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ORIGINAL ARTICLE

Bi-parentally Inherited Genetic Evidence for Male-Biased Dispersal in Common Moorhen (*Gallinula chloropus*)

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Abstract

Dispersal is a life history trait that has relevant effect on both the dynamics and the genetics of species and sex-biased dispersal depends on how resource competition affects each of the sexes. In this study, a total of 210 blood samples including 121 Common Moorhen (*Gallinula chloropus*) females and 89 males were collected from 18 diverse areas during the breeding season. Based on 8 microsatellite markers analyses, we found that the most genetic diversities from female populations were higher than those from the males, where only 2 male individuals were identified as the long-distance dispersal. Analyses of sex-biased dispersal conducted over all sampling sites indicated that m_{AI} (female $m_{\mathrm{AI}}=0.195$, male $m_{\mathrm{AI}}=-0.265$, $P=0.01$), F_{ST} (female $F_{\mathrm{ST}}=0.045$, male $F_{\mathrm{ST}}=0.026$, $P=0.020$), and r (female $r=0.118$, male $r=0.064$, $P=0.010$) in females were all significantly higher than those in males at the 0.05 level, which suggested a male-biased dispersal pattern in this species. Our Mantel test results suggested a significant isolation-by-distance pattern for females but not for males, which corresponded to the more frequent dispersal and gene flow in males than in females. This dispersal pattern could be explained by the special life history trait and mating system that Common Moorhen pair formation occurs before they leave the flock in the spring to establish territories and its females initiate courtship more frequently than males and compete with each other to pair with small males with large fat reserves. The philopatric female could benefit most from knowledge of a particular area because they may win more intrasexual competitions in the breeding season and be able to produce more offspring if they are familiar with the local resources.

Keywords Life history · Long-distance dispersal · Mating system · Microsatellite marker

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Introduction

Dispersal is a life-history trait relevant to the dynamics and the genetics of species. (Prugnolle and De Meeus 2002), and the sex-biased dispersal study has recently received particular attention in evolutionary biology (Bani et al. 2017). The most species dispersal is male-biased in mammals while female-biased in birds (Greenwood 1980), but counter-examples also exist in other species (Goudet 2001; Nagy et al. 2007), as a result of resource competition (Illes 2015). Female philopatry and male dispersal usually occur where females can defend high quality resources with relatives (Wrangham 1980). Generally, reproductive enhancement through increasing access to mates or resources and the avoidance of inbreeding promote to dispersal differences between sexes (Greenwood 1980; Prugnolle and De Meeus 2002).

For difficulty to obtain dispersal estimate from direct field observations, molecular evidence can help provide a more nuanced understanding of a species' social structure and behavior (Baden et al. 2014; Harris and Al 2009). It is a trend that the different parameters from bi-parentally inherited genetic markers were used for sex differences in migration rates (Bani et al. 2017; Prugnolle and De Meeus 2002). Based on different population genetic models, it is possible to detect contrasted population differentiation among sexes when their allele frequencies are equally randomized between sexes in the offspring (Prugnolle and De Meeus 2002).

Common Moorhen (*Gallinula chloropus*) is a worldwide distributed species (Taylor and van Perlo 1998; Wang et al. 2006), which is as abundant as its vernacular name implies in China (Wang et al. 2006) and tolerant of wide range of climatic conditions but vulnerable to low temperature (Taylor and van Perlo 1998). It usually exploits a wide range of natural and manmade eutrophic freshwater wetlands with fringing vegetation, occurring on both still and moving water (Sidle 1994; Wallau et al. 2010). Moorhen is usually an opportunist and could colonize new or restored wetland habitats (Ruan et al. 2018; Zhu et al. 2018; Worthington 1998), especially when they occur within the normal dispersal range (Miller et al. 2015). Using the radio-marker, Takano and Haig (2004) found the different seasonal movement and home range of the Mariana Common Moorhen between sexes, whereas Miller et al. (2015) used the mitochondrial and microsatellite markers to detect the interisland dispersal between Guam and Saipan in Mariana Common Moorhens. In this study we used microsatellite markers to detect whether there was sex-biased dispersal in this species as no study has previously used molecular genetics to test for sex biases in dispersal in this species or measured the degree of relatedness between dispersing individuals.

Methods

Sample Collection

A total of 210 blood samples including 121 females and 89 males were collected from 18 diverse areas during the breeding season (Fig. 1), where approximately 0.3 mL of blood was collected from each individual via brachial puncture with a 26-gauge needle into a heparinized tube and preserved for subsequent genetic analyses. The sample collection in this experiment was performed under the national ethical guidelines (Regulations for Administration of Affairs Concerning Experimental Animals, China, 1988) for animal husbandry and humane treatment strictly. Based on the geographical distance and apparent genetic barrier (e.g., river and huge mountain between adjacent populations) from sampling sites, all samples were separately grouped into 7 populations (Fig. 1).

DNA Extraction and PCR Amplification

Genomic DNA was extracted using the procedure described in Ruan et al. (2005), and then the individual sex was identified by PCR and gel electrophoresis with the primer pair P2 (5′-TCTGCATCGCTAAATCCTTT-3′) and P8 (5′-CTCCCAAGG ATGAGRAAYTG-3′) (Griffiths et al. 1998). PCR was performed in 25 μL volumes,

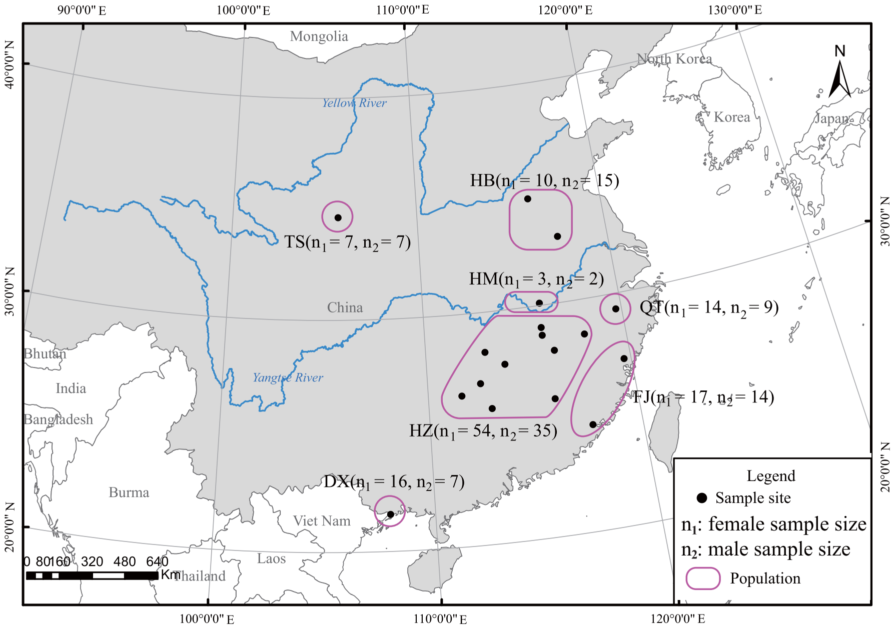


Fig. 1 Sample sites of Common Moorhen. All samples were incorporated into 7 large populations

which contained 2×EasyTaq SuperMix (TransGen Biotech Co., Ltd., Beijing, China), 5 µmol of each primer and 100 ng of template DNA. The thermocycler conditions consisted of an initial 10 min denaturation at 94 °C followed by 35 cycles of 30 s at 93 °C, 30 s at 47 °C, and 72 °C for 1 min. A final 10 min extension at 72 °C completed each reaction. Nuclear microsatellite genotypes were obtained at 8 loci and amplified by the primer pairs Crex7 and Crex8 from Gautschi et al. (2002), EFLZAP27 and CANSNX14 from Gregory and Quinn (2006), and Pho06, Pho53, Pho84, and Pho100 from Grueber et al. (2008). PCR was performed in a 10 µL reaction volume including 1×PCR buffer (Promega, Inc.), 0.5 µM of each primer, 2.5 mM $MgCl_2$, 100 µM of each dNTP, and 1U Taq DNA polymerase (Promega, Inc.). The thermocycling conditions included 2 min denaturation at 93 °C followed by 30 cycles of 30 s at 93 °C, 30 s at the annealing temperature, and elongation at 72 °C for 1 min. A final 10 min extension completed each reaction. Sequencing was carried out using an ABI 3100 automatic sequencer. ABI GENESCAN ANALYSIS software was used to assess the fragment size based on the internal GeneScan 500 [Rox] lane standard. ABI Genemapper was used to score allele sizes.

Genetic Analysis

We used FSTAT 2.9.3.2 (Goudet 2001) and Genepop 3.4 (Rousset 2008) to assess deviations from the Hardy–Weinberg equilibrium (HWE) and linkage equilibrium (LD). MicroChecker 2.2.3 (Van Oosterhout et al. 2004) was applied to check for misscoring from null alleles, stuttering and large allelic dropout. The program GDA 1.1 (Xu et al. 2002) was applied to calculate allelic richness and observed (H_E) and expected heterozygosity (H_O) over loci. The HP-Rare program (Kalinowski 2005) was used to obtain rarefied estimates of allelic richness within these units to better account for differences in sample size.

Sex-Biased Dispersal Analysis

Firstly, GENECLASS 2.0 (Cornuet et al. 1999) was carried out to detect the first-generation migrants among populations, which could identify the individuals that were sampled from but not born in the population. We used a frequencies-based method (Paetkau et al. 1995) and Monte Carlo re-sampling of 1000 individuals per locality (Paetkau et al. 2004), followed by four different sex-biased dispersal tests, including the variance in assignment indices (ν_{AI}), mean assignment indices (m_{AI}), differentiation values among populations (F_{ST}), and relatedness index (r), for set of adult individuals as described in Steinfartz (2009) and Illes (2015). The FSTAT 2.9.3.2 program (Goudet 2001) was used to compare ν_{AI}, m_{AI}, F_{ST} and r for males and females separately. The significances of different tests results were determined by performing 10,000 randomizations. A higher ν_{AI}, a lower m_{AI}, a lower F_{ST}, and a lower r suggest a weaker genetic structure for the more dispersing sex (Lawson and Perrin 2007; Steinfartz 2009). Given that detection of sex-biased dispersal reaches maximum power for each of these measures under different combinations of the dispersal rate, bias intensity, and sampling scheme, we tested each of the 4 measures to assess their performance at each of these scales.

Program STRUCTURE 2.2.3 (Pritchard et al. 2000) was used to identify the male/female number of genetic clusters and to assign each analyzed individual to one of the identified clusters, respectively. Analyses were performed using assumed numbers of clusters (*K*) ranging from 1 to 18 in male and 19 in female, and were implemented by using an initial 2×10^5 burn-in steps followed by 2×10^6 analysis replicates. We applied the correlated allele frequency model and the admixture model (Falush et al. 2003). Ten replicate analyses were performed for each value of *K*. The criteria that identify the most likely number of clusters were defined following Pritchard et al. (2000) and Evanno et al. (2005), and the evaluation were conducted in the website of STRUCTURE HARVESTER (Earl and vonHoldt. 2012).

MANTEL 1.18 was used to calculate the correlation (Mccoy 1963) between matrices of geographic distance (the natural logarithm of spatial distance) and genetic distance to determine if the population differentiation mode fit the pattern of isolation-by-distance. Pairwise ratios of $F_{ST}/(1-F_{ST})$ were used for microsatellite data as calculated by ARLEQUIN 3.1 (Excoffier et al. 2006). The significance of the Mantel Test correlation was assessed using 10,000 random permutations of matrices.

Result

Population Genetics

Hardy–Weinberg equilibrium test over loci showed no deviation from Hardy–Weinberg equilibrium. We also did not find any linkage disequilibrium. The results from Microchecker do not support scoring errors due to stuttering, nor large allele drop outs for all 8 loci. The most genetic diversities (including A_p, H_O and H_E, Table 1) in female populations were higher than those in males. But only A_p values in female were significantly higher than those in male at the 0.05 level ($t=3.396$, $P=0.015$,

Table 1 The genetic diversity in Common Moorhen

Population	Female			Male			All		
	A (A_p)	H_O	H_E	A (A_p)	H_O	H_E	A (A_p)	H_O	H_E
HZ	4.38 (2.46)	0.64	0.52	4.38 (2.18)	0.61	0.54	4.75 (2.97)	0.63	0.53
QT	3.13 (2.32)	0.80	0.50	3.50 (2.08)	0.73	0.51	3.63 (2.74)	0.77	0.50
FJ	3.63 (2.45)	0.74	0.55	3.38 (2.17)	0.74	0.56	3.88 (2.85)	0.74	0.55
DX	3.63 (2.39)	0.63	0.51	2.50 (1.94)	0.57	0.48	3.63 (2.70)	0.61	0.50
HM	2.50 (2.57)	0.67	0.59	2.00 (2.14)	0.64	0.50	2.75 (2.86)	0.63	0.56
HB	2.88 (2.29)	0.61	0.50	3.25 (2.00)	0.60	0.49	3.50 (2.66)	0.61	0.49
TS	2.25 (1.91)	0.45	0.35	2.75 (2.07)	0.69	0.52	2.75 (2.42)	0.57	0.44

N sample size, *A* allelic richness, A_p rarefied allelic richness estimates accounting for differences in sample size, H_E expected heterozygosity, H_O observed heterozygosity *df* = 6, Paired-samples *T* test). Compared to the female data, the male did not show consistent genetic diversity trends among populations (Table 1). In female, the highest genetic diversities were found respectively in HM ($A_p = 2.57$ and $H_E = 0.59$) and QT ($H_O = 0.80$), and the lowest genetic diversities were all found in TS ($A_p = 1.91$, $H_E = 0.45$ and $H_O = 0.35$), whereas in male, the highest genetic diversities were separately in HZ ($A_p = 2.18$) and FJ ($H_E = 0.\ 56$ and $H_O = 0.74$), and the lowest genetic diversities were all found in DX ($A_p = 1.94$, $H_E = 0.57$ and $H_O = 0.48$).

Sex-Biased Dispersal

The first-generation migrants were tested among populations in GENECLASS, where only 2 male individuals were identified as the first-generation migrants ($P < 0.01$), one from QT to HB and the other from HZ to TS. Both of them were long-distance dispersal, but no female individual was detected as long-distance dispersal. Analyses of sex-biased dispersal conducted over all sampling sites indicated that m_{AI} (female $m_{AI} = 0.195$, male $m_{AI} = -0.265$, $P = 0.01$), F_{ST} (female $F_{ST} = 0.045$, male $F_{ST} = 0.026$, $P = 0.020$), and r (female $r = 0.118$, male $r = 0.064$, $P = 0.010$) in females were significantly higher than those in males at the 0.05 level (Table 2). Meanwhile, ν_{AI} was lower in females than that in males, but this difference was not significant at the 0.05 level (female $\nu_{AI} = 3.625$, male $\nu_{AI} = 3.982$, $P = 0.450$). The m_{AI}, F_{ST}, and r tests indicated that the dispersal partners were more related than were random individuals of the same sex in the population. In general, all of the index values in sex-biased dispersal analyses suggested a male-biased dispersal pattern.

STRUCTURE analyses provided no evidence of genetic structure. Among the values of K investigated, both the male and female greatest average likelihood score was observed for the $K = 2$ case [log marginal likelihood = − 1461.69 (male) and − 1874.12 (female), Fig. S1]. Use of the Evanno et al. (2005) ΔK approach (Fig. S2) also suggested that there were 2 clusters. Notwithstanding both analyses suggested the presence of 2 genetic clusters, the results of admixture analysis based on these clustering showed no strict relationship to geographic distribution (Fig. S3).

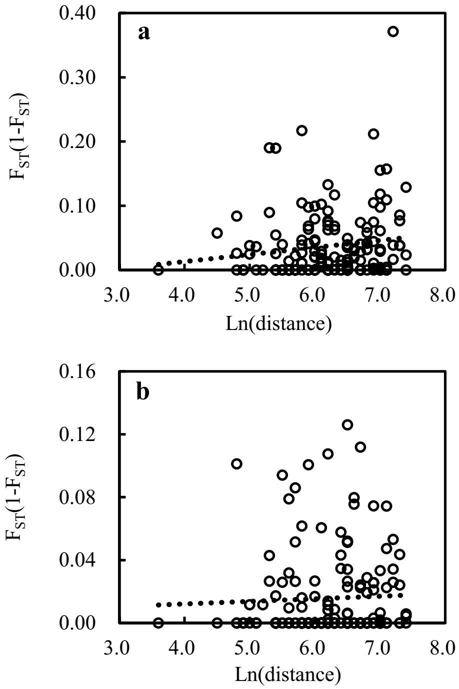
Our Mantel test results suggested that female genetic distances ($F_{ST}/(1 - F_{ST})$) significantly correlated to geographic distances (Ln distances) ($r = 0.184$, $P = 0.047$, Fig. 2), which could be thought as an isolation-by-distance pattern, whereas male genetic distances didn't significantly correlate to geographic distances ($r = 0.062$, $P = 0.316$).

Table 2 Microsatellite genetic parameters for sex-biased dispersal calculated from 18 sample sites of Common Moorhen

	m_{AI}	v_{AI}	F_{ST}	r
Female	0.195	3.625	0.045	0.118
Male	− 0.265	3.982	0.026	0.064
P values	0.010*	0.450	0.020*	0.010*

Differentiation among populations (F_{ST}), relatedness (r), mean assignment (m_{AI}), and variance of the assignment (v_{AI}) for male and female Common Moorhen, *P* values are from two-sided tests where * = significant at $P < 0.05$

Fig. 2 Isolation-by-distance in Common Moorhen population. The open circles indicate the pairwise observed values of F_{ST}/($1-F_{ST}$) of Common Moorhen. The broken line represents the regression line of F_{ST}/($1- F_{ST}$) on the natural logarithm of spatial distance (km) between Common Moorhen. **a** Female and **b** Male



Discussion

Our results indicated male-biased gene flow among Common Moorhen populations, which were supported by our results including genetic diversity, assignment test, four sex-biased dispersal tests and Mantel test. Firstly, the most genetic diversities from female populations were higher than those from the males, which could be explained by female philopatry and male dispersal. Our assignment tests also confirmed only 2 male long-distance movements among populations of the Common Moorhen. Long-distance male dispersal events can promote increases in genetic diversity and decreases in genetic differentiation during colonization (Petit et al. 2011). Moreover, the sex-biased dispersal analysis of the Common Moorhen indicated a significantly different m_{AI}, F_{ST} and r but non-significantly different ν_{AI} between the sexes (Table 2). To detect sex-biased dispersal, these tests differ in their sensitivity to various parameters (Goudet 2001). For example, ν_{AI} should be the most sensitive measure at lower dispersal rates, whereas m_{AI} and F_{ST} measures should be a more sensitive indicator when intermediate and higher dispersal rates come into play, respectively. Since three of four different sex-biased statistics proved a significant male-biased dispersal in Common Moorhen, here, we can conclude that this is a major demographic characteristic of Common Moorhen populations, which could also be supported by the Mantel test results. Our Mantel test results suggested a significant isolation-by-distance pattern for females but not for males, which corresponded to the more frequent dispersal and gene flow in males than in females.

Firstly, the male-biased dispersal pattern was correlated to Common Moorhen's special life history trait in China. This species has two different life history types, i.e., non-migratory in the south and migratory in the north of China (Wang et al. 2006). The northern breeding populations must migrate to the south for wintering and return in spring (Taylor and van Perlo 1998). As a migratory waterfowl species, some Common Moorhen males follow females from the wintering grounds to the female's natal area (Petrie 1986; Taylor and van Perlo 1998; Zink and Barrowclough 2008), which could result in the expectation of male-biased dispersal and even homogenize the populations. This process promotes genetic exchange between populations. Moorhens are predominantly socially monogamous, with pairs changing from year to year (Bannor and Kiviat 2002). During winter, Common Moorhen live in large flocks where pair formation occurs before they leave the flock in the spring to establish territories (Petrie 1986). Females initiate courtship more frequently than males and compete with each other to pair with males (Loyau and Schmeller 2012).

To interpret sex-biased dispersal is sometimes difficult due to the confounding effects of factors such as the mating system of the species (Prugnolle and De Meeus 2002). Sex roles in breeding season could highlight the different dispersal between two sexes. Understanding the evolutionary pressures leading to asymmetric dispersal of sexes and its ecological and genetic consequences will depend on our ability to determine its prevalence and magnitude in natural populations (Aars and Ims 2000; Clarke et al. 1997). These results could be explained by the fact that Common Moorhen females compete for males rather than vice versa (Loyau and Schmeller 2012; Taylor and van Perlo 1998). Most species of birds are faithful to their natal and breeding sites, although sex differences in dispersal could be found, which is usually explained by their reproductive enhancement through increased access to mates or resources and the avoidance of inbreeding (Greenwood 1980). Petrie (1983) found that the heaviest Common Moorhen females win most agonistic encounters and select small males with large fat reserves. Furthermore, females paired to fatter males initiate more clutches in a season because fat males can incubate for a longer time than thinner males. Here, the familiarity is the main result of inter-female competition for a private territory (Greenwood 1980). For instance, the close proximity of relatives could help to protect the resource in breeding. Thus, philopatry is a consequence of resource competition with the benefits accruing to the sedentary rather than the dispersing individuals (Greenwood 1980). Furthermore, using a radio-marker on Common Moorhen individuals to determine their home range, Takano and Haig (2004) found that females moved some farther and exhibited significantly smaller mean core areas than males in the dry season. Our investigation confirmed this difference when using genetic structure differences between sexes to detect sex-biased dispersal. For this species, the philopatric female may benefit most from knowledge of a particular area because they may win more intrasexual competitions in the breeding season and be able to produce more offspring if they are familiar with the local resources.

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Compliance with Ethical Standards

Ethical statement The sample collection in this experiment was performed under the national ethical guidelines (Regulations for Administration of Affairs Concerning Experimental Animals, China, 1988) for animal husbandry and humane treatment strictly.

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