quality (coloration [PC1] and size [PC2]), body size, and ambient temperature as a modulator by PGLMM.

Male's incubation investment ratio ($n = 71$)

Fixed effects

Intercept

Male ornament coloration (MPC1)

Male ornament size (MPC2)

Body mass

Tarsus length

Temperature (Temp.)

MPC1 × Temp.

Random effects

1| Population location

1| Population phylogeny
1| Year
Residual
Female's incubation investment ratio (n = 71)
Fixed effects
Intercept
Female ornament coloration (FPC1)
Female ornament size (FPC2)
Body mass

Tarsus length

Temperature
Random effects
1| Population location
1| Population phylogeny
1| Year
Residual

All data were standardised and centred. Bold items indicate statistical significance at a level of $p = 0.05$. 95% CI of estimat

Figure captions

Figure 1. The location of study site and associated mean daily ambient temperature during breeding season at the four study sites (Paisha Island and Bohai Bay from May to June, Qinghai Lake from May to July and Taitema Lake from in mid-April to July). The mean daily temperatue has significant different between four sites (ANOVA: $F_{3,361} = 348$, $p < 0.001$).

Figure 2. Coefficient estimates of the interaction between temperature (independent variable) and each dependent variable according to the PGLMMs. a) Coefficient estimates plot for each of male body mass (MMa), Female body mass (FMa), Male coloration (MPC1) and male's ornamental trait area size (MPC2) and their respective interactions with temperature. The centre points denote the means, the thick bars denote the 95% lower and upper confidence interval as calculated by PGLMMs simulated by bootstrapping with 1,000 iterations in R. b–d) Model predictions of the interaction between male body mass or ornamental traits and ambient temperature with male ornamental traits (b), female tarsus length (c), and male incubation investment (d).

Figure 3. Path models showing the influence of male and female body mass and male ornament color on parents' incubation investment in temperatures (a) below and (b) above the mean temperature across the four environments (23.782). The left bars show the average time (min) parents spent incubating the nest in a 3-hour period. Dotted lines with the double-ended arrow indicate correlations and solid lines with a single arrow indicate path coefficients. The black lines represent significant negative relationships and the red lines represent significant positive relationships. Non-significant paths were removed from the figure.

Figure 1

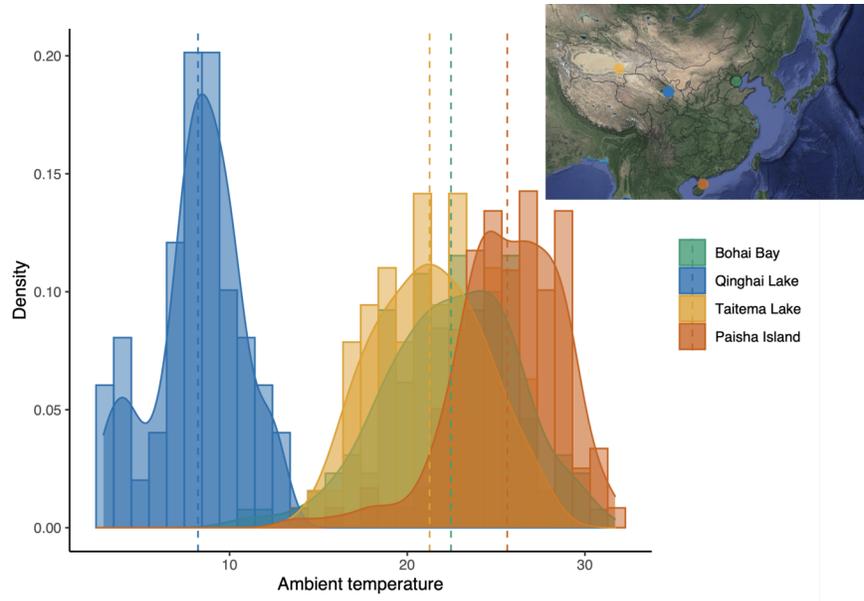


Figure 2a

Hosted file

image2.emf available at <https://authorea.com/users/660071/articles/663768-colder-ambient-temperatures-constrain-female-mate-preference-for-ornamental-traits>

Figure 2b

Hosted file

image3.emf available at <https://authorea.com/users/660071/articles/663768-colder-ambient-temperatures-constrain-female-mate-preference-for-ornamental-traits>

Figure 2c

Hosted file

image4.emf available at <https://authorea.com/users/660071/articles/663768-colder-ambient-temperatures-constrain-female-mate-preference-for-ornamental-traits>

Figure 2d

Hosted file

image5.emf available at <https://authorea.com/users/660071/articles/663768-colder-ambient-temperatures-constrain-female-mate-preference-for-ornamental-traits>

Figure 3a

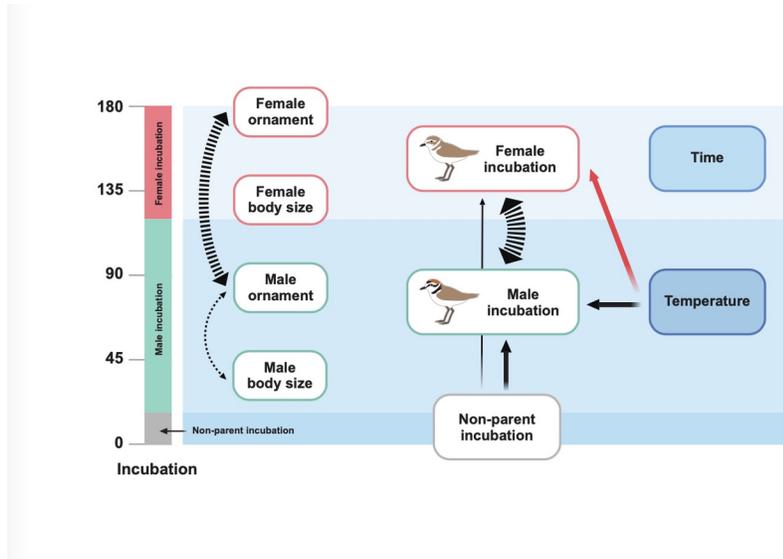


Figure 3b

