ORIGINAL ARTICLE

Breeding ecology of a high-altitude shorebird in the Qinghai–Tibetan Plateau

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Abstract

Shorebirds are facing global decline as a consequence of anthropogenic effects that include habitat loss, increased predation and climate change. Although some shorebirds are extensively studied, basic data on life history, ecology and behaviour are still lacking especially for populations where climate change is expected to have severe effects. Here, we provide the first detailed investigation of a high-altitude nesting shorebird in the Qinghai–Tibetan Plateau, the Tibetan Sand Plover *Charadrius atrifrons*. This alpine-breeding Central-Asian species recently split from the Lesser Sand Plover *Charadrius mongolus* that breeds in Eastern Siberia. Understanding the fundamental ecology and behaviour of alpine-breeding shorebirds is important for predicting the challenges these high-altitude species will face given the human-driven environmental changes that are likely to take place in these habitats. Here, we show that Tibetan Sand Plovers in the Qinghai–Tibetan Plateau have a short breeding season from mid-May to late-June, and exhibit social monogamy and bi-parental care of the clutch. Since they have low hatching success (18 of 57 nests hatched) and no chance of renesting, maintaining population size in the future may pose a challenge. To provide essential information for protection of this species in a vulnerable habitat, further demographic studies are warranted to better understand how climate change will mould adaptations of this specialised high-altitude species to their environment.

Keywords Sand plover · Breeding success · Incubation · Climate change · Plateau

Zusammenfassung

Strandvögel unterliegen weltweit einem Rückgang als Folge anthropogener Einflüsse wie Verlust des Lebensraums, zunehmende Verfolgung und dem Klimawandel. Obwohl einige Küstenvogelarten umfassend erforscht worden sind, fehlen noch immer grundlegende Daten zu ihrer Lebensweise, ihrer Ökologie und ihrem Verhalten, insbesondere für diejenigen Populationen, auf die der Klimawandel voraussichtlich besonders große Auswirkungen haben wird. Wir legen hier die erste detaillierte Untersuchung für einen Strandvogel vor, der hoch oben auf dem Qinghai-Tibet-Plateau brütet, dem

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Tibetregenpfeifer (*Charadrius atrifrons*). Diese in den Bergen brütende zentralasiatische Art wurde jüngst vom in Ostsibirien brütenden Mongolenregenpfeifer (*Charadrius mongolus*) abgespalten. Die Grundlagen von Ökologie und Verhalten von in den Bergen brütenden Strandvögeln zu verstehen ist wichtig für die Bewertung der Probleme, mit denen sich in größeren Höhen nistende Arten angesichts der für diese Lebensräume vorhergesagten anthropogenen Umweltveränderungen werden auseinandersetzen müssen. Wir zeigen hier, dass der Tibetregenpfeifer auf dem Qinghai-Tibet-Plateau eine kurze Brutsaison von Mitte Mai bis Ende Juni hat, sozial monogam lebt und sich die Betreuung des Geleges mit dem Partner teilt. Da der Bruterfolg gering ist (in 18 von 57 Nestern gab es Nachwuchs) und keine Chance auf eine erneute Brut besteht, könnte ein zukünftiges Problem die Erhaltung der Populationsgröße sein. Um wichtige Informationen für den Schutz dieser Art in einem gefährdeten Lebensraum zu bekommen, sind weitere demografische Studien erforderlich. Nur dann kann man besser verstehen, wie der Klimawandel die Anpassungen solcher spezialisierter Hochgebirgsarten an ihre Umwelt beeinflussen wird.

Introduction

Organisms exhibit adaptive behavioural modifications in response to changing environments to improve their survival and reproductive success (Sih 2013; Wong and Candolin 2015). However, recent anthropogenic activities have led to rapid and extensive changes in the environment including the climate, causing a staggering decline in global biodiversity (Parmesan and Yohe 2003; Arneth et al. 2020). In light of these challenges, it is of vital importance to understand the interactions between ecology and behavioural and physiological adaptations in wild populations with the intention of informing conservation decisions.

Shorebirds (plovers, sandpipers, and allies of Charadriiformes) are a group of bird species that breed in a variety of habitats on all continents including Arctic tundra, Antarctic, and sub-Antarctic islands, temperate wetlands, to deserts and tropical marshes (Kosztolányi et al. 2009; del Hoyo et al. 2018). Breeding populations also include coastal populations that breed on sand dunes and salt-marshes, species that breed in mountain forests and those that breed in high-altitude alpine meadows in Eurasia and South America at 3500 m or above (Que et al. 2015; Wiersma et al. 2016; del Hoyo et al. 2018). Their successful adaptations to various environments have resulted in extremely diverse social behaviours and life history traits within and between species, which include various forms of polygamy and parental care strategies (Székely et al. 2000, 2023, 2006; Thomas and Székely 2005; Thomas et al. 2007; Song et al. 2020). In addition, some shorebirds have migratory life-styles whereas others are all-year round residents (Székely et al. 2006; del Hoyo et al. 2018; Kubelka et al. 2022). Therefore, shorebirds are an ideal group of organisms in which to study ecological adaptations especially from a social behaviour point of view (Kempenaers 2022; Székely et al. 2023).

More recently, a line of comparative studies has shown that the variable mating and parenting behaviours in shorebirds are associated with the ambient environment (Vincze et al. 2013, 2017; Halimubieke et al. 2020). However, a limitation of those comparative studies is that life history and ecological data are scarce from regions that are highly vulnerable to climate and environmental changes such as deserts, Arctic regions and plateaus. More baseline data on breeding ecology from extreme environments is crucial to have a clearer idea about the relationship between breeding behavioural evolution and the ambient environment. Another challenge is that the ongoing climate change has had a significant impact on the shorebird population viability. A recent study by Kubelka et al. (2018) revealed that the Arctic shorebirds have experienced a worldwide increase in nest predation over the past 70 years due to climate change disrupting the trophic relationships between species. Regions like the Arctic are more sensitive to climate change as the consequences of warming are expected to be more pronounced (Overland et al. 2019; Choudhary et al. 2021), thus the breeding ecology of species from those areas is not only crucial for understanding the interactions between behavioural adaptation and environment, but also important for mapping the impact of climate change, human disturbance, and habitat degradation on global biodiversity (Pearce-Higgins et al. 2017; Kubelka et al. 2018; Amano et al. 2020).

Here, we focus on the breeding ecology of a Tibetan Sand Plover *Charadrius atrifrons* that breeds at an alkaline lake on the Qinghai–Tibetan Plateau. Tibetan Sand Plovers are facultative high-altitude breeders that include three subspecies *schaeferi*, *atrifrons*, and *pamirensis* in Qinghai–Tibetan Plateau and the adjacent Pamir Plateau. They were previously known as a subspecies of Lesser Sand Plovers *Charadrius mongolus* until a recent genome-based study elevated them to the full species *Charadrius atrifrons* (Wei et al. 2022). The breeding population at Qinghai Lake belongs to the subspecies *schaeferi*, and their wintering grounds can be found in coastal southern China and Greater Sundas (del Hoyo et al. 2018). The breeding ecology of Tibetan Sand Plovers is a missing piece of key information in global shorebird research as it can provide crucial information on the breeding ecology and behavioural adaptations of high-altitude species. Moreover, high-altitude environments are important habitats for shorebird breeding, and are also sensitive to global warming and anthropogenic activities (Li 2019;

Liu et al. 2021; Hua et al. 2022). However, research efforts to understand the conservation of shorebirds in high-altitude environments have been scant compared with their Arctic counterparts (Meltofte et al. 2007; Lanctot 2013; Kubelka et al. 2018; Sandercock 2020; Shaftel et al. 2021). Thus, understanding the breeding ecology of this plateau shorebird population can give us a comparative perspective to better understand the impact of climate change on global shorebird conservation. In this study, we aim to understand the breeding ecology and behaviour of Tibetan Sand Plovers to assist conservation decisions. Particularly, we focus on (i) breeding ecology that include nest biometrics, nest distribution, individual morphological features and breeding phenology; (ii) breeding success (specifically the nest success); and (iii) breeding behaviour (i.e. social mating system and incubation behaviour).

Materials and methods

Study site

Fieldwork was conducted at Qinghai Lake (36°50′30.78″N, 100°44′37.92″E), the largest lake in China, located on Qinghai–Tibetan Plateau with an elevation of 3200 m above sea level. There are approximately 50–100 Tibetan Sand Plover pairs breeding on the eastern lake shore each year (Fig. 1). Breeding data were collected from 2015 to 2019 ($N = 57$ nests), data from 2017 were excluded due to its low quality resulting from a limited fieldwork effort.

Data collection

Clutch size and egg volume

Data collection in the field followed the methods of Székely et al. (2008). We searched for nests using a mobile hide and a car intensively along the lake shore, we recorded the nest location with GPS. For each found nest, egg length and width were measured using sliding callipers, which were later used to calculate clutch volume. Douglas' formula (1990) was used to calculate egg volume: $V = K_v * L * W^2$, where $K_v = 0.5$, $L =$ egg length and $W =$ egg width. Clutch volume was calculated as the sum of all egg volumes per nest.

Egg-laying date

We estimated the egg-laying date based on the floatation stage of each egg in a transparent jar with clean water, and by backdating the number of days that the egg had already been incubated compared with the day it was found (Noszály and Székely 1993). We controlled for breeding phenological differences between years by converting egg-laying dates into Julian dates (Grolemond and Wickman 2011), and calculating the relative egg-laying date of each year using the z-transformation (mean = 0, SD = 1).

Nest success

Nests were monitored every 2–5 days until 20 days of incubation and then were checked every day until hatching to obtain nesting success data. The fate of nest was recorded as either successful (at least one chick hatched) or failed
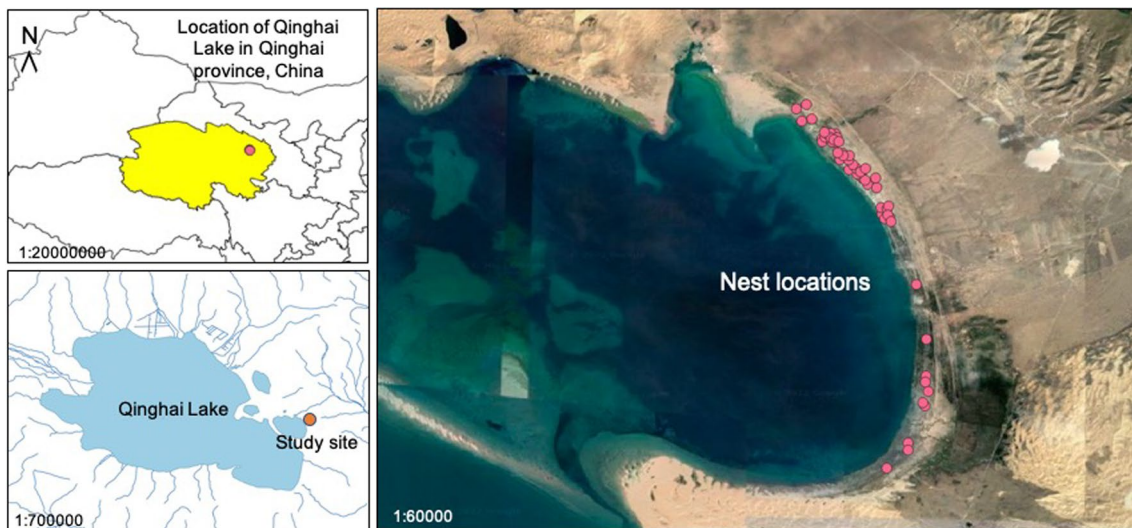

Fig. 1 The distribution of Tibetan Sand Plover nests at Qinghai Lake ($N = 57$ nests)

(no chicks hatched due to predation, destruction, abandonment, eggs disappeared < 18 days after estimated laying date, eggs did not hatch, or the nest was flooded). Nest fates were considered as unknown if all eggs disappeared close to the predicted hatching date, although the parents were not observed with chicks, or if the nests were still active at the time when fieldwork was finished (Please see Figure S1 nest fate determination flow chart for more details, Engel and Székely 2023).

Individual morphometrics

The parents of each nest were captured with a walk-in funnel trap placed over the nest, and were banded with a unique combination of three-color rings and an alpha-numeric metal ring. Wing, bill and tarsus length were measured to the nearest 0.1 mm and the bird was weighed with a digital balance to the nearest 0.1 g.

Incubation

Infrared cameras (Bushnell® trophy trail cameras, model 119,466) were used to record activities at nests; they were set up and hidden approximately 1 m away from the nest after the capture of parents, and captured images with a one-minute interval for 72 h. Then MATLAB_R2021a (9.10.0.1649659) was used to process the incubation photos. The incubation behaviours were defined as the behaviour taken by parents to maintain eggs at an appropriate development temperature (including keeping the eggs warm and shading the eggs), so as to distinguish 3 states: no birds, male incubation, female incubation. To ensure that the cameras did not negatively impact the behaviour of incubating birds, the cameras were positioned at a safe distance (at least 1 m from the nest) and concealed well (Kosztolányi et al. 2009; AlRashidi et al. 2011; Vincze et al. 2017). The first hour of data of each nest was removed from the analyses. Additionally, the final segment of recording, which was less than 60 min in duration for each nest, was also trimmed to improve the suitability of the data for analysis. Nests with at least continuous 24 h of behaviour data were used for analysis ($N = 7$ nests, the median number of days per nest used for analysis = 3 days, range: 1–3 days).

We extracted nest attendance (the proportion of time either parent incubated the eggs during the camera's observation period), incubation bout (the period of time from one parent arriving at the nest to the other parent taking over incubation, including periods when the parent is not actively incubating the nest) and exchange gap (the time between incubation bouts when neither parent was incubating the nest) for further analyses. Daytime and night were defined by the solar altitude angle (with "night" being defined as the sun being > 6° below the horizon).

Statistical analysis

Visualisation of the nest distribution was created using QGIS version 3.26.2 (QGIS Development Team, 2022). Three Generalized Linear Mixed Models (GLMMs) were built, employing Poisson, Gaussian (referred to as Linear Mixed-effect Models), and binomial error distributions. These models were applied to investigate the relationships between clutch size and egg-laying date, egg volume and egg-laying date, and nest success and egg-laying date, respectively. In all models, Year was incorporated as a random effect to account for inter-annual variations. Additionally, another GLMM using Gaussian error distribution, was employed to examine the associations between average egg volume and female body mass, including the Year as a random effect as well. The p values of the GLMMs were calculated using the Wald test (Ward and Ahlquist 2018). The daily survival rate (DSR) of the nests was estimated using the Kaplan–Meier curve (Sedgwick 2014), which described the proportion of nests that survived within the given time interval relative to the total nests. Kaplan–Meier curves were plotted using the R packages "survival" and "survminer" (Biecek and Kassambara 2021; Therneau 2023). Survival curve fitting was achieved through the "survfit" function in the "survival" package, the significance of differences between survival in different years was assessed using a chi-squared test in the "survdiff" function, and the final visualisation of survival curves was accomplished through the "ggsurvplot" function in the "survminer" package. The normal distribution of the morphological data was examined utilizing a Shapiro–Wilk test (Shapiro and Wilk 1965). A Wilcoxon test was used to evaluate differences in sexual size dimorphism, and the differences in nest attendance or incubation bouts between sexes.

Results

Breeding ecology

We recorded 57 Tibetan Sand Plover nests between 2015 and 2019 along the eastern shore of Qinghai Lake (Fig. 1)—an approximately 10 km length of coastline (estimated by Google LLC 2023). Nests were found inland up to 200 m from the shoreline. The breeding habitat was short grassland, sand dunes, white sand and stony grassland, but most nests were shallow scrapes in exposed sand on an open site without much vegetation (Fig. 2a). The nesting materials were tiny pebbles and marine shells. Egg-laying started from early May and lasted until late-June with the egg-laying peaks from late May to mid-June (Figure S2). The duration of incubation period was 26.3 days ($SE = \pm 1.6$ day, $N = 14$ nests).
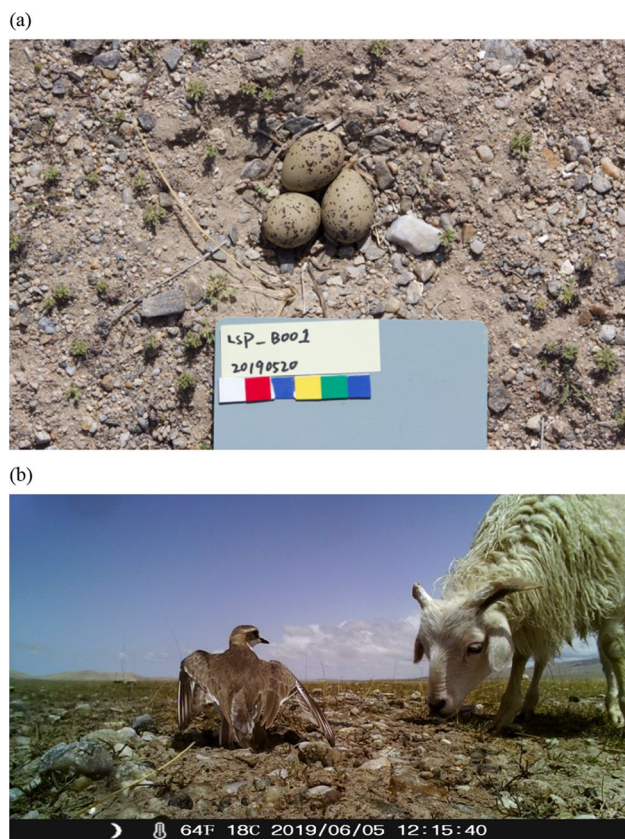
(a)

(b)

Fig. 2 **a** A Tibetan Sand Plover nest at Qinghai Lake. **b** A nest camera footage showing a female protecting her nest from grazing sheep

Among the 55 nests with egg data (data for 2 nests is missing), 41 nests had three eggs, 12 nests had two eggs, and 2 nests had only one egg. The mean clutch size of the Tibetan Sand Plover nests was 2.71 eggs per clutch ($SE = \pm 0.1$), and clutch size was not related to the relative egg-laying date (GLMM, estimate $= -0.39$, $p = 0.75$, Wald test statistic $= -0.32$, $N = 55$ nests). The mean length and breadth of eggs were 36.5 mm (33.8–40.4 mm; $N = 137$ eggs, $SE = \pm 0.1$) and 25.8 mm (24.3–27.8 mm; $N = 137$ eggs, $SE = \pm 0.1$), respectively, and mean egg volume was 11.9 cm^3 (10.1–14.3 cm^3; $N = 137$ eggs, $SE = \pm 0.1$). Egg volumes were unrelated to the relative egg-laying date

(GLMM, estimate $= -0.86$, $p = 0.34$, Wald test statistic $= -0.97$, $N = 137$ eggs).

Fifty-four adult Tibetan Sand Plovers (18 males and 36 females) were captured, and we found sexual size dimorphism in body mass and tarsus length—adult females were significantly heavier than males, and males had a longer tarsus than females. Neither wing length nor bill length differed between males and females (Table 1). Female body mass did not predict the average egg volume (GLMM, estimate $= 21.6$, $p = 0.41$, Wald test statistic $= 0.83$, $N = 30$ females).

Nest success

Among the nests with confirmed nest fate, 18 hatched (annual nest success rate: 37.11%) and 23 nests failed ($N = 41$ nests in total). Among the failed nests, at least 8 nests were confirmed predated (nest cameras identified nest predators are Tibetan sand fox *Vulpes ferrilata*, European badger *Meles meles*, and Red-billed Chough *Pyrrhocorax pyrrhocorax*), one was trampled by grazing herds, one was abandoned by parents, and 13 nests disappeared during early incubation stage (i.e. before the 18th day of incubation). The fate of 16 nests was unknown.

DSR decreased from 0.94 to 0.24 in 2018 during the course of breeding season, and from 0.96 to 0.39 in 2019 (Fig. 3; Table S1), so that nests initiated earlier in the breeding season survived better than nest produced later (GLMM, estimate $= -14.48$, $p = 0.02$, Wald test statistic $= -2.27$, $N = 41$ nests; Fig. 4). DSR was not different between years ($p = 0.70$, chi-squared test, Fig. 3). Data from 2015 and 2016 were not included in DSR analyses due to the missing information of nest fate or egg-laying date.

Breeding behaviour

We found that Tibetan Sand Plovers are socially monogamous based on our observations, since we have not noticed renesting after a successful or failed breeding. Across breeding seasons, due to total lack of re-capture, we did not find any evidence that supports between-year mate fidelity in this population.
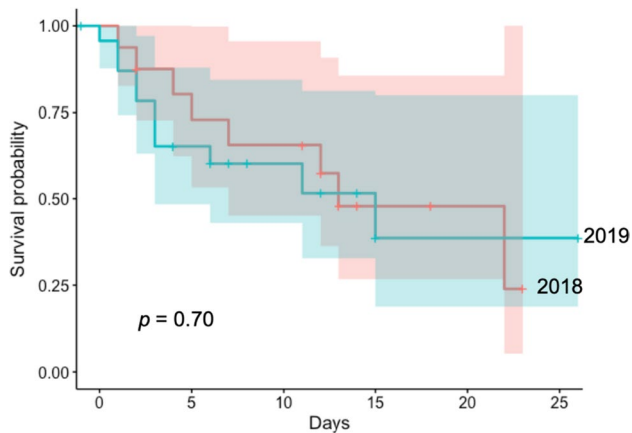
Table 1 Body size of breeding adult male and female Tibetan Sand Plovers at Qinghai Lake, China ($N = 18$ males, 36 females)

Traits	Males		Females		*p* value
	Mean ± se	Min–Max	Mean ± se	Min–Max	
Body mass (g)	63.1 ± 0.9	57.3–70.4	65.1 ± 0.8	45.9–74.7	**0.02**
Wing length (mm)	133.7 ± 0.6	128.0–139.0	135.2 ± 0.8	125.0–148.0	0.16
Tarsus length (mm)	35.2 ± 0.3	33.6–37.2	34.3 ± 0.2	31.7–37.9	**0.02**
Bill length (mm)	17.9 ± 0.2	16.3–20.0	17.7 ± 0.2	16.0–21.1	0.49

se standard error

Statistically significant results of Wilcoxon test are presented in bold

Fig. 3 Estimated daily survival rates for nests of Tibetan Sand Plover at Qinghai Lake, in relation to age of nests (days). Data from 2018 and 2019 were used (N=43 nests), data from 2015 and 2016 were not used due to the missing information. Shading represents 95% confidence intervals. p value represents the result of the chi-squared test
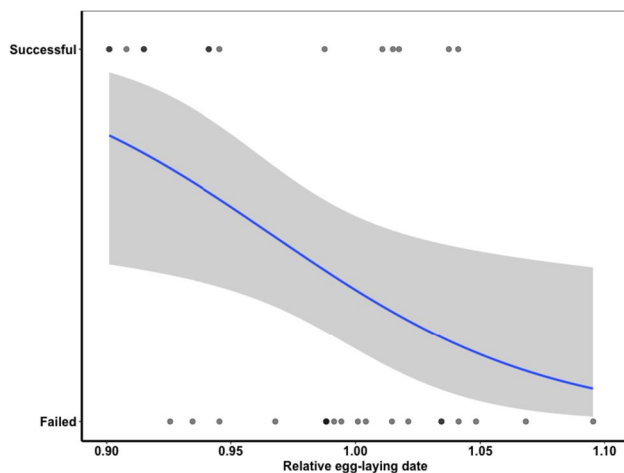

Fig. 5 Nest attendance rate in Tibetan Sand Plovers based on continuous 24 h recording of 7 nests. Box plots depict median (horizontal line inside the box), 25–75th percentiles (box), 25th and 75th percentiles minus or plus 1.5×interquartile range (whiskers), the ends of whiskers represent the minimum and maximum value, outliers are shown in circles

nest attendance is higher during the night than during midday (Fig. 6b). For further details, please see the supplementary materials (Figure S3).

Discussion

The breeding ecology of high-altitude shorebird species appears to be overlooked compared to the Arctic species (Pienkowski 1984; Meltofte et al. 2007; Kubelka et al. 2018). Here, we provide the first detailed report on the breeding ecology of a high-altitude Tibetan Sand Plover population at Qinghai Lake, that might also be relevant for the species as a whole and the conservation of other high-altitude populations. Our study provided the following key findings.

The plateau Tibetan Sand Plover population has a short breeding season which occurs from mid-May to late-June. This is a similar breeding length to their arctic counterparts (Meltofte et al. 2007), but rather short compared to other *Charadrius* plover populations from a similar latitude. For example, field data show that the Kentish Plover (*Charadrius alexandrinus*) population at Bohai Bay, Eastern China (39°08′ N, 118°46′ E to 39°14′ N, 118°52′ E,) has a breeding season from early May to late July (Huang and Que 2019, unpublished fieldwork report). We believe one of the main constraints for a short breeding season is the temperature, the average temperature in May and June at Qinghai Lake region is around 10.6 °C (Song et al. 2020; Cedar Lake Ventures, Inc. 2023), and a short window of suitable

Fig. 4 Nest success in relation to relative egg-laying date in Tibetan Sand plovers (GLMM, estimate=− 14.48, p=0.02, N=41 nests). Logistic linear regression line is shown in blue and standard error is shown in grey

Both parents incubate the eggs and show a high overall daily nest attendance, with parents incubating their eggs 94.4% of the time in a 24-h day (median, IQR 93.2%–96.7%, N=7 nests, Fig. 5). Females' and males' daily nest attendance rate were 45.4% (median, IQR 43.8%–51.3%) and 46.4% (median, IQR 42.2%–52.1%), respectively, with no difference between sexes (p=0.65, Wilcoxon test, N=7 nests, Fig. 5, see Figure S3 in Supplementary Material). However, we found a sex-specific pattern in daily nest incubation since males incubated primarily at night, with some contribution of daytime incubation, while females mainly incubated during the day with little contribution at night (p<0.001, Wilcoxon test, Fig. 6a). Furthermore, the daily
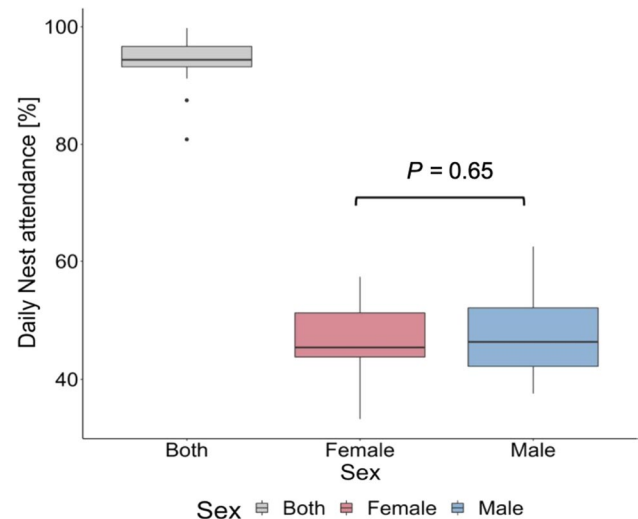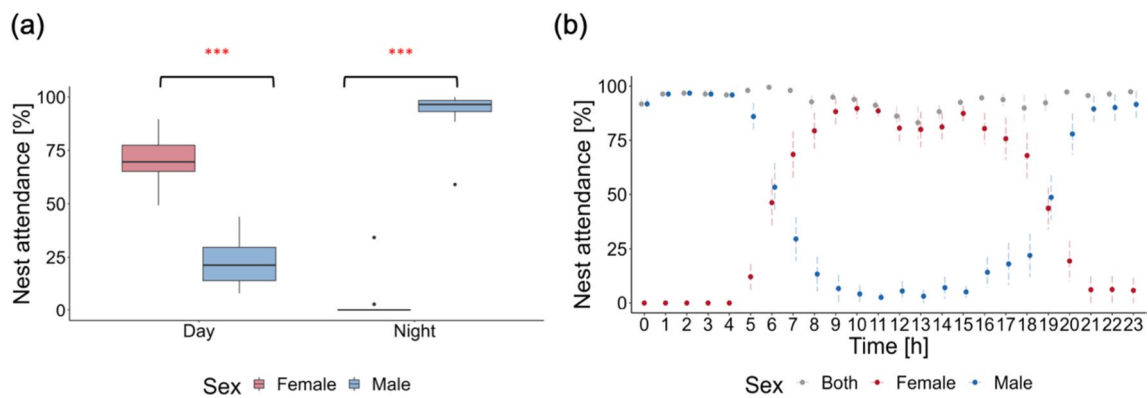
Fig. 6 a Diurnal variation in nest attendance in male and female Tibetan Sand Plovers. Medians, upper and lower quartiles, as well as extreme values are shown, ***$p < 0.001$. **b** Daily variation in overall (grey), female (red) and male (blue) nest attendance. Points depict hourly average nest attendance of all nests ($N = 7$ nests, 16 days), with standard errors shown in dash lines

temperature may have resulted in a short breeding season. Several other studies found that birds in high elevation had a shorter breeding season due to the temperature constraint (Lu et al. 2010; Hille and Cooper 2015; Boyle et al. 2016). Thus, we suggest that the cold temperatures at higher elevations are associated with a later start of egg laying, resulting in shorter breeding seasons.

We also reported the nest data of Tibetan plover, including clutch size and egg volume, although we did not find any temporal change in clutch size and egg volume throughout the breeding season. In terms of morphological features, Tibetan Sand Plover show a sexual difference in plumage (del Hoyo et al. 2018), here we further found that there is a sexual difference in body mass and tarsus length—females are heavier, whilst males have longer tarsi. Several factors may contribute to these sexual size dimorphisms (SSDs) observed in Tibetan Plovers. Across taxa, the evolution of SSD has been associated with natural selection for larger female body mass as it is linked to increased fecundity (Blanckenhorn 2000; Fairbairn 2007; Dos Remedios et al. 2015). Thus, the greater mass of female Tibetan Sand Plovers may reflect selection for breeding in harsh plateau environment, where the production and incubation of eggs demand substantial energy. At the same time, given the high fecundity, larger females may be favoured by males. However, it is important to note that the body mass is not always strongly related to fecundity among many birds (Lislevand et al. 2009; Dos Remedios et al. 2015). In Tibetan Sand Plovers, we did not find empirical support for a correlation between female body mass and fecundity, as indicated by the average egg volume (Ding et al. 2023). Nevertheless, the robustness of our analyses may be influenced by the lack of comprehensive long-term reproductive success data and the temporal fluctuation in female body mass during the breeding season. Sexual selection may favour larger male body size in many species (Székely et al. 2000; Bertin and Cezilly

2003; Lislevand et al. 2007). In the case of Tibetan Sand Plovers, we hypothesise that the longer tarsi in males may be advantageous for the courtship displays (Rice et al. 2020) or nesting behaviour. For instance, males with longer tarsi might be better at reaching into deeper cavities to help excavate nest sites, thus better at attracting a mate. This hypothesis could ideally be tested by examining whether males with longer tarsi have a higher rate of mating success since they are likely to have more mates (Lv et al. 2020). Nevertheless, as a result of insufficient data regarding courtship behaviour and the long-term success of mating, we are now unable to evaluate this hypothesis. SSD could also reflect demographic processes, such as mortality differences between juvenile or adult males and females in relation to body size (Badyaev et al. 2001, Kersten and Brenninkmeijer 2008), or a sex-specific growth rate at the pre-/post-natal stage (Müller et al. 2012, Helle et al. 2013; Blanckenhorn 2005, Hasumi 2010, Zhang and Liu 2013). Tests of these hypotheses, however, will require a longer-term monitoring of demographic processes. To sum up, it is necessary to conduct further experimental and long-term studies on the implication of SSD on natural or sexual selection, and related processes in Tibetan Sand Plover, as SSD and natural or sexual selection play a critical role influencing reproductive success across species (Darwin 1871; Székely et al. 2007; Shuster 2009), therefore, are critical to long-term conservation of this plateau population.

Investigating the breeding behaviour of the Tibetan Sand Plovers, we found that this population exhibits social monogamy with bi-parental care of the clutch. Previous studies have suggested that high ecological pressures (e.g. harsh and stochastic ambient environment, low food and mate availability, high predation pressure) may promote monogamy and bi-parental care in bird species, as monogamy and bi-parental care are advantageous for offspring survival (Székely and Reynolds 1995; Welch 2003;

Candolin et al. 2007; Thomas et al. 2007; Bulla et al. 2014; Saalfeld and Lanctot 2015; Eberhart-Phillips 2019). Consequently, we speculate that the observed social monogamy and bi-parental care in Tibetan Sand Plovers may be adaptations to the cold ambient environment and high nest loss, which facilitate both parents to cooperate and continuously incubating the nest, thereby mitigating the thermal stress and other ecological pressures contributing to nest loss. This could be supported by the observation that social monogamy and bi-parental care are not exclusive to Tibetan Sand Plovers alone within the Qinghai Lake region, their sympatric counterpart, the Kentish Plovers, also exhibit similar breeding behaviour (Halimubieke et al. 2018, 2019; unpublished fieldwork reports). Interestingly, in the Arctic region, where similar environmental pressures exist, highly diverse mating and parenting behaviours have been documented across different shorebird species, suggesting the multifaceted interplays of different ecological factors and phylogenetic composition may have resulted in various behavioural adaptations (Meltofte et al. 2007; Bulla et al. 2014, 2016; Saalfeld and Lanctot 2015; Kubelka et al. 2018). However, it is important to acknowledge the limitation of our study due to the paucity of ecological data in Qinghai Lake region, thus we need further experimental studies to explore alternative explanations for these observed behaviours. Future research should involve long-term monitoring of breeding behaviours over a longer time scale and cover a larger area to verify our present findings and uncover additional adaptive evidence. Understanding the ecology of breeding behaviour is crucial, as it carries potential implications for the conservation of Tibetan Sand Plovers and other avian species facing similar ecological challenges.

We also found a male-biased nocturnal incubation in Tibetan Sand Plovers, which is uncommon in their Arctic counterparts (Pienkowski 1984; Wanders et al. 2023). We suggest that this could be because less colouration can reduce the risk of predation, thus female incubating during the day can improve egg survival (Ekanayake et al. 2015); however, it does not explain why male-biased nocturnal incubation is not common in Arctic shorebirds where the ecological constraints are similar to Qinghai Lake. Therefore, we speculate that the existence of a relatively longer night at Qinghai Lake may have resulted in a different foraging strategy in Tibetan Sand Plovers, where females can take advantage of the higher food abundance at night to compensate for the energy deficit during the day (Kuwae 2007), whereas such advantages may be less prominent in Arctic species, leading to a non-biased incubation pattern. Although remain untested, such behavioural divergence is a strong evidence showing that the breeding ecology might be different between Arctic and plateau species despite the similar ecological environment and life history traits.

Finally, we found that Tibetan Sand Plovers exhibit low nest success, resembling their counterparts in the Arctic region (Troy 1996; Kubelka et al. 2018; Freeman et al. 2023). Like many other plover species, the Tibetan Sand Plovers prefer open and less vegetated habitats for nesting (Fig. 2), which makes them vulnerable to predators and anthropogenic activities (Amat and Masero 2004; Colwell et al. 2005; Zefania et al. 2008; Kosztolányi et al. 2009; AlRashidi et al. 2011). We found that the main source of confirmed nest failure in this plateau population comes from predation, and nest cameras identified the nest predators as the Tibetan sand fox *Vulpes ferrilata*, badger *Meles meles*, and Red-billed Chough *Pyrrhocorax pyrrhocorax*. We also observed nest failures were associated with the trampling by livestock or sometimes the tourist cars on the lake shore. Breeding grounds on the lake shore are often grazed by herds (sheep and horses), causing disturbance to the incubating birds (Fig. 2b); and eggs can easily be trampled by the running herds driven by the shepherds. We believe that the nest failure of this population is likely to be underestimated as there were 16 nests (33.3% of the nests monitored) with unknown nest fates, among which 10 nests disappeared after at least 18 days of incubation, and 6 nests were still active by the time fieldwork terminated. Furthermore, due to limitations in historical data and the demographic monitoring, we lack the necessary information to gauge any temporal changes in breeding success, and how other demographic processes (e.g. mortality rate, fledglings' survival rate, sex ratio) may impose impacts on breeding success and the overall survival of Tibetan Sand Plovers.

We found that the early breeders had a higher nest success. This is a common pattern seen in many migratory bird species (van de Pol et al. 2006; Borgmann et al. 2013; Plaschke et al. 2019), and a range of mechanisms have been proposed to explain this association. For example, early breeders are able to able to lay replacement clutches; and early breeders are often the higher-quality individuals (Borgmann et al. 2013; see Morrison et al. 2019). In Tibetan Sand Plovers, increased nest success among early breeders is likely attributed to their opportunities to secure higher-quality habitats and territories, which may offer reduced predation risk to eggs or chicks and improved resource availability, ultimately enhancing offspring growth and survival (Arnold et al. 2004; Jonzen et al. 2007). Nonetheless, it is necessary to monitor breeding success on a broader spatial and temporal scale, identify predators, and estimate survival rates to gather information on conservation status. Furthermore, the importance of collecting high-quality ecological data, quantifying anthropogenic disturbances, and assessing the impact of climate change and anthropogenic pressures on breeding success should not be underestimated.

Although our study encountered constraints in collecting data on pivotal components of breeding behaviours

including some components of the mating system (such as re-mating or divorce across years), brood care behaviours, and the dynamics of long-term breeding and reproductive success (i.e. fledgling success), this study provides fundamental data on the breeding behaviour and fills up a gap in our knowledge of the breeding ecology and behavioural adaptation to high-altitude breeding environments in alpine shorebirds. The breeding biology of the Tibetan Sand Plover is mainly characterised by a late start of egg laying, a short breeding period and low breeding success. We hypothesise that the breeding success is largely influenced by the predation and disturbance of anthropogenic activities although we cannot exclude alternative explanations. We posit that the monogamy and bi-parental care of the individuals is an adaptation to harsh environmental conditions such as high altitude, cold ambient temperature and high nest loss. In addition, comparison of Tibetan Sand Plovers and their Arctic counterparts has revealed that behavioural differences exist even among species with similar ecological and life-history syndromes. Future research in this area may provide valuable insights into effective conservation strategies, and eventually will help us to understand how climate change differentially impacts shorebird conservation in different regions.

Data availability Data are available in the following Github repository: https://github.com/narhulan29/Tibetan_sand_plover_Journal_of_Ornithology.git

Declarations

Conflict of interest The authors have no conflict of interest to declare.

Ethical approval All aspects of the fieldwork complied with the Law of the People's Republic of China on the Protection of Wildlife, and were authorized by the Animal Welfare & Ethical Review Body (AWERB) at University of Bath. Birds were ringed and handled by trained people aiming to cause as little disturbance to birds as possible.

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