



Erratum. In the original publication of this article the last two paragraphs of the Introduction were missing from the PDF. The error was corrected on 9 January 2022.

Avian Behavior, Ecology, and Evolution

Nest predation risk influences the Varied Tit's life history strategy in response to temperature and precipitation

El riesgo de depredación en los nidos influye en la estrategia vital del Carbonero variado en respuesta a la temperatura y las precipitaciones

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ABSTRACT. Life history strategy is of great significance to the survival and reproduction of any individual because it determines individual fitness. Strategies are shaped by diverse factors: temperature, precipitation, and nest predation risks may be some of them. From a four-year study, we analyzed the role of temperature, precipitation, and nest predation risk in relation to change in the life history strategy of the Varied Tit (*Sittiparus varius*). Specifically, clutch size was negatively related to both ambient temperature and nest predation risk. The reproductive success rate was negatively related to both temperature and precipitation, but only when the predation risk was low. First-egg laying date was not significantly related to any recorded factors. These results help us better understand the evolution of life history and inform us regarding management decisions for wild population conservation.

RESUMEN. La estrategia de vida es de gran importancia para la supervivencia y la reproducción de cualquier individuo, ya que determina la eficiencia individual. Las estrategias están condicionadas por diversos factores: la temperatura, las precipitaciones y el riesgo de depredación de los nidos pueden ser algunos de ellos. A partir de un estudio de cuatro años, analizamos el papel de la temperatura, la precipitación y el riesgo de depredación de los nidos en relación con el cambio en la estrategia de vida del Carbonero variado (*Sittiparus varius*). Específicamente, el tamaño de la puesta se relacionó negativamente tanto con la temperatura ambiental como con el riesgo de depredación de los nidos. La tasa de éxito reproductivo se relacionó negativamente tanto con la temperatura como con las precipitaciones, pero sólo cuando el riesgo de depredación era bajo. La fecha de puesta del primer huevo no se relacionó significativamente con ningún factor registrado. Estos resultados nos ayudan a comprender mejor la evolución de historias de vida y nos informan sobre las decisiones de gestión para la conservación de las poblaciones silvestres.

Key Words: clutch size; first-egg laying date; nest predation; precipitation; reproductive success rate; temperature

INTRODUCTION

Animals exhibit extraordinarily diversified life history strategies (e.g., clutch size, offspring number; Simons and Martin 1990, Mainwaring and Hartley 2012). This is composed of a set of physiological, behavioral, and ecological characteristics, that vary at both the interspecific and intraspecific levels in accordance with selective pressures on individuals (Tuero et al. 2018). Given limiting resources, individuals also face trade-offs of resource allocation between current versus future reproduction and survival. This shapes patterns of covariation between life-history traits, resulting in a variation of slow-fast life-history gradient of virtually all taxa. The continuum of life-history strategies ranges from a combination of fast development, short life, and high reproduction rate, and a combination of slow development, long life, and low reproduction rate (Wolf et al. 2007, Nielsen et al. 2016, Dammhahn et al. 2018, Jablonszky et al. 2018). But how much of it can be predicted from environmental contexts remains highly controversial.

Species may adjust life history strategy in breeding behavior to changes in environmental characteristics, thereby offsetting potential negative effects. For instance, food availability affected clutch size and breeding investment of Horned Larks (*Eremophila alpestris*; DuRant et al. 2013). Dark-eyed Juncos (*Junco hyemalis*)

shifted to a “standpat” life history strategy (smaller clutch size, longer life span) as food resources became more restricted after elevation increase (Tieleman 2009). When spring was extremely cold or warm, Eurasian Tree Sparrows (*Passer montanus*) delayed laying date to reduce temperature regulation cost (Dolenec et al. 2011). Based on these known behaviors, we predicted that when ambient temperature fluctuates, birds may change their life history strategies. When temperature increases, breeding individuals would compete to occupy the territory earlier to ensure favorable reproduction condition.

Another aspect of environmental fluctuation is precipitation. Tuero et al. (2018) indicated that precipitation level had a significant negative impact on nestling growth patterns of Fork-tailed Flycatcher (*Tyrannus savana*) and Scissor-tailed Flycatcher (*Tyrannus forficatus*). High frequency of precipitation events reduced the reproductive success rate of Dickcissels (*Spiza americana*; Rosamond et al. 2020). However, most studies investigating the effect of temperature and precipitation have mainly concentrated on extreme events and not accounted for year-to-year changes in temperature and precipitation. Even fewer empirical studies have quantified relationships between changing weather and resident songbirds' life history strategy. Against this backdrop, identifying and quantifying the effect of

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temperature and precipitation on life history strategy are vital to conservation, particularly for locally distributed species (Norris 2004, Thomas et al. 2004).

Nest predation is one of the main causes of nest failure in most birds. It also plays an important role in the evolution of life history (Martin 1995). Ricklefs (1969) estimated that predation accounted for 55% of egg losses and 66% of nestling losses in six passerine species. Nest predation hypothesis predicts that an individual will reduce its reproductive efforts when higher risk of nest predation reduces the value of current reproduction (Lack 1948, Slagsvold 1982). However, empirical results show differential effects. In a 32-year study, mean clutch size of Great Tit (*Parus major*) was reduced by about one egg in the year following peak nest predation (Julliard et al. 1997), whereas in a four-year study across 12 passerines, parents did not change their clutch size when the risk of nest predation was lower (Fontaine and Martin 2006). This might be because these long-term studies failed to consider the potential impact of accompanying climatic factors; therefore, they did not show a comprehensive picture of nest predation risk on species life history strategy. Accordingly, we questioned whether the effects of temperature and precipitation on life history strategies would change under the influence of nest predation risk.

The Varied Tit (*Sittiparus varius*) is a small forest, secondary cave-nest passerine endemic to East Asia. Studies have shown that predation by natural enemies is the main cause of reproduction failure (Yamaguchi 2005). Our aim here was to explore how temperature, precipitation, and nest predation risk were associated with the life history strategy in Varied Tits. We used first-egg laying date, clutch size, and reproductive success to measure the influencing factors. We predicted that individuals might exhibit a large clutch size and high breeding success at high temperature and low precipitation because food resources are abundant in such favorable climate conditions. We also predicted that these impacts would differ under different predation risk, because of individuals' trade-off between current reproduction and future ones.

METHODS

Study areas and species

This study was carried out annually from early March through mid-July from 2017 to 2020 in Liaoning Xianrendong National Nature Reserve (122°53'24" E–123°03'30" E, 39°54'00" N–40°03'00" N), Zhuanghe, Liaoning, China. Adjacent to the Yellow Sea, it is in a warm, temperate climate zone with humid monsoons. A variety of secondary cave-nest birds are distributed in the protected zone, including Cinereous Tits (*Parus cinereus*), Yellow-rumped Flycatchers (*Ficedula zanthopygia*), Daurian Redstarts (*Phoenicurus auroreus*), Marsh Tits (*Poecile palustris*), Eurasian Nuthatches (*Sitta europaea*), and Varied Tits. Snakes and chipmunks are common nest predators.

Field methods

Artificial nest boxes were used to attract breeding pairs and gather reproduction data. Artificial nest boxes had been installed 11 years before this study began, and were supplemented or replaced every year. All nest boxes were approximately 16 cm × 14 cm × 34 cm (length × width × height), with an entrance hole of 5 cm

or 3.5 cm in diameter. Most natural nests are 2–4 m away from the ground, and the artificial nest boxes were also placed at a similar height. All nest boxes had a sliding top through which we monitored breeding events. Details on nest boxes and their distribution can be found in Jiang (2022). The study area was divided into four parts (Fig. 1). The straight-line distance of each sampling point was at least 3 km, and there were obvious physical features in topography separations (such as artificial facilities, mountains, rivers, valleys, etc.). In addition, the nest predation risk in each sample area was estimated as the number of preyed nest boxes/total number of nest boxes occupied. Each sample area was identified as either a high nest predation risk (≥ 0.5) area or low nest predation risk (< 0.5) area according to the calculated nest predation risk rate.

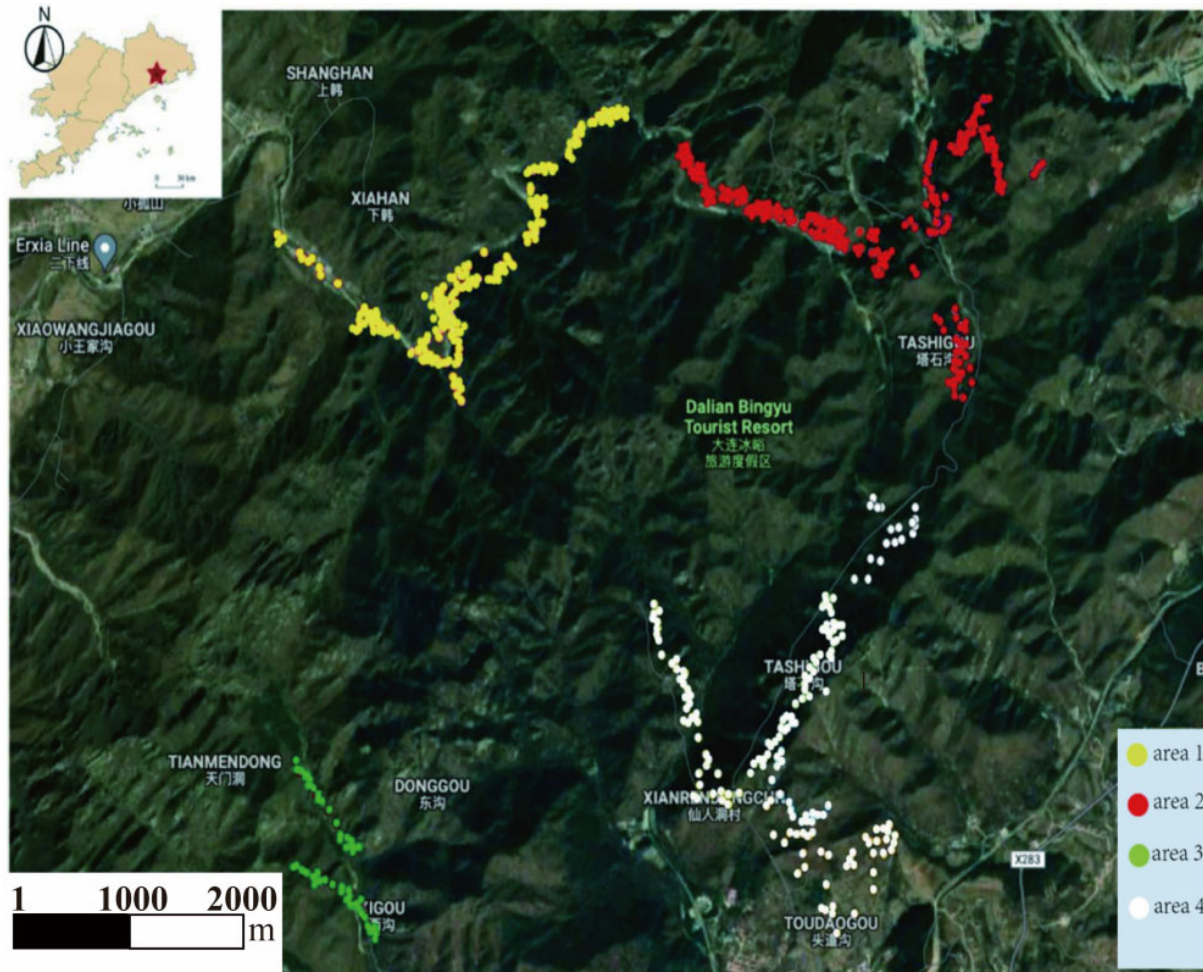
Adults were captured with mist nets in March each year. For those that had never been caught before, they were taken from the nest when their chicks were 6–12 days old. All birds caught were marked with a numbered aluminum band and a unique combination of colored leg bands, and had their physical parameters measured. Individuals were identified through the colored rings in the following experiments. Contents of nest boxes were checked at least once every four days from March to July to identify which ones were used. Occupied boxes were inspected more frequently, about every other day, until the chicks flew out. During this period, the clutch size and fledgling number were recorded. The first-egg laying date was then back-calculated from the number of eggs assuming that one egg was laid every day. The reproductive success rate was calculated as the number of fledglings/clutch size.

We photographed failed nests and noted possible reasons. Nests destroyed by chipmunks (*Tamias sibiricus*) were easily distinguished by the remaining egg-shells. Nests preyed by snakes were usually empty and the nest cup was pressed down. We used the predation situation in year $i-1$ to represent the potential nest predation risk of this sampling point in year i . Daily average temperature and precipitation data provided by the Liaoning Xianrendong National Nature Reserve were used.

Statistical analyses

First-egg laying dates were noted in Julian date, where 1 April = 91. We took into account the autocorrelation between the first-egg laying data and the average temperature and average precipitation in the two months before the first-egg laying data. Average temperature and precipitation of April and May were used to test the effects of temperature and precipitation and predation risk on first-egg laying date. To analyze the impact of climate on clutch size and reproductive success rate, we used the average temperature and precipitation of the first two months before the first-egg laying date of the focal nest. The effects of temperature and precipitation and nest predation risk on the life history strategy (first-egg laying data, clutch size, reproductive success) were tested with generalized linear mixed models (mean precipitation, mean temperature, and nest predation risk as the covariates, year and site as random effect variables). We also considered the interaction of climate and nest predation risk. All statistical tests were performed with SPSS 19.0. The level of significance was set at 0.05. Data are reported as mean \pm SE.

Fig. 1. Area of reproductive parameters sample collection of the Varied Tits (*Sittiparus varius*) from Liaoning Xianrendong National Nature Reserve, China. Each color represents an area. The straight-line distance of each sampling area was at least 3 km, or there were obvious geographical separations (such as artificial facilities, mountains, rivers, valleys, etc.).



RESULTS

Across the study, 451, 434, 410, and 391 nest boxes were investigated in 2017, 2018, 2019, and 2020, respectively. Each year those occupied (fewer than half) were mainly by Varied Tits and Cinereous Tits, whereas few were occupied by Marsh Tits and Daurian Redstarts.

First-egg laying dates of Varied Tits were between 18 April and 17 May, with mean on 24 April ($SD = 13.11$). Varied Tits' clutches contained six to eight eggs with mean clutch size being 6.9 ± 1.07 . The average reproductive success rate in the past four years was 0.38 ± 0.42 .

Clutch size reduced with increasing temperature and nest predation risk, but did not seem to change with precipitation (Table 1). The relationships between temperature and precipitation and reproductive success rate were both affected by predation risk (Table 1). Separate analyses on high and low predation risks showed that the reproductive success rate was

negatively related with ambient temperature when the predation risk was low ($\chi^2 = 4.965$, $\beta = -0.034$, $SE = 0.0154$, $P = 0.026$; Fig. 2), but no significant relationship was found at high nest predation risk ($\chi^2 = 1.414$, $\beta = -0.033$, $SE = 0.0277$, $P = 0.234$). The reproductive success rate was only negatively related with precipitation when nest predation risk was low ($\chi^2 = 88.830$, $\beta = -0.015$, $SE = 0.0015$, $P = 0.039$; Fig. 3), and also no significant relationship was found at high nest predation risk ($\chi^2 = 0.014$, $\beta = 0.004$, $SE = 0.0302$, $P = 0.907$). None of these factors seemed to influence the first-egg laying date of Varied Tits (Table 1).

DISCUSSION

We focused on how predation risk interacted with temperature and precipitation, and how this affected Varied Tits' breeding strategy. The results showed that the reproductive success rate decreased with increasing temperature when nest predation risk was relatively low. Warmer temperature increased the odor of the nest and usually increased the nest predation rate for the whole

Table 1. Relationships between the life history strategy (first-egg laying date, clutch size, and reproductive success rate) and temperature, precipitation, and nest predation risk of the Varied Tit. The model for first egg laying date had the statistics: $\chi^2 = 18.127$, BIC = 1425.089, $P < 0.01$; the model for clutch size had the statistics: $\chi^2 = 34.722$, BIC = 511.639, $P < 0.01$; and the model for reproductive success rate had the statistics: $\chi^2 = 20.262$, BIC = 224.350, $P < 0.01$.

	χ^2	SE	β	P
First egg laying date (n = 181)				
(Intercept)	0.138	529.5497	-196.905	0.710
Temperature	0.307	37.2946	20.672	0.579
Precipitation	0.06	3.6798	-0.898	0.807
Nest predation	0.495	644.6200	453.55	0.482
Temperature*Precipitation	0.202	0.2475	0.111	0.653
Temperature*Nest predation	0.503	44.1814	-31.343	0.478
Precipitation*Nest predation	0.296	0.9771	-0.531	0.587
Clutch size (n = 181)				
(Intercept)	197.306	0.5910	8.302	0.000**
Temperature	7.352	0.1077	-0.292	0.007**
Precipitation	2.697	0.0878	0.144	0.101*
Nest predation	5.350	0.9540	-2.207	0.021*
Temperature*Precipitation	1.440	0.0069	-0.008	0.230
Temperature*Nest predation	3.348	0.1954	0.358	0.067
Precipitation*Nest predation	0.005	0.1819	0.013	0.942
Reproductive success rate (n = 181)				
(Intercept)	7.228	0.2673	0.719	0.007**
Temperature	0.216	0.0487	0.023	0.642
Precipitation	8.746	0.0397	-0.117	0.003**
Nest predation	0.00	0.4314	0.004	0.992
Temperature*Precipitation	1.415	0.0031	0.004	0.234
Temperature*Nest predation	4.423	0.0884	-0.186	0.035*
Precipitation*Nest predation	9.471	0.0822	0.253	0.002**

Note: β is the regression coefficient, * means $P < 0.05$, ** means $P < 0.01$.

brood by attracting predators (Crick 2004). In addition, as temperature increased, the dominant predator of the study site (snakes) woke up earlier from hibernation and bred earlier (Brown and Shine 2006), thus reducing reproductive success. Breeding birds may also actively reduce feeding rates to reduce potential nest predation risk (Skutch 1949), which may negatively impact chicks, reducing reproductive success rate.

Reproductive success rate also decreased with increasing precipitation when the predation risk was relatively low. This pattern could partially be explained by an insufficient food supply and excessive energy consumption caused by temperature regulation, because high precipitation increased the costs of thermo-regulation, which might consequently result in lower breeding success (Slobodník et al. 2013). Other studies also reported consistent results (e.g., Méro et al. 2014, Coppes et al. 2021), showing that precipitation may relate to the reproductive effectiveness of birds. At times, when nest predation risk was high, both temperature and precipitation were no longer associated with reproductive success rate. This might be because, when the nest predation risk on the breeding sites was high, the regulating effect of temperature and precipitation on the density of predator was reduced, and therefore the effect of temperature and precipitation on the reproductive success rate was weakened (Young et al. 2015).

Fig. 2. The impact of temperature on reproductive success rate under two levels of nest predation risk. The reproductive success rate decreased with increased temperature only when the nest predation risk was low (n = 117, t = -2.203, $P = 0.026$, $r^2 = 0.041$). The solid line is the linear regression line for the low predation nests.

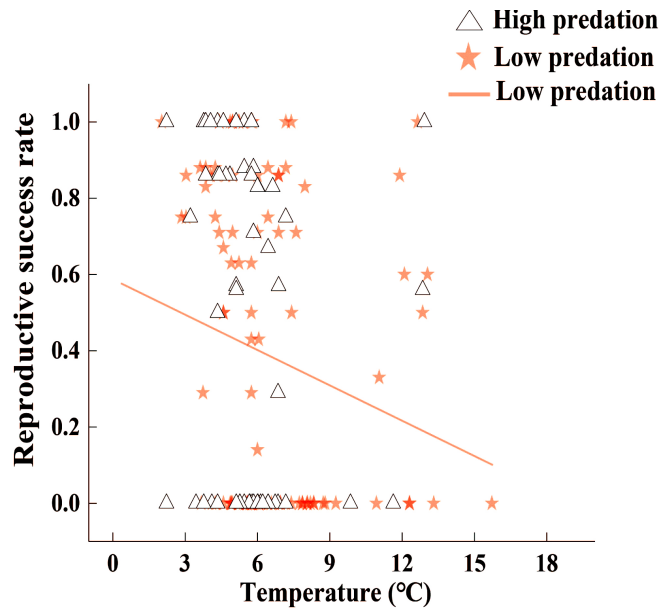
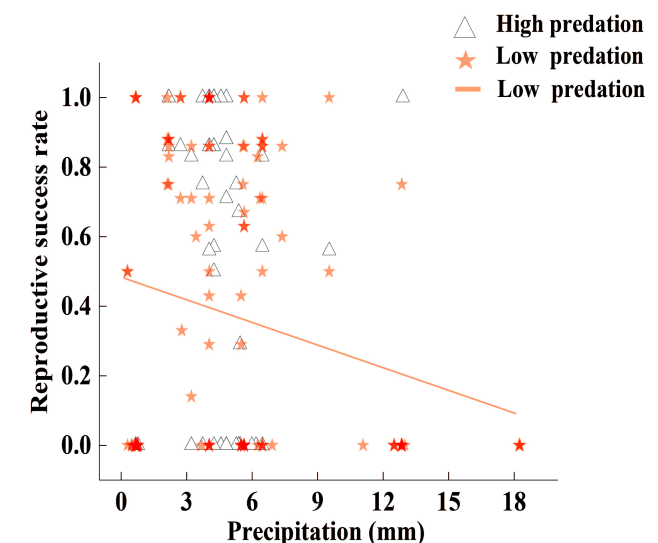


Fig. 3. The impact of precipitation on reproductive success rate under two levels of nest predation. The reproductive success rate was negatively related with precipitation when the nest predation risk was low (n = 112, t = -1.7733, $P = 0.039$, $r^2 = 0.195$). The solid line is the linear regression line for the low predation nests.



The clutch size of Varied Tit was negatively related with ambient temperature. A warmer temperature could provide a more favorable ambient environment for females that might cause them to change their life history strategies, e.g., an increase in clutch size. However, females might also make a trade-off between the number and post-hatch quality of offspring, because large clutch size not only consumes more hatching energy, but also is more prone to changes in offspring phenotype because of uneven incubation temperatures (Hope et al. 2021). A warmer temperature might also cause faster caterpillar development, and birds had to speed up to keep up with their food resources. One way of doing this was by laying fewer eggs and shortening the duration of incubation (Matthysen et al. 2011). Conspecific and heterospecific density might also affect this relationship (e.g., Møller et al. 2020), because reduction in clutch size could potentially improve reproductive adjustment with lower trophic levels (Bleu et al. 2017). There were several explanations for this observed negative relation between clutch size and temperature that imply more complex effects of climate warming on bird reproduction.

Our results indicated that the clutch size was negatively related with nest predation risk. Life-history theory predicts that an individual should reduce its reproductive efforts by laying a smaller clutch size when high risk of nest predation reduces the value of current reproduction (Stearns 1992). If parental survival declines with clutch size, a reduction in clutch size will improve parental survival prospects and future reproduction, thereby spreading the risk of nest predation between broods and ultimately increasing lifetime reproductive success (Slagsvold 1984, Martin 1995). Apart from this, smaller broods may shorten the breeding period when the nest is susceptible to nest predators and reduce the number of nest visits that could attract the attention of predators (Skutch 1949, Martin et al. 2000). It can be seen from these results that nest predation risk can exert strong selection on the evolution of life-history strategies (Ibáñez-Álamo et al. 2015).

However, we did not find significant relationship between temperature or precipitation and first-egg laying date, or between nest predation risk and first-egg laying date in Varied Tits. The current research on the relationship between the first-egg laying date and these two factors is still controversial. Although most research considered the first-egg laying date as the event that needs to be related to the time of maximum food availability (Tomás 2015), one possible explanation for this result is that slight precipitation and temperature fluctuations do not change food availability severely enough to affect birds' life history strategy. But to a certain extent, this shows that Varied Tits did not respond to changes in climate and nest predation risk by advanced or delayed first-egg laying date.

CONCLUSIONS

In conclusion, our finding reveals the impact of temperature, precipitation, and nest predation risk on life history strategy and shows that these three factors together affect the life history strategy of Varied Tits. The results contribute to our understanding of the evolution of life history. It confirms that we must pay attention to the potential negative impacts of climate fluctuations on wild populations. Conservation measures could be thus proposed to a nature reserve: we can speculate that the

impact of climate fluctuation is far greater than just increasing temperatures and rainfall patterns and protecting the nestlings from the predators can mitigate the negative impacts of climate fluctuation on species of conservation concern.

Author Contributions:

YJ and DW conceived the ideas and designed methodology; FS and XM collected the data; YJ and FS analyzed the data; YJ and FS led the writing of the manuscript. YJ and FS contributed equally to this article. All authors contributed critically to the drafts and gave final approval for publication.

Acknowledgments:

This project was supported by the National Natural Science Foundation of China (No. 31872231 to DW, No. 32000316 to YJ). We really appreciate the support of Liaoning Xianrendong National Nature Reserve. We want to thank all data contributors for their help covering a period from 2017 to 2020 (2017–2018, Ruiqiang MA and Chengan LI; 2019–2020, Pengyu LI and Luming BAI).

Data Availability:

The data that supports the findings of this study are available in the supplementary material of this article.

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Appendix 1. Data used in this article

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