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Genetic evidence for male-biased dispersal in Elliot's Pheasant (*Syrmaticus ellioti*) in China

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Abstract Sex-biased dispersal, in which individuals of one sex tend to disperse and breed at a greater distance from their natal site than individuals of the opposite sex, appears to be common in vertebrate organisms and is very important to population structures and dynamics. Many studies have documented the dispersal patterns of monogamous birds; however, observations and data are few for polygynous birds. In our study, we report on the indication of sex-biased dispersal in Elliot's Pheasant (*Syrmaticus ellioti*), a vulnerable species endemic to China, using polymorphic DNA microsatellite loci (105 individual birds and seven loci) and mitochondrial DNA control-region sequences (63 birds). Contrary to the traditional concept that males are the more philopatric sex and females the more dispersing sex in birds, all the genetic information extracted from the two markers suggests that male-biased dispersal is predominant in Elliot's Pheasant. We argue that polygynous species in Galliformes without lekking behavior are more likely to exhibit male-biased dispersal patterns, consistent with the expected results based on the polygynous mating system of Elliot's Pheasant.

Keywords Elliot's Pheasant, sex-biased dispersal, microsatellite, mtDNA

Introduction

Dispersal is a central topic in ecology and evolution, because it is a fundamental life history trait that has important effects on both dynamics and genetic structures of populations (Clobert et al., 2001). If animals are less active, their genetic structure will be strong because of divergence and inbreeding in local populations. In contrast, in animals which show high dispersal patterns, few spatial genetic structures should be expected. Because of cost/benefit asymmetries of dispersal in animals, the sexes often show different dispersal tendencies. One special case is sex-biased dispersal, in which individuals of one sex tend to disperse and breed at a greater distance from their natal site than individuals of the opposite sex (Wolff and Plissner, 1998). Several hypotheses are put forward to explain this phenomenon. A prior mechanism expected to affect dispersal patterns is the mating system (Greenwood, 1980), with male-biased dispersal in mate-defense systems associated with most polygynous species and female-biased dispersal in resource-defense systems linked to most monogamous species. Intrasexual competition would also lead to differences in dispersal between the two sexes which mostly involves intense competition (Dobson, 1982). Waser and Jones (1983) emphasized the importance of inbreeding avoidance and parent-offspring competition in addition to the mating system. Moreover, recent studies have suggested that kin selection and social interaction may play an important role in sex-biased dispersal (Devillard et al., 2004). Physiologically, hormone levels may also exert an effect (Smale et al., 1997). There is no consensus on the evolutionary origins of sex differences in dispersal.

To date, considerable attention has focused on the patterns of sex-biased dispersal. An increasing number of studies have been carried out in many species, mostly in birds and mammals (Nyakaana and Arctander, 1999;

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Piertney et al., 2000; Dallimer et al., 2002; Kerth et al., 2002; Moller and Beheregaray, 2004; Maki-Petays et al., 2007) and to a relatively limited extent in other taxa, such as fish (Cano et al., 2008), reptiles (Dubey et al., 2008; Johansson et al., 2008; Lukoschek et al., 2008; Ujvari et al., 2008), amphibians (Austin et al., 2003; Palo et al., 2004) and insects (Doums et al., 2002). As data has accumulated, it has become increasingly obvious that general patterns of sex-biased dispersal can be found; for example, male-biased dispersal is pervasive in mammals and female-biased dispersal predominates in birds (Greenwood, 1980; Dobson, 1982). Although dispersal tends to be female-biased in birds, many counter examples exist (Clarke et al., 1997; Gibbs et al., 2000; Dallimer et al., 2002). Some studies also document that there are no differences between the two sexes in dispersal (Clarke et al., 1997; Maki-Petays et al., 2007). Many studies have suggested that the most common pattern for monogamous birds is female-biased dispersal (Greenwood, 1980; Dobson, 1982). However, the mechanism about possible sex-biased dispersal in polygynous birds is still not clear.

Elliot's Pheasant (*Syrmaticus ellioti*) is a vulnerable species endemic to China, found in Jiangxi, southern Anhui, Zhejiang, Fujian, Guangdong, Guangxi, Hunan, Guizhou and Hubei provinces (Delacour, 1977; Cheng et al., 1978; Li, 1996; Ding, 1998; BirdLife International, 2009). It is a bird of the Galliformes which has a polygynous mating system with the male typically having two or three mates (Ding et al., 1990). Many kinds of forests, e.g. broadleaf forest (both evergreen and deciduous), evergreen and deciduous broadleaf mixed forests, as well as coniferous and broadleaf mixed forests are used by Elliot's Pheasants as their habitat (Ding and Zhuge, 1988, 1989). Given present day clearing of forests and their replacement with single species plantations, deforestation, slash and burn systems, collection of firewood and other forest products, loss, fragmentation and degradation of habitats have become major threats for this species (Ding et al., 2000; BirdLife International, 2009). Since Elliot's Pheasant is a land-dwelling bird and its flight capacity relatively weak, an understanding of its dispersal behavior and pattern in the fragmented habitats is particularly important for its conservation and habitat management. Several studies have indicated that Elliot's Pheasant has a pre-nuptial dispersal between wintering sites and breeding sites during the early breeding season (Shi and Zheng, 1995; Peng and Ding, 2005). However, little is known about the sex differences in dispersal.

In our investigation, we have used both microsatellite DNA loci and mtDNA haplotype variation to detect the dispersal pattern of Elliot's Pheasant, to test whether this bird with its polygynous mating system has a male-biased dispersal pattern based on the significant impact of the mating system on the dispersal pattern of this species and to have a better understanding of the dispersal pattern to make action plans for future conservation and habitat management for this threatened species.

Materials and methods

Samples (Table 1) used in this study were obtained from Fujian, Hunan, Guizhou and Gutianshan areas and at adjacent areas of Zhejiang, Anhui and Jiangxi (Jiang et al., 2007). We used 105 samples (47 males, 39 females and 19 samples without sex information) for microsatellite analysis. A total of 63 samples (30 males, 29 females, 4 samples without sex information) were used for mtDNA analysis, in which 33 samples were from previous work by Jiang et al. (2007). These two sample sets were used for microsatellite and mtDNA analysis respectively.

Molecular analysis

DNA extraction and mtDNA amplification

Protocol of DNA extraction and mtDNA amplification were used as described by Jiang et al. (2007).

Microsatellite

Seven polymorphic microsatellite loci (SE02, SE03, SE04, SE05, SE06, SE07 and SE08) were used as described by Jiang et al. (2006). PCR products were loaded on a 6.5% acrylamide gel and run on a LI-COR 4200 automatic sequencer of standard size (50–350 bp IRDye700, LI-COR). Gel images were analyzed using SAGA GT software. In order to minimize the errors of genetic typing, we repeated this six times to ensure consistent sizing of alleles.

Table 1 Total number of genetically sampled birds (N_T), number of females (N_F) and number of males (N_M) in each of the study area for microsatellite analysis

Study area	N_T	N_F	N_M
Gutianshan area	16	4	10
Fujian	27	9	11
Hunan	20	8	6
Guizhou	42	18	20
Total	105	39	47

Statistical analysis

mtDNA data

The program CLUSTAL X (Thompson et al., 1997) was used to align mtDNA control region sequences. The identification of variants and haplotypes was performed by MEGA4.0 (Kumar et al., 2008).

Microsatellite data

Microsatellite genotypes were tested for linkage disequilibrium (LD) within the whole population for each pair of loci using GENEPOP software (Raymond and Rousset, 1995). This program was also used to conduct tests for the Hardy-Weinberg equilibrium (HWE) employing the Markov chain method. Expected (H_E) and observed (H_O) heterozygosities were estimated with the program Cervus2.0 (Marshall et al., 1998). We used Weir and Cockerham's (1984) unbiased estimators for the calculation of F-statistics.

Sex-biased dispersal analyses

1) Microsatellites DNA

In order to test for possible differences in migration rates between males and females, five different tests, i.e., gene diversity (H_S), differentiation among populations (F_{ST}), relatedness (r), mean assignment index (*mAIc*) and variance of the assignment index (*vAIc*) were carried out separately for both sexes over all populations. Whether these parameters differ significantly between the two sexes was determined using the approach of Goudet et al. (2002), as implemented by 10000 randomizations in FSTAT version 2.9.3 (Goudet, 2001).

Statistically significant dissimilarity in genetic parameters can be expected when sex-biased dispersal occurs. Allelic frequencies should be more homogeneous for individual birds of the dispersing sex, thus F_{ST} and r are expected to be higher for the more philopatric sex and for the within-group H_S is expected to be lower (Goudet et al., 2002). The assignment values of individual birds (*AIc*) determine the probability of an individual genotype originating in the population from which it was sampled (Favre et al., 1997). The distribution of *AIc* is centered round a mean of 0. A positive value indicates a genotype more likely than average to occur in its sample and the bird is more likely a resident. In contrast, a negative value suggests that it is potentially a disperser. Because the *AIc* values for residents tend to be higher than for immigrants, under sex-biased dispersal, *mAIc*, for the more philopatric sex is expected to be higher than that for the sex that disperses most (Goudet et al., 2002). Because of the increased probability that members of the dispersing sex will include both residents and immigrants, *vAIc* for the sex dispersing is expected to be higher (Favre et al., 1997). Goudet et al. (2002) has pointed out that the efficiency and power of these indices, used to detect sex-biased dispersal, depend on dispersal rates, extent of the bias, sampling and markers used.

2) Mitochondrial DNA

Since mtDNA is maternally inherited, males do not transmit their mtDNA haplotypes to their offspring. If a male animal dies or migrates to a different population, his haplotype will not be available. In contrast, females can contribute their haplotype to the next generation. When female animals or their female offspring disperse to different populations, they will leave a copy of their haplotypes. Compared with males, females have a greater potential power to homogenize mtDNA genetic structures through dispersal (Escorza-Trevino and Dizon, 2000). If the mtDNA genetic structure in females is stronger than in males, it would probably be assumed that the result provides compelling evidence for male-biased dispersal (O'Corry-Crowe et al., 1997). Many studies have used mtDNA to infer patterns of sex-differential dispersal (O'Corry-Crowe et al., 1997; Escorza-Trevino and Dizon, 2000; Lukoschek et al., 2008).

Gender-specific hierarchical AMOVA were conducted for mtDNA, performed in the software package Arlequin3.11 (Excoffier et al., 2005).

3) Comparison between microsatellites DNA and mtDNA

When sex-biased dispersal occurs in animals with relatively complex social behavior the patterns of population structure, based on uniparentally inherited markers, e.g. mtDNA, may differ from those based on biparentally inherited nuclear markers. The rationale is as follows: for uni-parentally inherited markers, only one sex contributes to a part of the genome of its offspring. In contrast, for bi-parental markers, both sexes make contributions (Prugnolle and de Meeus, 2002).

For species with male-biased dispersal, population differentiation based on microsatellites will be weaker than that based on mtDNA. This approach has been successfully used in several studies (e.g. Gibbs et al., 2000; Hoarau et al., 2004; Maki-Petays et al., 2007).

A comparison of the differentiation level of the genetic structure in microsatellite and mtDNA can infer patterns of sex-biased dispersal. The overall differentiation for microsatellites and mtDNA was estimated by AMOVA, implemented in program Alequin 3.11.

Results

There was substantial variation at each locus as shown by the number of alleles and the observed and expected heterozygosity (Table 2). For the seven microsatellite loci, the number of alleles per locus ranged from 6 to 11 (average of 8.86), with a total of 62 alleles across 7 loci. H_O was generally low, ranging from 0.261 for SE02 up to 0.782 for SE06.

A total of 47 males and 39 females were included in the microsatellite analysis, where genetic parameters of the population were estimated separately for each sex. F_{ST} and r were significantly higher for females than males (female $F_{ST} = 0.142$, male $F_{ST} = 0.059$, $p = 0.020$; female $r = 0.198$, male $r = 0.092$, $p = 0.040$). *mAIc* was negative in males (–0.593), but not statistically significantly different ($p = 0.060$) from the positive mean assignment index in females (0.715). Neither was the difference in the variance of assignment index significant, although the level in males was on average higher (Table 3). Furthermore, males displayed significantly higher gene diversity, H_S (males = 0.724, females = 0.654, $p = 0.025$).

AMOVA, based on mtDNA, showed stronger genetic structure and hierarchical partitioning of genetic variation in females ($F_{ST} = 0.350$) than in males ($F_{ST} = 0.290$).

Simple comparisons between differentiation based on haplotype and based on allele frequencies are feasible, although the two markers of mtDNA and microsatellite represent two different genetic data. The result showed that the overall differentiation based on mtDNA was almost six times higher (mtDNA: overall $F_{ST} = 0.320$; microsatellite overall $F_{ST} = 0.058$).

Discussion

As our results show, we have used indirect methods to examine dispersal in Elliot's Pheasant by 1) comparing different genetic indices and genetic differentiation patterns estimated separately for both sexes by microsatellite and mtDNA; 2) comparing the level of genetic structures obtained from two markers with different inherited modes: microsatellite and mtDNA. All indices estimated suggest that males have a higher dispersal rate than females in Elliot's Pheasant. The indications given by the differences in relatedness and gene diversity show statistically significant differences. Assignment tests show that the mean of *AIc* (*mAIc*) and the variance in *AIc* (*vAIc*) are consistent with the prediction of male-biased dispersal, although there are no statistically significant differences. This may due to the relatively low efficiency and power of the assignment tests (Goudet et al., 2002). Also, no significant differences in *vAIc* were expected from the fact that both sexes disperse in the spring (Peng and Ding, 2005), so distributions of both male and female *AIc* values include immigrants, resulting in more overlaps. The result from the assignment index test is supported by *F*-statistics, given that the male F_{ST} is significantly smaller than the female F_{ST}. In contrast to the result from the variation in the mtDNA control region, the level of overall genetic differentiation is much lower in microsatellite variation. In addition, gender-specific hierarchical AMOVA shows a higher partition of genetic variation in females than in males for mtDNA. Lower levels of the mtDNA genetic structure in males than in females probably suggests a strong dispersal pattern of male-biased dispersal (O'Corry-Crowe et al., 1997).

Table 2 Genetic diversity of Elliot's Pheasant (*Syrmaticus ellioti*) at seven microsatellite loci

Locus ID	Range of allele sizes	N_a	H_E	H_O
SE02	202–230	7	0.618	0.261
SE03	266–276	6	0.641	0.269
SE04	168–185	9	0.856	0.411
SE05	263–287	11	0.767	0.461
SE06	299–327	11	0.878	0.782
SE07	196–225	8	0.719	0.607
SE08	300–345	10	0.767	0.737

N_a, number of alleles; H_E, expected heterozygosity; H_O, observed heterozygosity.

Table 3 Differentiation among populations (F_{ST}), gene diversity (H_S), relatedness (r), mean assignment index (*mAIc*) and variance of the assignment index (*vAIc*) for male and female Elliot's Pheasant (*Syrmaticus ellioti*) based on microsatellite analyses

	F_{ST}	H_S	r	*mAIc*	*vAIc*
Males	0.059	0.724	0.092	–0.593	10.024
Females	0.142	0.654	0.198	0.715	8.979
p [a]	0.020*	0.025*	0.040*	0.060	0.682

[a] p-values are from two-sided tests where * indicates significance at $p < 0.05$.

Seielstad et al. (1998) stressed that the results from the comparison between two classes of genetic markers should be interpreted carefully. The disparity in the level of genetic differentiation may be due to their different effective population sizes and rates of mutation (Chesser and Baker, 1996). Gibbs et al. (2000) used the approach suggested by Seielstad et al. (1998) to assess the effect of these genetic differences on levels of differentiation in the yellow warbler and found that the expected level of divergence, based on haploid mtDNA, was almost four times higher than that based on diploid microsatellite markers. Similarly, in our study, the differentiation based on mtDNA is almost six times higher than that of microsatellite loci. In addition to the genetic characteristics of the two types of markers, there must be another reason to explain the difference. Combining with the outcomes from the other two methods we used in this study, it is difficult to explain the result from the comparison between mtDNA and microsatellites as anything but a biased dispersal between male and female Elliot's Pheasants.

Suggestions have been made explaining that males and females differ in their movement patterns. The more common mechanism to explain the pattern is that sex-biased dispersal may be associated with their type of mating system (Greenwood, 1980). In polygynous mating systems, local mate competition is dominant and often observed on male-biased dispersal species. In contrast, female-biased dispersal is highly correlated with a monogamous mating system due to competition for local resources (Greenwood, 1980; Dobson, 1982; Favre et al., 1997). The dispersal pattern of Elliot's Pheasant conforms to the expected result based on the polygynous mating system of this species. Elliot's Pheasant has a polygynous breeding system in which the male has two or three mates (Ding et al., 1990). In successful breeding attempts of Elliot's Pheasant, females nest and hatch on their own and males take no part in nest construction, incubation or care of the chicks. In this context, males make little contribution to parental investment but invest more in male-male competition for females. Males are therefore more likely to exhibit strong local mate competition. Because getting more mates is more important than being familiar with local resources for male reproductive success, dispersing males can increase their breeding opportunities and fitness (Hamilton and May, 1977). On the other hand, females who invest highly in their offspring show competition for local resources. They benefit from being philopatric due to their familiarity with the food resources for successful breeding. Another important mechanism may be related to avoid inbreeding. In Elliot's Pheasant, females typically reproduce only once per breeding season. The opposite is that males may copulate repeatedly, so males can avoid mating with related individuals and hence lower the negative impact of inbreeding by dispersing. The males can sometimes be somewhat aggressive towards hens, so female philopatry in Elliot's Pheasant may also be advantageous for defending themselves against males. However, the dispersal pattern of male-bias is not applicable to all polygynous birds. Most grouse and pheasant species also have polygynous mating systems. Lekking behavior is common in grouse species, e.g. Sage Grouse (*Centrocercus urophasianus*) (Dunn and Braun, 1985), in which several males display in a ground where females come and choose mates. In this case, defending resources is important for males to attract females, hence it is advantageous to be more philopatric for males. In contrast, females have more choices to get the best mates by dispersing (Wolff and Plissner, 1998). All five grouse species listed by Clarke et al. (1997) show female-biased dispersal, although examples of no sex-biased dispersal exit (Maki-Petays et al., 2007). The lek mating system was not found in Elliot's Pheasant from field observations (Ding et al., 1990). Local mate competition among males may be stronger than local resource competition among females, as is the case in the male-biased dispersal pattern in Elliot's Pheasant. We are of the opinion that polygynous birds of Galliformes without lekking behavior are more likely to exhibit a male-biased dispersal pattern.

Our field study has shown that the movement routes of Elliot's Pheasant are selective when dispersal occurs in the spring. The major factors affecting dispersal are the number of shrub species, canopy height of shrubs, slope and abundance of shrubs (Peng and Ding, 2005). This suggests that the dispersal behavior of this pheasant is affected by habitat characteristics and availability. Hence, the increasingly serious problems of habitat loss, fragmentation and degradation are bound to limit the dispersal of Elliot's Pheasant and then cause the recession of population fitness. To some extent, the dispersal behavior can weaken the negative effect of habitat fragmentation, for it will expand the distribution area of the species. How to reduce the impact of habitat fragmentation on the dispersal of Elliot's Pheasant by improving the suitability of habitat and decreasing the level of fragmentation is vital for the sustained survival of this species. Since males need a larger range of activities than females, their reactions to habitat fragmentation are much more sensitive. Combined with the male-biased dispersal pattern of Elliot's Pheasant, it is particularly important to create favorable conditions for male Elliot's Pheasants to enhance their dispersal capacity in habitat management, such as habitat recreation and corridors establishment. Specific measures should be explored further in future studies.

Although our genetic evidence has shown strong male-biased dispersal in Elliot's Pheasant, more research should be carried out to support our argument that polygynous birds without lekking behavior are more likely to exhibit male-biased dispersal patterns in Galliformes. As well, ultimate mechanisms, the adaptive significance and the evolutionary implications of male-biased dispersal patterns should be detected more in future studies, which is vital for the conservation and management of Elliot's Pheasant.

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有关白颈长尾雉雄性偏倚扩散的遗传学证据

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摘要：一种性别的个体倾向于比另一性别的个体扩散到离出生地较远的地方，这种现象称为性别偏倚扩散。性别偏倚扩散现象在脊椎动物中很常见，对种群结构和种群动态有着非常重要的作用。许多研究已经证明了一夫一妻制鸟类的扩散模式，然而有关一夫多妻制鸟类的研究和数据还是很少。白颈长尾雉（*Syrmaticus ellioti*）是中国特有的濒危物种。本研究中，我们使用多态性DNA微卫星位点（105个个体和7个位点）和线粒体DNA控制区序列（63个个体）来研究白颈长尾雉的性别偏倚扩散模式。传统的观点认为，鸟类中雌性个体比雄性个体更具扩散性。与此不同的是，本文中两种遗传标记所得的遗传信息都表明，白颈长尾雉的扩散模式是雄性偏倚的。我们认为，在鸡形目中，不具群集展示行为的一夫多妻制物种更加倾向于雄性偏倚扩散模式。该推论与基于白颈长尾雉一夫多妻的婚配体制所得到的结果是相一致的。

关键词：白颈长尾雉，性别偏倚扩散，微卫星，线粒体DNA