

# Research progress in avian dispersal behavior

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**Abstract** Dispersal, defined as a linear spreading movement of individuals away from others of the population is a fundamental characteristic of organisms in nature. Dispersal is a central concept in ecological, behavioral and evolutionary studies, driven by different forces such as avoidance of inbreeding depression, density-dependent competition and the need to change breeding locations. By effective dispersal, organisms can enlarge their geographic range and adjust the dynamic, sex ratio and genetic compositions of a population. Birds are one of the groups that are studied intensively by human beings. Due to their diurnal habits, diverse life history strategies and complex movement, birds are also ideal models for the study of dispersal behaviors. Certain topics of avian dispersal including sex-biased, asymmetric dispersal caused by differences in body conditions, dispersal processes, habitat selection and long distance dispersal are discussed here. Bird-ringing or marking, radio-telemetry and genetic markers are useful tools widely applied in dispersal studies. There are three major challenges regarding theoretical study and methodology research of dispersal: (1) improvement in research methodology is needed, (2) more in-depth theoretical research is necessary, and (3) application of theoretical research into the conservation efforts for threatened birds and the management of their habitats should be carried out immediately.

**Keywords** birds, dispersal, dispersal distance, natal dispersal, breeding dispersal

## 1 Introduction

Dispersal is a form of movement and a basic characteristic of organisms in nature. Dispersal study is an important field in ecology, behavior biology and evolutionary biology (Ferriere and Galliard, 2001; Begon et al., 2006).

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Dispersal results in the extension of distribution range, the changes in age structure, sexual ratio as well as population structure (Hanski and Gilpin, 1997; Newton, 2003; Lester et al., 2007; Sugden and Pennisi, 2006). By effective dispersal, organisms can avoid inbreeding depression, intraspecific competition and kin competition (Begon et al., 2006; Newton, 2003; Clobert et al., 2001). Since the 1940s, studies focusing on dispersal behavior have been reported (Greenwood and Harvey, 1982). In recent years, dispersal has been increasingly accepted as an important subject in ecology and dispersal ecology and has become a hot topic in ecology research (Bullock et al., 2002).

Birds are one of the animal groups that are studied intensively by human beings (Clark et al., 2004). Due to their diurnal habits, diverse life history strategies and complex movements, birds are also ideal models for the study of dispersal behaviors. The 115<sup>th</sup> and 121<sup>st</sup> Annual Congress of American Ornithologists' Union had special symposiums on avian dispersal (Clark et al., 2004; Walters, 2000). A series of paper about avian dispersal have also been compiled and published in two special issues in *Condor*, a worldwide renowned ornithological journal in 2000 and 2004. An increasing number of research on avian dispersal showcases that dispersal has emerged as a new frontier in ornithological research (Clark et al., 2004; Walters, 2000).

## 2 The concept and causes of dispersal behavior

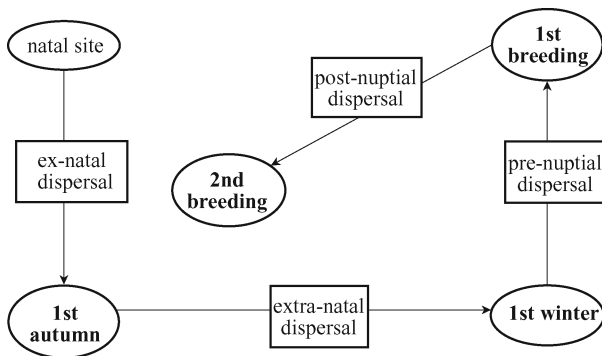
### 2.1 Definition and classification of dispersal

Early in the 1960s, Howard (1960) defined dispersal as a constant movement between natal site and breeding site. Later, Greenwood and Harvey generalized the definition of dispersal as a linear spreading movement of individuals away from others of the population, including natal dispersal (the movement between the natal site and the place where first reproductive activity takes place) and breeding dispersal (dispersal between two successive breeding sites)

(Greenwood and Harvey, 1982; Greenwood, 1980). The key parameter of measuring dispersal is the dispersal distance. Compared with avian migration, another important movement in the life history of birds, there is no fixed distance or direction in dispersal. Moreover, a dispersal individual may not return to the origin point (Begon et al., 2006; Newton, 2003).

Apart from the two types of dispersal mentioned above, Newton (2003) proposed a third category: non-breeding dispersal, i.e., individual moves between the wintering sites of consecutive years. The three types of dispersal are relevant in that natal dispersal is the movement by juveniles and immatures while breeding and non-breeding dispersal are the adults' movement.

It is doubtless that animals not only exist in the breeding sites and natal sites, but also occupy a home range for hunting, roosting, displaying and other daily activities (Burt, 1943). Zheng (1995) defined a bird's home range as "a range that birds constantly traverse and move around". To understand the definition of dispersal more thoroughly, it is useful to combine Greenwood's definition of dispersal with home range and thus the life history and home range can be linked (Kenward, 2001; Kenward et al., 2002a, 2002b). In principle, animal dispersal can be termed as the following types: *ex-natal* dispersal, the movement from natal site to the first settled home range; *extra-natal* dispersal, the movement from the first home range to the first wintering site; *pre-nuptial* dispersal, the movement from wintering site to breeding site during the early breeding season; *post-nuptial* dispersal, the movement between two mating or breeding.



**Fig. 1** Definitions of dispersal combined with "home-range" concept. Ellipses represent home ranges in different life-times (Kenward et al., 2002a, 2002b)

Taking the differences in age, sex and life history phase of the birds into account, we suggest that avian dispersal should include the following types: dispersal of the adults, the linear movement between two successive home-ranges, happening between the wintering site and the breeding site or two consecutive breeding sites during a same breeding season; dispersal of juveniles, the linear movement between two successive home ranges before the first breeding attempt, including movement from the

natal site to the first home range, wintering site and first breeding site of the juveniles and movement between the summering site and the wintering site of immatures.

## 2.2 Causes of dispersal

Compared with the philopatric individuals, dispersal individuals may be at greater risk from predators. Thus, individuals who take dispersal strategy may suffer a lower survival rate (Smith, 1974) or consume more energy in movement (Belichon et al., 1996). From this point, dispersal behavior appears to decrease the fitness of organisms. However, dispersal has been considered as one of the fundamental features of organisms and may have a selective advantage. The following three widely accepted viewpoints may well explain the reasons.

### 2.2.1 Inbreeding avoidance hypothesis

Begon and Motro believed that close inbreeding will incur inbreeding depression and in particular, when closely related individuals breed, their offsprings are likely to have a higher abnormality rate and mortality rate. Thus, inbreeding avoidance is a selective force favoring natal dispersal of juveniles (Begon et al., 2006; Motro, 1991). The offsprings of inbreeding are more likely to carry recessive deleterious alleles than outbreds (Frankham et al., 2005). Inbreeding leads to reductions in heterozygosity and increases the risk of mortality and thus, decreases the fitness of descendants (Keller and Waller, 2002). There is overwhelming evidence of inbreeding depression in wild bird populations, for instance, in the Great Tit (*Parus major*) (Greenwood et al., 1978) and song sparrows (*Melospiza melodia*) (Keller et al., 1994). Natural selection can be thus expected to be in favor of any behavior that avoids the adverse effect of inbreeding depression such as kin recognition and dispersal. The sex-biased dispersal ability in most birds may well be consistent with the inbreeding avoidance hypothesis. Superb Fairy-wren (*Malurus cyaneus*) is a cooperative breeder, in which immature males and other non-breeding individuals act as helpers in order to enhance the productivity (Cockburn et al., 2003). Unlike other fairy-wren species, females disperse further than males to avoid breeding with their sons. Whenever a male partner dies or the son becomes a senior helper, mother in the breeding territory would move out and disperse, which is a female's tactic for incest avoidance.

### 2.2.2 Competition avoidance hypothesis

If the resources (e.g. food) in nature distributes in a patchy manner, according to the optimal foraging theory, animals will distribute themselves and decide their stay times among the patches according to the quality of each patch (Lester et al., 2007). The Ideal Free Distribution (IFD) model predicts that the distribution of individuals at equilibrium

matches with the resources across patches, meaning that if all competitors with equal resources acquisition ability, can move between patches without cost, and have perfect information on the resource supply and competitors' distribution, each competitor is expected to go to the patch where it gains the maximum energy intake (Fretwell and Lucas, 1970). In order to achieve the IFD state, two fundamental assumptions must be fulfilled so that each individual must access and utilize the resources freely and the availability of patches will decrease as the number of competitors increase. Obviously, the competitive abilities are varied in different individuals and thus, they will gain unequal payoffs, which contradict the second assumption of the IFD theory. In this case, a "despotic" distribution will emerge (Harper, 1982). As stated above, patchily distributed resources and different competitive abilities between individuals can lead to intraspecific or interspecific competition. One direct consequence of competition is density-dependent dispersal (Lambin et al., 2001; Sutherland et al., 2002). Individual birds have a high tendency to travel further in the year when the population size increases and the food or the nesting sites become scarce in response to overcrowding (Lack, 1954). The level of pressure from intraspecific competition may influence the dispersal distance (Arcese, 1981). Besides the food and nest site (Löfgren et al., 1986; Delestrade et al., 1996; Newton, 1993), it is true that the juveniles disperse at a further distance in the year when the new fledging rate is high (Greenwood et al., 1978; Nilsson, 1989). Waser (1985) believed that competition for those limited and scarce resources during the avian breeding season is a driving force for certain species. There are also selective benefits of dispersal when individuals are born in a harsh natal territory (Newton and Marquiss, 1993).

Dispersal will be beneficial, avoiding kin competition because close kins are also competitive against each other. This was explained with a classic modeling by Hamilton and May (1977) that even in very stable habitats, dispersers have greater payoffs than philopatry counterparts. This is true in the Siberian Jay (*Perisoreus infaustus*), in which social system sibling conflicts often happen. Inferior individuals are driven out of their natal territories by their dominant cons and dispersed (Ekman et al., 2002).

### 2.2.3 Changing the breeding locations hypothesis

Birds have different habitat preferences and extents of fidelity to breeding sites (Alcock, 2005). Some species switch into a new nesting when another breeding attempt comes while others prefer to retain the old one. Dispersed individuals may have experienced failure of breeding or low reproductive rate and eventually disperse to choose more suitable sites or mates (Dow and Fredga, 1983; Gavin and Bollinger, 1988; Dale et al., 2004).

Individual dispersal has significant influences on the genetic structure and population composition. However, the basic cause of dispersal is not very clear and there is no

single answer to this question (Johnson and Gaines, 1995). Much efforts are needed on the study of the influences of dispersal behavior on the gene flow and fitness between populations and the influences of decision-making in life history components of dispersed individuals on the population dynamic (Clobert et al., 2001). There may be variations in morphology, behavior and genes between dispersers and non-dispersers within a same population, though to what extents these variations influence the individual fitness are not clearly understood so far (Gaines and McGlenaghan, 1980).

## 3 The main research subjects of avian dispersal

The primary objective of the avian dispersal study is to reveal the proximate and ultimate factors that affect the dispersal behavior. The patterns and mechanisms of avian dispersal are diverse and causes of dispersal are also species-specific as we stated above. One point is certain, that such diversity is the consequences of different selective forces on different species in long-term evolutionary history (Gaines and McGlenaghan, 1980). Moreover, closely-related bird species may show some similarity in dispersal patterns (Delestrade et al., 1996; Negro et al., 1997). Presently, studies have been focused on the factors shaping the bird species to disperse (Stenseth and Lidicker, 1993), including sex-biased (Blums et al., 2003), age-dependent (Pyle, 2001), density-dependent (Cam et al., 2004), body condition (Garant et al., 2005), social status (Baglione et al., 2003), habitat and landscape (Breininger, 1999), food (Coles et al., 2003), parasite (Brown and Brown, 1992) and climate change (Walls et al., 2005).

### 3.1 Sex-biased dispersal

In many bird species, males and females often differ in their liability of dispersal with one sex dispersing further than the other. By meta-analysis of several species, Greenwood and Harvey conclude that there is sex-biased dispersal in bird species, where the most common pattern is that females move further than males (Greenwood and Harvey, 1982; Greenwood, 1980). Greenwood explained that the details of mating systems generate asymmetries in the costs and benefits in the two sexes and thus, the sex-biased dispersal is dependent on the different roles of each sex in different mating systems. The key driving force is to reduce possibility of inbreeding and thereby, the dispersed gender will gain fitness benefits from such behavior, not only by means of dispersal distance, but also the proportion of dispersed individuals in a population, Clarke et al. (1997) found the tendency of female-biased dispersal in a wide range of species and supported Greenwood's conclusion. Nonetheless, male-biased dispersal exists in several species.

Based on Greenwood's theory, a large number of studies on avian dispersal have been carried out, investigating the relationship between sex-biased dispersal and varied mating systems. There are 17 species of Tetraonidae in the world with various mating system patterns in this family. In resource or female defense polygyny, females tend to disperse in order to choose non-kin individuals as mates to avoid inbreeding. Females have further distance than males in birds which have such a mating system like the Black Grouse (*Tetrao tetrix*) (Caizergues and Ellison, 2002) and Ruffed Grouse (*Bonasa umbellus*) (Small and Rusch, 1991). But in monogamous species like the Hazel Grouse (*Bonasa bonasia*), on the contrary, males have longer mean dispersal distances (Moss et al., 2006). Group-living bird species (especially in the family Corvidae), like the Black-throated Butcher Bird (*Calocitta formosa*), were reported to have a male-biased dispersal (Langen, 1996), while the Scrub Jay (*Aphelocoma coerulescens*) was found to be female-biased (Woolfenden and Fitzpatrick, 1986). Yaber and Rabnold (2002) found that no matter which sex disperses, the strategy that the non-disperser holds is to protect its territory and social status in the social population in order to mate with more partners while the disperser struggles to consolidate the social status in a new social system and gain more chances to mate. In doing so, potential inbreeding is effectively avoided and these tactics will help produce the balance of sexual conflicts in cooperative breeding species.

### 3.1.1 The effects of body condition on dispersal

Dispersal is a process of energy consumption and may result in a lower survival rate during the movement. Furthermore, in the process of immigration and settlement at new territories, organisms have to face the competition from other individuals. Therefore, body condition plays an important role in the decision-making of dispersal (disperse or not), time to disperse (early or late) and distance to travel (long or short) (Nilsson and Smith, 1998; Dufty and Belthoff, 2001). Generally, natural selection will favor individuals with sufficient deposited energy and suitable body conditions to disperse. The tradeoffs between body condition and dispersal are relevant to the success of dispersal and dispersal distance (Belthoff and Dufty, 1998). Selecting weight and tarsus length as parameters of body condition of the Greater Flamingo (*Phoenicopterus ruber*), Barbraud et al. (2003) found that individuals with better qualifications have a longer dispersal distance. A study also revealed that the dispersal time of the juvenile Marsh Tit (*Parus palustris*) is positively proportional to weight and individuals with a higher hierarchy of the Western Screech Owl (*Otus kennicottii*) disperse earlier and further (Ellsworth and Belthoff, 1999). However, there are some contrary cases that inferior individuals disperse earlier and further (Arcese, 1981). Stronger competitors do not disperse or merely

take short-distanced movement, but they impel inferior individuals to disperse (Gese et al., 1996).

Some studies reveal that dispersal distance is associated with individual's hormone level. Appetite and mobility of individuals are stimulated and increased in the Western Screech Owl and the Long-eared Owl, when the contents of corticosterone in the blood rise to certain levels induced by some endogenic and extragenic factors (Belthoff and Dufy, 1998). Studies of the Spanish Imperial Eagle (*Aquila adalberti*) revealed that inferior individuals which disperse later have higher levels of carbamide and uric acid in the blood (Gonzalez et al., 1989).

### 3.1.2 Dispersal process and habitat selection

Early empirical studies on dispersal emphasize on estimating directional distance but not the details of the dispersal process per se. In fact, the process of dispersal is very complicated and more important (Begon et al., 2006). Birds opt to select suitable habitats for the sake of increasing the survival rate and breeding success by effective dispersal process (Clobert et al., 2001; Wheelwright and Mauck, 1998; Altwegg et al., 2000). The avian dispersal process is divided into three phases: emigration, transience and immigration. An effective dispersal should include all three phases (Lester et al., 2007). From the population ecology's point of view, emigration means loss of the habitat and a new habitat is obtained through immigration, and these two phases are connected by transience (Andreassen et al., 2002). The emigration mechanisms, especially the factors that influence dispersal, have been discussed above. While in the latter two periods, birds are wandering to select novel habitats and gain the breeding opportunities (Doerr and Doerr, 2005). Because of the long-term ignorance and shortage of valid study approaches, the precise mechanisms of transience and immigration are poorly understood (Doerr and Doerr, 2005; Stamps, 2001; Kenward et al., 2002a, 2002b). Efforts have been made to find out physical factors (such as animal sense), landscape and microhabitat factors that determine the transience process (Gundersen and Andreassen, 1998). A study of the spring dispersal of the Elliot's Pheasant (*Syrnaticus ellioti*) pointed out that the major factors acting as barriers of dispersal, such as shrub species, canopy height of shrubs, slopes and abundance of shrubs, have significant influence on the Elliot's Pheasant's dispersal (Peng and Ding, 2005). Organisms acquire new habitats when in the emigration phase, which is composed of searching, entering, prospecting and settling down. Habitat imprinting and conspecific attraction are the proximate factors determining emigration (Doerr and Doerr, 2005). Serrano and Tella (2003) studied the factors governing the dispersal rate of the Lesser Kestrel (*Falco naumanni*) in northeast Spain and suggested that prospecting birds were reluctant to make settlement decision by using the number of conspecificity in the patch

as the cue of indication of habitat quality, but not the patch size. Through meta-analysis of several groups in the animal kingdom, Davis and Stamps (2004) conclude that habitat selection in natal dispersal is in fact a consequence of the imprinting behavior formed from the natal area. The individuals' habitat preferences are closely relevant to the environmental stimulators which juveniles undergo at natal sites, the so called Natal Habitat Preference Induction (NHPI).

### 3.2 Long distance dispersal

Long distance dispersal regularly occurs amongst waterbirds, predators and herbivores passerines, whose breeding performance greatly rely on annually fluctuating resources and nesting sites. For instance, diving ducks in North America show site fidelity to deep permanent water bodies. On the other hand, dabbling duck breeds at shallow impermanent water bodies (Johnson and Grier, 1988). In droughty years, Northern Pintails (*Anas acuta*) tend to travel further northwards to the Arctic Circle for breeding and the breeding dispersal distance can cover as extraordinarily long as thousands of kilometers (Smith, 1970). Long distance dispersal has also been reported in some species of nocturnal predators such as the Long-eared Owl, the Tengmalm's Owl (*Aegolius funereus*), woodpeckers and passerines, because of the lack of nest resources (trunk holes) and food resources (Schloss, 1984; Ferral et al., 1997). By the use of molecular tools such as allozymes and mtDNA, the genetic diversity of the Australian Magpie (*Gymnorhina tibicen*) demonstrates that gene flow exists between two subpopulations over 1599 km. Hence it is clear that the dispersal distance of the species is much further than the previous record (Baker et al., 2001).

## 4 Approaches to the study of avian dispersal

Marking birds for individual study is basic and common in avian dispersal study. By direct observation of the marked individuals, data on presence and absence can be collected to reflect the rate of emigration as well as dispersal distance in each generation (Lensink, 1997). Major methods of marking birds to study dispersal are discussed in the following.

### 4.1 Bird-ringing

Bird-ringing is carried out by capturing birds and marking them with metal rings inscribed with the number and place of marking. Information will be produced by recapturing. Bird-ringing brings to light the flyways of migration (Zhang and Yang, 1997). Once a banded individual is recovered, resighted or reported dead, the information

of redistribution will reflect the movement of the marked individual. As a traditional technique, bird-ringing is widely used in avian dispersal study (Clobert et al., 2001; Delestrade et al., 1996). The merits of bird-ringing are easy-handling and that large numbers of samples can be obtained. When the number of marked individuals is large enough (such as 100–1000) and the recovery rate reaches above 0.04%, survival rate and dispersal could be calculated by computer programs such as MARK and M-SURGE (White and Burnham, 1999; Choquet et al., 2004). The ring is usually less than 1% of the bird's average body mass. At present, no studies have reported that banding has the adverse effects on the normal behaviors of marked individuals (Walters, 2003). In addition to the traditional metal rings, it is more convenient to identify individuals by the combination of different color rings, which makes recognition of individuals possible. Nice (1937) was the first one to use color-ringing to study the life history of the Song Sparrow (*Melospiza melodia*). 47% of the individuals banded every year were found dead or dispersed. Since then, bird-ringing has become a popular and basic technique for dispersal studies. For instance, Reed and Oring (1993) had shown the dispersal pattern and survival rate of Spotted Sandpiper (*Actitis macularia*) after a 18-year recovery project and discussed the application of long distance behavior in shorebirds. After the analysis of the recovery data in 25 years by multivariate regression, the dispersal distance of the Polish population of White Storks (*Ciconia ciconia*) proved to be 94 km on the average, and the individual dispersal distance is positively related to the sex and birth year (Chernetsov et al., 2006).

Although bird-ringing is easy, the limitations are also obvious. First of all, the study scale is restricted to a small area by recapturing and resightings (Newton, 2003). Even for color ring resightings, marked individuals can only be spotted at a limited distance, normally less than 2 km. Topography and vegetation sometimes interfere with the observation (Kenward et al., 2002a, 2002b). Secondly, few individuals are reported again through recovery or resightings. Considering the great amount of human and material resources and a relatively long-cycled study period, the result may not be worthwhile. It was reported that the recovery rate of geese and cormorants was typically close to 25% and merely 1% among passerines. Even in species like the House Sparrow (*Passer domesticus*), a widely distributed passerine in Europe, only 1%–2% return rates were recorded (Walters, 2003).

### 4.2 Radio-telemetry

Radio-telemetry is used for gathering bird data by attaching radio transmitters on them. A tagged bird can be located through the received radio wave by the researcher. The technique is used to answer questions like where (location and home range), how (physiology and survival)

and what (behaviors and related topics) (Kenward, 2004). Compared with bird-ringing, radio-telemetry allows the researcher to collect individual redistribution data beyond the vision of the observer at any time (Kenward, 2004). It upgrades the study scale to a geographical level and makes all-day monitoring for the daily activity of animals possible. More importantly, bird-ringing only reflects marked redistribution in a manner of linear distance while radio-telemetry is able to trace the actual route of movement and the accurate time at the starting point. For the study of birds with better dispersal abilities, like pheasants and birds of prey, radio-telemetry is the most commonly used technique (Kenward, 2001; Kenward et al., 2002a, 2002b; Kenward, 2004). For example, after a nine-year monitoring, Caizergue and Ellison found that female Black grouse chicks tend to disperse further than male ones. Dispersal events mainly occur in the autumn. However, the survival rate calculated with the Kaplan-Meier model shows no sex difference (Caizergues and Ellison, 2002), indicating that the dispersal behavior may not result in the decrease of fitness (O'Riain et al., 1996). Dispersal of the Lanyu Scope Owl (*Otus elegans botelensis*) was investigated by a combination of radio-telemetry and color-ringing resightings. The results proved frequent seasonal movement within the island and the dispersal were related to the age and sex (Severinghaus, 2003).

Although radio-telemetry is one of the most common methods used in avian dispersal study nowadays, there are several disadvantages. The first is the trade-off between the body mass of studied birds and the weights of the transmitters. Naturally, the weight of tag battery affects the longevity of transmitters as well as the distance at which signals are received. The lighter the battery, the shorter life and distance it has. Large and heavy transmitters are not suitable to be fitted on small birds. The second is the adverse effects of transmitters on the normal behaviors of animals. So far, no evidence indicates that transmitters will bias the dispersal behavior. However, it does have influence on the survival of birds (Kenward, 2001). The method of attachment of the transmitter to the bird may be important. Reynolds et al. (2004) compared the effects of tail-mount and backpack on the Goshawk (*Accipiter gentilis*) and discovered that the former method significantly decreased the survival rate. Last but not least, the precision of locating birds, operation protocol and the cost of telemetry should be taken into consideration by researchers.

#### 4.3 Methods of molecular biology

Molecular biology technique is superior to other direct marking methods not only because it is convenient to obtain abundant samples, but also because it may reveal the influences of genetic structure on the present population caused by historical dispersal events (Newton, 2003; Waser and Strobeck, 1998). Therefore, with the

development of molecular biology, researchers have been able to study dispersal patterns using a variety of genetic markers such as allozymes, mtDNA, RAPD, minisatellite DNA and microsatellite DNA, which increases the temporal and spatial scales of avian dispersal studies (Dobson, 1994; Horn et al., 1996).

Dispersal pattern could be better examined by making comparisons of the genetic distance between captured individuals and other individuals within the population *via* genetic markers. Marking-recapturing data sometimes are combined to speculate whether the individuals emigrate from other places (Waser and Strobeck, 1998; Kendall and Nichols, 2004; Powell, 2004). In a study of dispersal pattern of corvidae species in North America with different mating systems, the degree of microsatellite variations was positively related to the dispersal distance. This indicates that dispersal distance has influences on the population structure (Peterson, 1992). Wang and Trost (2001) studied the natal dispersal pattern of the Yellow-billed Magpie (*Pica hudsonia*) by RAPD analysis and found that some adult males show fidelity to the natal site while the females dispersed. The genetic distance was consistent with this dispersal pattern, where the genetic distance between males was closer than between the females. It is believed that such a dispersal pattern is the result of status-dependent competition in the population. Individuals of higher rank exclude the inferior males and females from their natal places and disperse. DNA analysis is commonly used in detecting cryptic dispersal patterns, which are difficult to study by direct markers. By the analysis of the genetic diversity of mtDNA from 12 subpopulations of the Grey-crowned Babbler (*Pomatostomus temporalis*) from Australia to New Guinea, gene flow exists between two subpopulations over 1390 km. However this species has been proven to be a weak disperser in earlier studies (Edwards, 1997).

Another molecular biology method for the study of avian dispersal is to estimate the population differentiation within the population and among different geographical populations. The degree of population differentiation can be determined by calculating  $F_{st}$ .  $F$  statistics by using various types of polymorphic genetic markers.  $F$  statistics is also used to reveal the genetic differentiation within a population (Rousset, 2001). The smaller  $F_{st}$  value means that the fewer differences between subpopulations, indicating that more frequent gene flow and high dispersal rate happened between subpopulations and *vice versa* (Rousset, 2001). This method is commonly used to study evolutionary processes like dispersal and gene flow among subpopulations. For instance, Austin et al. (1994) investigated the genetic diversity of 11 breeding colonies of the Short-tailed Shearwater (*Puffinus tenuirostris*) in southeastern Australia. The result show very little genetic differentiation among different colonies and that some haplotypes are almost shared in every population. Hereby, it is believed that the species

distributed in a limited area in the past and later on the population size and distribution range experienced a fast growth. The Fairy Prion (*Pachyptila turtur*) distributed in an extensive range in the South Pacific Ocean but the observed genetic diversity was low if considering its population size. Ovenden et al. (1991) suggests such a pattern reflects the site fidelity of the species and it is also possible that the species has experienced a bottleneck or founder effect in the past.

#### 4.4 Other methods

Satellite tracking, stable-isotope analysis and hormone analysis are also useful techniques for avian dispersal study. Birds with vast home ranges such as migrating waterbirds and birds of preys require studies in a larger geographical scale. Satellite-tracking in this case will be a suitable method to study such kind of species, with which marked individuals can be precisely traced. However, one disadvantage is that the cost of satellite-tracking is extraordinarily high (Kenward et al., 2002a, 2002b). Satellite-tracking has only been applied to studying the movement of some large-sized and critically endangered species such as the Black-faced Spoonbills (*Platalea minor*) (Ueta et al., 2002), the Siberian Crane (*Grus leucogeranus*) (Kanai et al., 2001) and Steller's Eagle (*Haliaeetus pelagicus*) (Meyburg and Lobkov, 1994). Moreover, Rempel et al. (1995) introduced a technique locating birds using a GPS system. Weimerskirch et al. (2006) applied such a system to the study of the dispersal behavior of the Wandering Albatross (*Diomedea exulans*) in South Pacific Ocean.

In recent years, stable-isotope analysis has gradually become popular in the study of the relationship between organisms and their living environment (Maguas and Griffiths, 2003). Researchers are able to get the information of the home range and migrating data by analyzing isotopes from different tissues of birds. Stable-isotope provides the information of longitude avian movements. For example, through moult sites were estimated by analyzing the profiles of the feathers of North American birds (Hobson, 2005). By comparison of the content of  $\delta^{13}$  and  $\delta^{15}$  in the feather samples of the breeding population of the Barn Swallow (*Hirundo rustica*) before and after the nuclear disaster in Chernobyl, Ukraine in 1986, researchers found that the heterogeneity in isotope from females were higher than males, indicating that females were probably from different sites, thus it was a female-biased dispersal of the Barn Swallow. The variance of stable-isotope contents in that area was significantly higher than the controlled area, suggesting that more individuals from other places emigrated into that area and the subpopulation of Chernobyl played a sink role in a "source-sink" population model (Møller et al., 2006). Hormone analysis has been one of important approaches to provide proximate clues of avian dispersal behavior (Schwagmeyer et al., 2005). One example is that the level directly determined the natal dispersal of the

Western Screech Owl (Belthoff and Dufty, 1998). Although these novel methods have been shown to be effective in some studies, immature protocols and expensive costs limit their popularity. However, they are expected to have promising futures in application.

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## 5 Prospectives

Both the number and the research level of avian dispersal have steadily increased since the 1990s (Nathan, 2003). Individual marking has been commonly used to answer questions such as who is dispersing, when and how long it disperses, in order to detect the ecological effect of dispersal on the individual and the population including the survival rate, breeding success, and population dynamics regulation (Lambin et al., 2001; Sutherland et al., 2002; Lack, 1954; Arcese, 1981; Nilsson, 1989; Löfgren et al., 1986; Delestrade et al., 1996; Newton, 1993; Waser, 1985; Newton and Marquiss, 1993; Hamilton and May, 1977; Ekman et al., 2002). However, these studies can only show the recent proximate reasons. To understand the effects on population geographical distribution, genetic structure, interspecific dynamics, community and ecology system, we obviously need more comprehensive approaches to enlarge the spatial and temporal scales of studies (Nathan, 2001; Kokko and López-Sepulcre, 2006). With the improvement of methodology and the introduction of more accurate and indirect marking methods such as molecular biology and stable isotope analysis, many limitations of traditional methods can be overcome. Approaches combining direct and indirect marking methods are expected to be used more in the future. Moreover, the application of theoretical protocols of current methods to the practical study of dispersal needs more attention.

Observation, experimentation and modeling are three primary steps for ecological research. Modeling can well mimic the target model and help predict future trends (Zhang, 2000). There were only 4% theoretical study papers among 317 papers submitted to one recent meeting of the American Ornithologists' Union, and such a small proportion reflects the neglect of theoretical study in avian ecology for a long time. Since the 1990s, a number of field experiments about dispersal distance, dispersal pattern, and dispersal process have been undertaken and explained the ultimate and proximate factors and dispersal behavior of birds. However, compared with the enormous bird species, their diversities of life history, in addition to the limitations of current empirical work, much more theoretical studies are required (Clobert et al., 2001). By modeling model species, one could accurately describe and forecast the avian dispersal pattern. The use of optimization approach can also predict the optimal dispersal an individual performs. Evolutionarily stable strategy (ESS) may shed light into the computations

of the fitness differentiation between dispersers and non-dispersers within a population. On the other hand, current studies mainly focus on single species. Meanwhile, there is a lack of comparative studies which will be useful to explore the variations of dispersal patterns among species and provide novel insights into the evolution of dispersal behavior.

New selection pressures including habitat alternation, global warming and invasive species caused by human activities will no doubt greatly affect the causes, process and outcomes of avian dispersal. Relevant studies have become a hot topic (Kokko and López-Sepulcre, 2006). The loss and degradation of habitats have led to the restrictions on migration and dispersal, thus resulting in the degradation of population fitness and evolutionary potential (Ferrière et al., 2004). The decrease of genetic diversity and effective population size has become threatening causes for many species (Frankham et al., 2005). Dispersal plays important roles in expanding the distribution area and buffering those adverse effects of habitat fragmentation of habitats (Simberloff, 1988), which is significant for endangered species conservation. Local population dynamics and connection depend on the dispersal between individuals among different roosting patches. Therefore, dispersal behavior has a positive effect on sustaining the dynamic of metapopulation (Hanski and Gilpin, 1997). We suggest that studies of avian dispersal should be combined with practical conservation efforts for threatened birds and the management of their habitats. For instance, dispersal ability can be fortified by habitat recreation and habitat corridors establishment (Macdonald and Johnson, 2002).

Chinese ornithologists paid little attention to study of avian dispersal in the past. However, one national project funded by the National Natural Science Foundation of China namely "The Phylogeny Relatedness and Dispersal Patterns of Endangered Galliformes in China" led by Professor Guangmei ZHENG was established in 2004. Multi-approaches including field ecology, molecular ecology and biological geography were employed to study phylogeny, evolution, dispersal patterns and influential factors of dispersal behavior of Crossoptilon, Tragopan, Syrmaticus, Chrysolophus and some progress have been made. This project has greatly stimulated the avian dispersal study in China. We expect that more efforts will be made in galliformes and passerine birds in the future.

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