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Dispersal patterns of Reeves's pheasant based on genetic and behavioral evidence

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Abstract

Dispersal is an important life history trait that plays a crucial role in avoiding inbreeding. Uncovering the dispersal pattern of a threatened species facilitates conservation efforts. Most species of Galliformes are forest-dwelling terrestrial birds with a weak dispersal ability and high conservation priorities. However, little is known about the dispersal behavior and dispersal pattern of Galliformes species such as Reeves's pheasant *Syrmaticus reevesii*, a globally vulnerable species endemic to China. Here, we integrated behavioral and genetic analyses to investigate the dispersal pattern of Reeves's pheasant. Our results revealed that both females and males would disperse, although the overall dispersal pattern was more likely to be male-biased. Reeves's pheasant population had a low level of genetic diversity and a mild level of inbreeding. Speculation low genetic diversity was resulted from fragmented habitat, and male-biased dispersal may reduce the opportunity of inbreeding. Our research indicated that sex-biased dispersal patterns may be a behavioral mechanism adopted by wildlife to avoid inbreeding in a fragmented habitat.

Key words: animal behavior, dispersal, Galliformes, genetic diversity, satellite tracking.

Dispersal generally refers to a unidirectional move of animal individuals from one place to another. It is a common behavior of almost all organisms and gradually evolves in animals under multiple selection pressures (Howard 1960; Greenwood 1980; Greenwood and Harvey 1982; Handley and Perrin 2007). Dispersal can expand the distribution area of animal populations (Diniz et al. 2019), affect the survival rate (Souchay et al. 2018) and reproductive success rate of individuals, and promote gene flow among different populations (Rózsa et al. 2016; Ha et al. 2020). Thus, it plays an important role in population structure, genetic diversity, population dynamics, and species evolution (Gajdárová et al. 2021). It is a key ecological and evolutionary process that allows individuals, populations, and species to cope with and adapt to the changing environment, and controls the spatial patterns of biological communities and ecosystems (Souchay et al. 2018). In addition, it can also increase the risk of diseases spreading and being preyed upon by natural enemies (Russo et al. 2019). Therefore, uncovering the dispersal patterns of species is of great significance to species conservation and biodiversity (Clark et al. 2004; Marschalek 2020; Gajdárová et al. 2021).

Due to an imbalance between the benefits and costs of dispersal for individuals of different sexes, dispersal distance and proportion of individuals dispersing often differ between males and females (Zheng 2015). This phenomenon is called sex-biased dispersal (Wolff and Plissner 1998). Sex-biased dispersal patterns have an important impact on the genetic structure and dynamics of species populations, such as avoiding inbreeding (Hu et al. 2017). Therefore, long-term field research on the sex-biased dispersal behavior of animals has attracted increasing attention (Greenwood 1980; Clarke et al. 1997).

With the rapid development of animal tracking and next-generation sequencing technologies, it has become possible for researchers to systematically study animal dispersal behavior (Handley and Perrin 2007; Clobert et al. 2012). There are a variety of methods for studying animal dispersal, including direct observational methods (e.g., ringing, radiotelemetry, and satellite tracking) and indirect molecular biology methods (e.g., Hu et al. 2017; Li et al. 2019). Among them, satellite tracking provides the most accurate location information and excludes the defects of other methods, such as low recovery rate of ringing, small radiotelemetry range, and large radiotelemetry error (Zheng 2015). Thus, satellite tracking is a better direct method for studying the behavior of wildlife, and has been widely used in studies on animal behaviors in recent years (Foley and Sillero-Zubiri 2020), despite its relatively high costs. Indirect molecular biology methods are based on population genetics, and can make up the defects of direct observation methods in terms of sample size (Zheng 2015). In addition, these methods are of great

significance in studying the dispersal behavior of species that are difficult to directly observe (Wen et al. 2022). For example, researchers have found evidence of female-biased natal dispersal in wild giant pandas *Ailuropoda melanoleuca* based on DNA extracted from animal feces and population genetic analysis (Hu et al. 2017). Direct observation methods always provide dispersal evidence of limited numbers of individuals, but indirect methods such as the population genetic method can provide credible dispersal evidence of populations, thus integrating genetic and behavioral evidence can help uncover the dispersal patterns of wildlife (Hu et al. 2017).

With the gradual accumulation of data, researchers have summarized the general dispersal patterns of birds and found that female-biased dispersal patterns are more common than male-biased patterns (Greenwood 1980; Clarke et al. 1997). However, only 6.58% of Galliformes species have been investigated in previous studies (see Supplementary Materials Part A for details). Thus, the research on Galliformes is still insufficient. Furthermore, an increasing number of studies have recently found male-biased dispersal patterns of several Galliformes species such as Elliot's Pheasant (*Syrmaticus ellioti*, Zheng 2015) and grey partridge (*Perdix perdix*, Šálek and Marhoul 2008), which is inconsistent with the results of previous studies that the dispersal patterns of Galliformes are female-biased (Clarke et al. 1997), and presents new challenges for researchers and conservation workers. It remains an open question whether Galliformes species have a male-biased or female-biased dispersal pattern.

Reeves's pheasant *Syrmaticus reevesii* is a Galliformes species endemic to China (Zheng 2017; Figure 1A). It is considered as a vulnerable species (IUCN 2018) and is listed as a national first-class protected animal in China. Reeves's pheasant was once widely distributed in the temperate and subtropical forests in central and southwestern China in the past (Cheng et al. 1978). With the increasing intensity of human activities, the habitat of Reeves's pheasant has become increasingly fragmented, and the previously continuous population of Reeves's pheasant has been split into two isolated geographic subpopulations (Wang et al. 2009) that are also patchy and scattered (Zhou et al. 2014; Tian et al. 2020). Driven by interests (Cheng et al. 1978), illegal hunting and other activities have led to a sharp decline in the number of populations (Zhou et al. 2017; Tian et al. 2022), and some isolated populations in patchy landscapes are facing the risk of extinction or have already gone extinct (Zheng 2015). Recent statistics have shown that the wild population of Reeves's pheasant was about 23,000 in 2009 (Tian et al. 2021). However, only 2,500–9,999 adult individuals capable of reproduction were estimated to remain in 2018 (IUCN 2018). Because of the drastic decline in its population size, Reeves's pheasant is listed in the Appendix of the *Convention on International Trade in Endangered Species of Wild Fauna and Flora* (CITES 2019).

As a typical forest-dwelling bird, Reeves's pheasant is highly vigilant. Despite substantial challenges when locating and observing this animal, detailed behavioral observations based on radiotelemetry technology have illuminated the basic movement ecology of this species (Zheng 2015). Reeve's Pheasant has a weak dispersal ability and high fidelity within its home range (Zheng 2015). During the breeding season (March–July), males occupy a certain area, while females visit multiple male territory owners to choose mates (Zheng 2015). Reeves's pheasant is a precocial bird, which makes it difficult to track young individuals. As a result, its dispersal pattern remains largely unclear. Therefore, this study aimed to identify the dispersal patterns of wild Reeves's pheasant and discuss the dispersal patterns and conservation strategy of Galliformes based on behavioral and genetic analyses.

Material and Methods

Study area and data collection

The study sites were located in the Pingjingguan Village, Guangshui City, Hubei Province (113°54′09″–113°55′21″E, 31°51′03″–31°52′40″N; Figure 1B). These sites were situated in the Dabie Mountains, one of the main distribution areas of Reeves's pheasant (Tian et al. 2022).

From 2019 to 2021, we captured a total of 87 (45 males, 42 females) adult Reeves's pheasants, collected blood samples
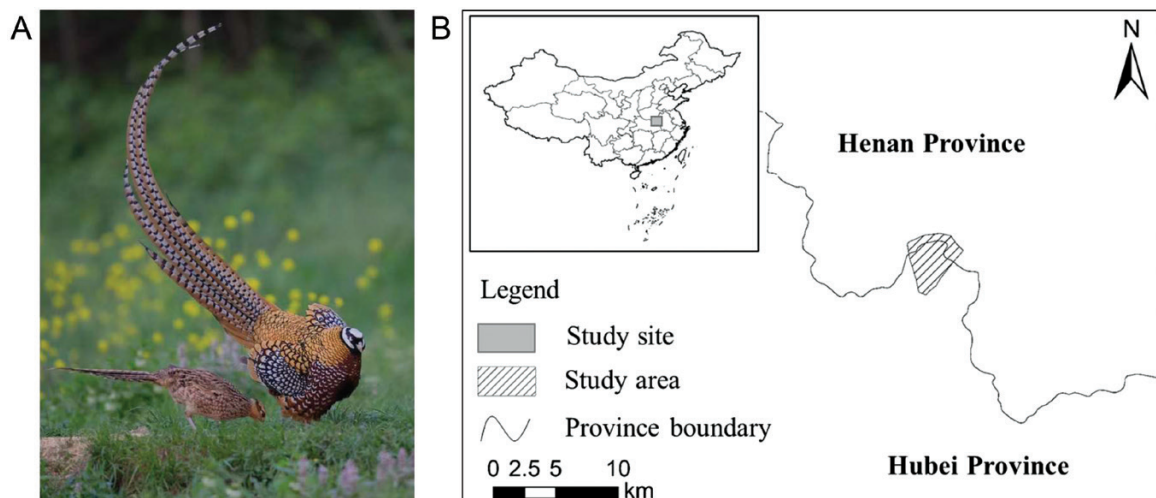

Figure 1 Female (left) and male (right) of the Reeves's pheasant A) (Taken by Peng Zhang), and location of the study area in China B). The upper left corner of Figure B) shows the geographical location of the study site (gray area) in China, and the bar-shaped area represents the study area in Hubei province. The black lines represent the province boundary. The source of the map was from https://www.webmap.cn.

from each individual, and recorded the longitude and latitude of each location in which each individual was recorded in detail. In addition, we tracked 42 (17 males, 25 females) of them with satellite trackers (LEGO, piggyback trackers, Druid Technology Co., Ltd., China. Supplementary Table S3). The tracker weighs less than 30 g, which is less than 3% of the body weight of an adult Reeves's pheasant individual. The frequency of the data recorded by the tracker was regulated according to the power. The tracking time was concentrated from March to July, which is the breeding season of Reeves's pheasant.

Molecular experiments and genetic data analyses

We carried out molecular experiments on blood samples from the 87 Reeves's pheasants captured in Pingjingguan (Supplementary Table S3). DNA was extracted from the blood samples using a Blood and Tissue Extraction Kit (Qiagen, Hilden, Germany) following the manufacturer's instructions. The microsatellite molecular markers (n = 9, Supplementary Table S4) and polymerase chain reaction (PCR) amplification conditions were the same as those used by Wang et al. (2009). We performed two amplification replicates of the DNA extracts from each individual to ensure genotype accuracy. If the amplification of the sample failed or the results of the two amplifications did not match, we conducted three amplifications again. The PCR products were separated according to size using a 3730XL Genetic Analyzer (Applied Biosystems, Vernon Hills, IL, USA) and were analyzed using GeneMapper 4.0.

We used the CERVUS 3.0.7 software (Kalinowski et al. 2007) to calculate the number of alleles (K), observed heterozygosity (H_O), expected heterozygosity (H_E), and polymorphism information content (PIC) of each microsatellite locus. Genepop 4.7.5 software was used to calculate the inbreeding coefficient (F_{IS}) of Reeves's pheasant and Hardy–Weinberg equilibrium and Gene-Linkage disequilibrium tests were conducted for each locus. The significance levels were corrected using the sequential Bonferroni procedure (Rice 1989). The loci that deviated from the Hardy–Weinberg equilibrium were removed in the following analysis.

Relatedness, paternity assignment, and inbreeding

The relatedness (R) was calculated using GenAlEx 6.5 based on the allele frequency of all the individuals (Lynch andRitland 1999). R values ranged from –1 to 1. Theoretically, the R values of first-class relatives (e.g., parent-offspring, full-sibs), second-class relatives (e.g., grandparent-grandchild, half-sibs), and third-class relatives (e.g., first-cousin) were 0.5, 0.25, and 0.125, respectively (Hu et al. 2017).

A maximum likelihood-based paternity assignment was conducted using the CERVUS 3.0.7 software (Kalinowski et al. 2007). All females and males identified in this study were taken as candidate mothers and fathers. The proportion of the candidate fathers sampled was set as 0.9, and the proportion of loci mistyped was set as 0.01 to tolerate genotyping errors. Paternity was assigned at both strict (95%) and relaxed (80%) confidence levels (Hu et al. 2017). After determining the parents of an individual, mating between individuals with $0.125 \leq R < 0.25$ was defined as mild inbreeding, with $0.25 \leq R < 0.5$ was defined as moderate inbreeding, and with $R \geq 0.5$ was defined as high inbreeding (Hansson et al. 2007).

Detection of dispersal patterns

To detect the dispersal pattern of Reeves's pheasant, we used three different methods, two of which are based on genetic data (spatial genetic autocorrelation analysis based on the genetic distance and spatial R distribution analysis based on the allele frequency) (Hu et al. 2017; Wen et al. 2022) and one of which is based on behavioral data (the ratio of the home range overlap) (Xu et al. 2009).

In the spatial genetic autocorrelation analysis, the data for 56 individuals (30 males and 26 females) collected in Pingjingguan in 2019–2020 were used. Based on the active location data for the individuals collected in Pingjingguan (9 males and 12 females 2020; 11 males and 16 females 2021; Supplementary Table S3), the home range was calculated using the 95% fixed Kernel method in ArcView 3.3, and least squares cross validation was used as the smoothing factor (Xu et al. 2009). We used the computational geometry function in ArcGIS 10.2 to calculate the mobility of 42 tracked individuals—that is, the distance between the centroid of the home range and the outermost location of the home range (Xu et al. 2009), which was about 400 m (mean = 403 m, unpublished). Because the accuracy of the spatial genetic autocorrelation analysis depends on the distance class size chosen and the associated number of samples per distance class (Peakall et al. 2003), we used two different strategies based on the use of different distance sizes to explore the difference in males and females in the spatial genetic autocorrelation. First, 400 m was used as the distance class size and four classes of autocorrelation analyses were performed using GenAlEx 6.5 (Peakall and Smouse 2012): all individuals, just males, just females, and female–male pairs, with at least 35 pairwise comparisons in each distance class. Second, we used multiple different distance class sizes (four increments of 400 m) to perform autocorrelation analyses of the four classes separately. Regarding the detection of the spatial autocorrelation, the null (H_0) and alternative hypotheses (H_1) were as follows: H_0 = a random distribution of genotypes in space (r = 0), whereas H_1 = nonrandom distribution of genotypes in space ($r <$ or > 0, Peakall et al. 2003). We tested the hypotheses via random permutation (1,000 repeats), which generated the distribution of the permuted r values under the assumption of no spatial structure via random shuffling of all of the individuals among the geographic locations. The 95% error bar about r within each distance class was generated via bootstrapping (1,000 repeats). Significant autocorrelation was concluded only when the observed r value fell outside the permutation 95% confidence intervals around the null hypothesis of zero, and the bootstrap 95% error bar about r did not intercept the x-axis at r = 0. The difference in the r values of the males and females was determined by comparing their 95% error bars (Hu et al. 2017; Wen et al. 2022). Because spatial autocorrelation is only likely to occur in the first few distance classes (e.g., Peakall et al. 2003; Banks and Peakall 2012; Hu et al. 2017; Wen et al. 2022), so we only reported the r value for the first distance class (Hu et al. 2017).

In the spatial relatedness distribution analysis, we analyzed the spatial distribution of R among all of the individuals, just females, just males, and female–male pairs within the different distance classes. The 95% confidence intervals of R for the different distance classes were obtained through 1,000 permutations implemented in SPAGeDi 1.5 (Hardy and Vekemans 2002).

In the analysis of the home range overlap ratio, we investigated the proportions and home range overlap ratio (I) of dyads with $R \geq 0.25$ for the different distance classes among the males, females, and male–female pairs, to account for the difference in the spatial genetic structure of the sexes. The Crosstabs test tool in SPSS 22.0 was used to test the differences in the proportion of dyads with $R \geq 0.25$ among the males, females, and male–female pairs. The formula for calculating the index I is

$$I = \frac{200S_{ab}}{(S_a + S_b)},$$

where I is the overlap ratio of the home range with values of 0 to 1. When $I = 0$, the home range of the two individuals does not overlap; and when $I = 1$, the home range of the two individuals completely overlaps. Sab is the area of the home range jointly occupied by individual A and individual B; Sa is the area of the home range of individual A; and Sb is the area of the home range of individual B.

One-way ANOVA analysis was conducted in SPSS 22.0 to analyze the differences in the overlapping proportions of I among different paired classes, the level of statistical significance is 0.05.

The mean values reported in this paper are expressed as the mean ± standard deviation.

Results

Microsatellite locus polymorphism of Reeves's pheasant

The K values at the nine microsatellite loci for Reeves's pheasant were 2–7 (4.222 ± 1.856), H_O was 0.475 ± 0.219, H_E was 0.487 ± 0.237, and PIC was 0.437 ± 0.223 (Table 1), and F_{IS} was 0.025, which indicated that a medium level of genetic diversity and no inbreeding were observed in Reeves's pheasant population. After correcting significance levels with the sequential Bonferroni procedure, there was no significant gene-linkage disequilibrium at any of the loci, but the SR19 locus deviated from the Hardy–Weinberg equilibrium.

Table 1 Polymorphism parameters of microsatellite locus of Reeves's pheasant

Locus	K	HO	HE	PIC
SR01	5	0.517	0.525	0.479
SR03	3	0.517	0.513	0.391
SR08	2	0.195	0.196	0.176
SR11	6	0.575	0.563	0.504
SR13	3	0.414	0.404	0.365
SR17	4	0.632	0.642	0.573
SR18	2	0.057	0.056	0.054
SR19*	7	0.701	0.816	0.788
SR20	6	0.667	0.670	0.607
Mean ± SD	4.222 ± 1.856	0.475 ± 0.219	0.487 ± 0.237	0.437 ± 0.223

K, number of alleles; H_O, observed heterozygosity; H_E, expected heterozygosity; PIC, polymorphism information content.
*Indicates that the locus deviated from the Hardy–Weinberg equilibrium.

Inbreeding of Reeves's pheasant

Of the 3741 pairs from the 87 Reeves's pheasants, the first-class relatives, second-class relatives, and third-class relatives accounted for 3.88% ($n = 145$), 11.31% ($n = 423$), and 10.16% ($n = 380$) of cases, respectively. Of the 1892 male–female pairs, the first-class relatives, second-class relatives, and third-class relatives accounted for 3.96% ($n = 75$), 11.52% ($n = 218$), and 10.84% ($n = 205$) of cases, respectively. A total of 3 mating pairs were identified from the 87 individuals. Among them, 1 pair had mild inbreeding ($0.125 \leq R = 0.227 < 0.25$), and the other 2 pairs had no inbreeding (Table 2). These results indicated that Reeves's pheasants had a low level of inbreeding.

Dispersal patterns of Reeves's pheasant

The results of the spatial genetic autocorrelation analysis revealed that male Reeves's pheasants had a significant negative autocorrelation in the first distance class (0–400 m, $r = -0.067$; Figure 2B), but there was no significant autocorrelation in any distance class among all individuals, females, and male–female pairs (Figure 2A, C, and D).

Analysis of different distance classes revealed that male pairs only exhibited significant negative autocorrelation in the first distance class (Figure 3B), while the other three types of pairings (all individuals, females, and male–female pairs) did not exhibit significant spatial autocorrelation in any of the distance classes (Figure 3A, C, and D). The spatial autocorrelation coefficient r of male pairs was still smaller than that of females at the dispersal distance of 0–1200 m.

The relatedness analyses revealed a similar sex-biased difference in the spatial genetic organization (Supplementary Figure S1). Further examination of the number of dyads with $R \geq 0.25$ also revealed that in the first distance class (0–400 m), the proportion of female dyads was higher than that of male dyads and female–male dyads (Figure 4), but there was no significant difference (Crosstabs test: $\chi^2 = 0.732$, $P = 0.694$). The I of male pairs and male–female pairs was obviously smaller than that of female pairs (males: $n = 19$, $I = 0.085 \pm 0.221$; females: $n = 28$, $I = 0.215 \pm 0.320$; male–female pairs: $n = 54$, $I = 0.137 \pm 0.217$), but there was also no significant difference (one-way ANOVA: $F = 1.665$, $df = 2$, $P = 0.194$).

These results suggested that both females and males dispersed. The overall dispersal pattern of Reeves's pheasant was more likely to be male-biased, as the proportion of male pairs with $R \geq 0.25$ increased with increasing distance (Figure 4). In particular, the proportion of male pairs and male–female pairs with $R \geq 0.25$ was lower than that of female pairs at close distances, and the overlap ratio of the home range was also notably lower.

Table 2 Parent pairs and their relatedness for the 87 individual Reeves's pheasants

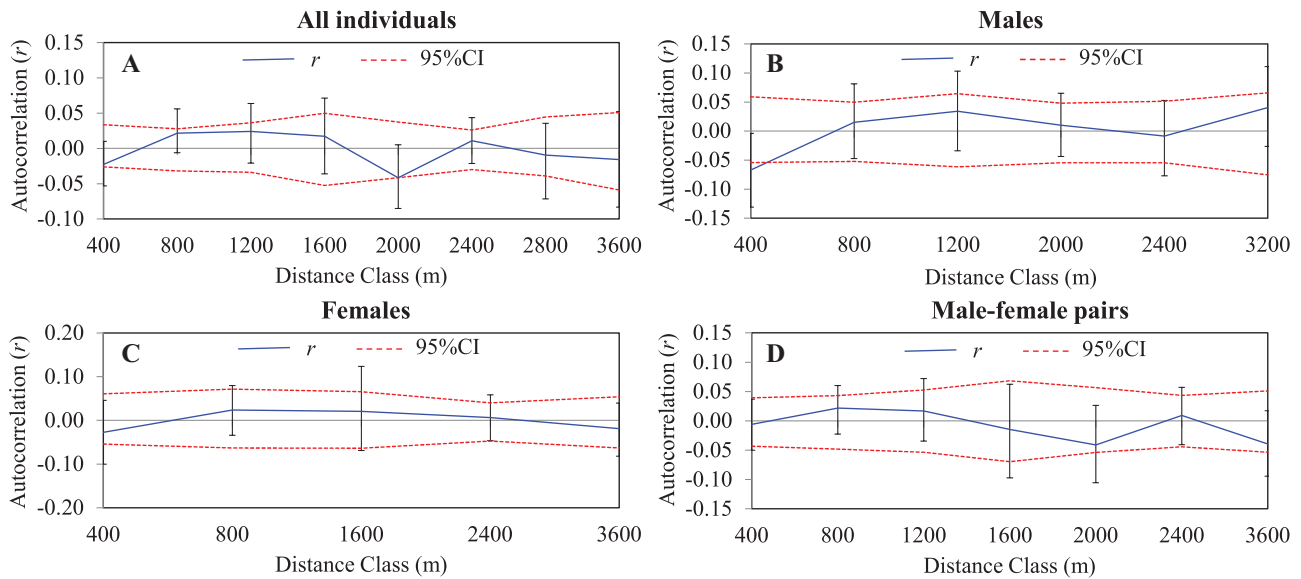| ID	Mather identified	Father identified	Trio confidence level (%)	Mating relatedness
M06	F82	M15	80	0.227
F18	F72	M66	80	−0.196
M64	F17	M85	80	−0.214

Figure 2 Spatial genetic autocorrelation analysis among (A) all individual pairs (*n* = 1540 pairs), (B) male pairs (*n* = 435 pairs), (C) female pairs (*n* = 325 pairs), and (D) male–female pairs (*n* = 780 pairs). The genetic autocorrelation coefficient (*r*) is a function of geographic distance, with the permuted 95% confidence intervals indicating random spatial genetic structure (dashed lines) and the bootstrapped 95% confidence error bars around *r*. The smallest distance class size, 400 m, is the mean mobility of Reeves's pheasants.
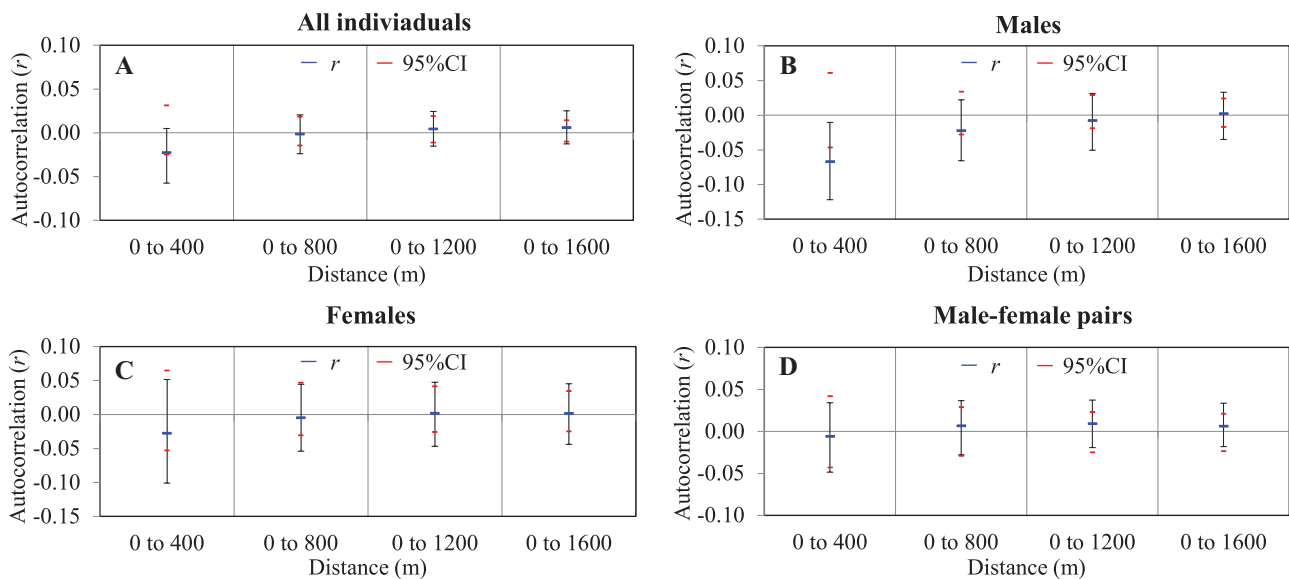

Figure 3 Spatial genetic autocorrelation analysis of Reeves's pheasant in different distance classes. A) all individual pairs; B) male pairs; C) female pairs; D) male–female pairs.

Discussion

It should be noted that the sample size of Reeves's pheasant in this study was relatively small for studying bird dispersal. Since terrestrial forest-dwelling birds are highly vigilant, it was extremely difficult to catch Reeves's pheasants in the field and to charge the trackers using solar energy in forests. As a result, most of our tracking equipment lost contact in about 3 months after the individuals were released because they ran out of battery power or could not communicate. Although the results of this study require a larger sample size for validation, we still described the genetic background and dispersal patterns of wild Reeves's pheasant from a genetic and behavioral perspective, thus improving our understanding of this threatened species.

The Reeves's pheasant population in the study area not only had a lower genetic diversity than populations in three protected areas and breeding base (*K*: 4.22 vs. 7.11; H_O: 0.48 vs. 0.55; H_E: 0.49 vs. 0.57, Wang et al. 2009) but also had a lower genetic diversity than wild Elliot's pheasant *Syrmaticus ellioti* populations (*K*: 4.22 vs. 8.86; H_O: 0.48 vs. 0.50; H_E: 0.49 vs. 0.75, Zheng 2015). Genetic diversity is positively correlated with population fitness (Markert et al. 2010). Therefore, it can be speculated that the Reeves's pheasant population in this area had a weaker adaptability to environmental changes than populations in protected areas and wild Elliot's Pheasant populations (Keller and Waller 2002).

Reeves's Pheasant population maintained a low level of inbreeding (F_{IS} = 0.025), consistent with the findings in
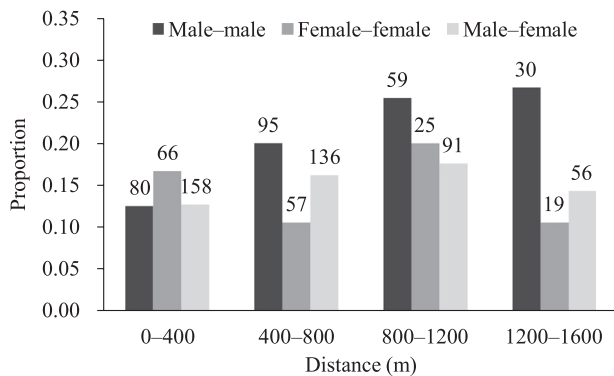
Figure 4 Proportions of dyads with $R \geq 0.25$ for different distance classes among males, females, and male–female pairs. The numbers above the bars denote the sample size.

Dongzhai, Jinzhai, Shennongjia, and Daxing (Wang et al. 2009). But the inbreeding phenomenon was detected in the studied population. There are three mating pairs were identified from the 87 individuals, and 1 pair were inbreeding. The habitat suitable for Reeves's pheasant in Pingjingguan is small and fragmented (Tian et al. 2020), and the population size is far lower than its historical records (Zhou et al. 2014; IUCN 2018). Limited and fragmented habitat and small population size increase the possibility of inbreeding. In addition, none of the individuals tracked in Pingjingguan in this study successfully crossed the provincial road during the study period. The geographical isolation of Reeves's pheasant in this area caused by the landscape barriers formed by man-made buildings may also induce inbreeding in this population (Frankham et al. 2002; Malcolm et al. 2006).

The avoidance of inbreeding hypothesis states that in a species, the dispersal of individuals of one sex will greatly reduce the likelihood of breeding with their close relatives, thus promoting the formation of sex-biased dispersal patterns (Waser and Jones 1983; Hu et al. 2017). There was a male-biased dispersal pattern of Reeves's pheasant, and the overlap ratio of the home range for male–female pairs with $R \geq 0.25$ was notably low. This indicated that the consanguineous male–female pairs were spatially isolated, which would reduce the probability of their encounters (Greenwood 1980; Clarke et al. 1997). Thus, male-biased dispersal may be an avoidance mechanism for Reeves's pheasant to avoid inbreeding (Hedrick and Kalinowski 2000; Townsend et al. 2003; Clobert et al. 2012).

In addition, the dispersal pattern of a species may also be related to its mating system and intrasexual competition (Zheng 2015). The mating system hypothesis states that a polygamous species is more inclined to have a male-biased dispersal pattern, and a monogamous species is more inclined to have a female-biased dispersal pattern (Greenwood 1980; Dobson 1982; Favre et al. 1997). The intrasexual competition hypothesis states that individuals of the sex with more intense intraspecific competition are more likely to disperse (Dobson 1982). Reeves's pheasant is a polygamous species, and male Reeves's pheasants will compete for territory during the breeding season, thereby obtaining the opportunity to mate (Zheng 2015). After the mating behavior, the female Reeves's pheasant leaves to lay her eggs, incubate them, and broods alone (Zheng 2015). These processes indicate that males invest relatively little in offspring, and their main

thought is to compete with other males for mates. Therefore, the male-biased dispersal pattern of Reeves's pheasant conforms to the mating system hypothesis and the intrasexual competition hypothesis. Zheng (2015) has reported similar results for Elliot's pheasant.

Previous studies have reported that the dispersal distance of female Reeves's pheasants is greater than that of males (243.65 vs. 171.45 m, Zheng 2015), and the dispersal may be female-biased. Similar findings have been reported in other polygamous Galliformes species, such as Dusky Grouse (*Dendragapus obscurus*, Jamieson and Zwickel 1983) and Lesser Prairie-Chicken (*Tympanuchus pallidicinctus*, Earl et al. 2016). Of course, there are some examples of species that have dispersal patterns without sex-biased changes, such as Greater Sage-Grouse (*Centrocercus urophasianus*, Cross et al. 2017) and Black Grouse (*Lyrurus tetrix*, Warren and Baines 2002). The breeding locations hypothesis states that low-quality habitats are not conducive to the survival and reproduction of animals, and animals improve their fitness through dispersal to find high-quality habitats (Shitikov et al. 2014; Zheng 2015; Engler and Krone 2021). In addition, the lack of mating opportunities may also cause some males to disperse farther away (Li et al. 2019). Therefore, the dispersal patterns of the same species in different regions may also be different.

According to the previous studies on 20 Galliformes species, female-biased dispersal is more common than male-biased dispersal (Supplementary Table S2). Previous studies have reported that among Galliformes, birds with a polygamous mating system but no flock behavior are likely to have male-biased dispersal patterns (Zheng 2015). Reeves's pheasant is a polygamous species and does not have flock behavior (Zheng 2015). Thus, this research somewhat supports this point of view. However, not all polygamous Galliformes with no flock behavior have male-biased dispersal patterns, such as willow ptarmigan (*Lagopus lagopus*, Piertney et al. 1998, 2000; Warren and Baines 2007; Hörnell-Willebrand et al. 2014) and rock ptarmigan (*Lagopus muta*, Caizergues et al. 2003; Novoa et al. 2020). In addition, previous studies have found that Galliformes with monogamous and flock behaviors may also have male-biased dispersal patterns, such as California quail (*Callipepla californica*) and Gambel's quail (*Callipepla gambelii*, Gee 2003). Galliformes is a complex group of bird species with diverse life histories, and current studies have failed to find a general rule for their dispersal patterns so far. We suggest that future studies need to pay more attention to wild Galliformes species and their dispersal behavior, especially to the species with unknown dispersal patterns. In addition, researchers should take multiple wild animal populations as research objects and compare their dispersal patterns with Galliformes so as to better understand the dispersal patterns and driving factors of Galliformes species.

For terrestrial species, the range and connectivity of suitable habitats are undoubtedly critical to their dispersal (Hu et al. 2017; Diniz et al. 2019). If a large number of habitats will continue to be lost and fragmented in the future, animal individuals will no longer be able to disperse far enough to communicate with other populations, which may reduce genetic diversity and increase the possibility of inbreeding (Frankham and Ralls 1998; Hedrick and Kalinowski 2000; Hu et al. 2017), thus negatively affecting the population's fitness and increasing the extinction risk of isolated populations (Pusey and Wolf 1996; Keller 1998; Slate et al. 2000; Keller and

Waller 2002). Reeves's pheasant has a weak dispersal ability (Zheng 2015) and a limited ability to cross artificial barriers. Therefore, we suggest that in order to effectively protect the scattered populations of this species and other related species, infrastructure construction in their distribution areas should be controlled within a moderate scale to avoid the formation of landscape barriers that would hinder species dispersal. Simultaneously, managers should take measures to increase the range of suitable habitats and connectivity of patchy habitats, such as by establishing nature reserves and ecological corridors (Zheng 2015).

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Author Contributions

J.X., J.L., and S.L. contributed to the conception of the study; S.L. performed the experiment; S.L., X.H., Y.W., and T.J. contributed significantly to the laboratory work, data calculation and analysis; S.L., S.T., and Z.L. wrote and edited the manuscript; J.X., J.L., X.H., and P.W. modified the manuscript; and J.X. contributed resources and funding. All of the authors have approved the final version.

Ethical Approval and Consent to Participate

The experiments in this study complied with the current laws of China. The study protocol and field procedures were approved by the forestry department and by the Ethics and Animal Welfare Committee of Beijing Forestry University (Approval No. EAWC_BJFU_2021018).

Conflict of interests

The authors declare that they have no competing interests.

Supplementary Material

Supplementary material can be found at https://academic.oup.com/cz.

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