

博士論文

**Dispersal process of barn swallows (*Hirundo rustica*)  
breeding in Izu Islands**

(伊豆諸島で繁殖するツバメの分散プロセス)

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# Chapter 1

## General Introduction

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### Population dynamics and dispersal of individuals

A population is an assembly of conspecific individuals in a certain area, and genetic interaction may occur by interbreeding of individuals within the area. Although individual behavior may influence the population dynamics, the dynamics and behavior of individuals were studied under different fields of ecology until Łomnicki first emphasized the influence of individual variation on a population (Łomnicki, 1980; 1988). He stated that emigration, the movement of individuals from a site, caused by unequal food resource partitioning between individuals in a heterogeneous environment, regulates population density and thereby leads to population stability.

Population structure changes with rates of birth, death, emigration, and immigration of individuals (Clobert *et al.*, 2001). In particular, the emigration and immigration of individuals, i.e., dispersal, can be crucial in understanding the spatial structure of a population and in predicting how species respond to environmental change (Bowler & Benton 2005). Dispersal differs from daily movement (e.g., searching for food within a home range). In general, dispersal occurs over a much larger area and its frequency is lesser than that of movement within the home-range area. Therefore, dispersal influences not only individual fitness but also population dynamics and genetics (Greenwood & Harvey 1982; Hanski, 1999; Clobert *et al.*, 2001). For

example, when an individual immigrates to a population at a site, the amount of resources and the number and/or behavior of conspecific resident individuals belonging to the population determine the resource intake rate and reproductive success of the immigrated individual, and vice versa.

Dispersal provides benefits for fitness, such as avoidance of competition between kin or non-kin individuals and avoidance of inbreeding (Clobert *et al.*, 2001). Together with environmental heterogeneity, these factors are considered evolutionary causes of dispersal (Clobert *et al.*, 2001). When habitat quality of sites varies spatially, temporal variation in the quality is likely to favor high dispersal rates. When habitat quality varies spatially but remains constant in time, dispersal is not likely to be favored. Moreover, as mentioned earlier, dispersal can be an efficient strategy for avoiding competition with relatives and avoiding inbreeding in natal sites. When dispersal has a detrimental effect compared to remaining in local sites, dispersal may not be selected. Dispersal behavior also carries fitness costs. The possible costs of dispersal behavior include increased mortality during searching and settlement because of loss of site familiarity (Larsen & Boutin, 1994), and decreased time available for other activities such as breeding (Jakob *et al.*, 2001).

In addition to the variation in dispersal costs and benefits in terms of space and time, these can vary among individuals according to their conditions. In other words, dispersal is a condition-dependent strategy (Massot *et al.*, 2002). In general, dispersal rate (dispersal distance and its proportion) vary with age and sex. For example, natal dispersal, i.e., the movement of first-year breeders between the natal site and the site where breeding first occurs, involves longer distances and is more frequent than breeding dispersal, i.e., the movement of adults between 2 breeding sites (Greenwood,

1980; Greenwood & Harvey, 1982). In addition, the negative fitness consequences of breeding with close relatives (i.e., inbreeding), and asymmetries in the level of intrasexual kin competition, which arise because of mating and the social systems, produce a sex bias in dispersal (Greenwood, 1980; Dobson, 1982; Goudet, 2001). Male individuals usually tend to disperse more than female individuals in the case of mammals; however, in the case of birds, female individuals tend to disperse more than male individuals (Dobson, 1982). According to Greenwood (1980), intrasexual competition is more important than intersexual competition. Therefore, juveniles should disperse more and avoid competition with the same-sex conspecifics, particularly with relatives. In a heterogeneous environment, dispersal behavior may be selected if the benefits of moving to a new site exceed the costs of movement. Thus, dispersal strategy can be described as condition dependent (Massot *et al.*, 2002), and the balance of costs and benefits may determine the dispersal strategy of individuals of a species.

## **Dispersal and habitat selection**

The dispersal process consists of 3 stages; emigration from a site, moving or searching for a new site, and immigration to a new site. During this process, animals such as birds and large mammals with the abilities of movement and cognition, are known to gather information about habitat quality and access it before selecting habitats (Cody, 1985; Dale *et al.*, 2006). To maximize fitness, individuals use several environmental and social factors as cues for their decision-making during the dispersal process (Doligez *et al.*, 2003). The environmental factors are resources, such as the quality and quantity of

food, and refuge from predators. The social factors include the presence, breeding performance, or behavior of conspecific individuals (Danchin *et al.*, 2004; Dall *et al.*, 2005); they are cues that indirectly represent the environmental factors. For example, breeding performance of conspecifics is a powerful cue for breeding habitat selection because it integrates the effects of all the environmental factors on breeding success (Doligez *et al.*, 2003).

Moreover, the age, sex, and the previous experience of individuals interact with each other and influence habitat selection. However, the manner in which these factors are related to each other and their relative influence on habitat selection are both unclear. In addition, only a few studies have simultaneously analyzed the effects of resource environmental and social factors on habitat selection (Müller *et al.*, 2005; Betts *et al.*, 2008).

## **Habitat selection at multiple scales**

How are biological processes related at different scales and how do they interact with each other is a critical ecological question (O'Neill *et al.*, 1989). A scale is defined in the ecological context as “the spatial or temporal dimension of an object or process, characterized by both grain and extent” (Turner *et al.*, 1989). The grain is the finest level of spatial resolution of an ecological data set, and the extent is the physical size or duration of an ecological observation (Turner *et al.*, 1989). Currently, most ecologists agree that the scale is important when acquiring and interpreting ecological data, and hierarchical aspects of ecological observation and analysis are commonly considered.

Why is the multiscale perspective more important to consider than the single scale? There are 2 possible reasons. First, the same ecological process might show different patterns at different scales. If we study a system only at a single scale, we cannot detect its actual dynamics. For instance, because the densities of conspecifics vary with the spatial scale, the density dependence of habitat selection differs at different spatial scales (Oatway & Morris, 2007). Second, observation at a single scale cannot detect all of the aspects of the ecological process. For instance, to investigate the natal dispersal of a species, we need to distinguish between 2 types of movement, i.e., local foraging movement which occurs at a fine scale and natal dispersal, which occurs at a larger scale.

The factors related to habitat quality differ geographically and change over time. As these factors may influence individuals at different scales, the fitness costs and benefits of dispersal may change with the spatial and temporal scales. Thus, habitat selection during dispersal can be viewed as a hierarchical process (Johnson, 1980). For example, during habitat selection, individuals search first in large extents, and make decisions at rough grains; subsequently, they begin to search in smaller extents and make decisions at finer grains. The environmental and social factors may interact with each other and affect the process of habitat selection differently in different spatial and temporal scales (Johnson *et al.*, 2002; Anderson *et al.*, 2005).

Previous studies found that the patterns of habitat use observed at a given spatial scale reflected the constraints of habitat selection at other spatial scales (Leonard, Taylor, and Warkentin, 2008; Mayor *et al.*, 2009). In addition, the spatial scale and temporal scale are related to each other, such that phenomena occurring at larger spatial scales occur slowly. Thus, to investigate habitat selection accurately, we should analyze

it at multiple spatial scales. In fact, a study on the habitat selection of juvenile fish compared the analysis at multiple spatial scales with that at a single spatial scale and showed that analysis at multiple scales better explained the variation observed in habitat use than analysis at a single scale did (Poizat & Pont, 1996). However, it is not known how environmental and social factors interact and influence habitat selection at various spatial scales (Ronce, 2007; Mayor *et al.*, 2009). Moreover, from a methodological viewpoint, the spatial scales chosen in many studies were arbitrary with no biologically relevant level such as home-range size. Wheatley and Johnson (2009) reviewed studies performed over 14 years, and only 29% of the observational scales they examined had biological rationales for their use. Despite the increasing interest in ecological scales, it is still not possible to predict ecological phenomena across observational spatial scales. Accurately choosing observational scales is important for understanding basic questions in ecology, and this choice should be based on ecological criteria rather than human constraints (Orians & Wittenberger 1991).

### **Study species and study areas**

Although the relationship between various factors (e.g., environmental factors and social factors) and habitat selection have received much attention, these relationships are still unclear which may be due to 2 reasons. First, the data collection method used for habitat selection analysis in most studies is inaccurate. Data pertaining to dispersal and habitat selection behavior are difficult to obtain with direct observation in the field (Clobert *et al.*, 2004), and most of these studies have been conducted on spatially continuous landscapes where the movements of individuals are not limited. Second, the

procedures used for assessing the effects of various factors on habitat selection are inadequate in many studies. Most studies do not simultaneously consider the effects of environmental and social factors (but see Müller *et al.*, 2005; Betts *et al.*, 2008). Moreover, as I cited in a previous section, many habitat selection analyses use only 1 spatial scale or the spatial scales are arbitrary selected (Wheatley & Johnson, 2009).

In this study, to overcome these 2 problems in habitat selection studies, I used an easily observable passerine species, i.e., barn swallows (*Hirundo rustica*), as the study species and observed individuals of them on islands with spatially patchy landscapes.

Barn swallows are small (in my study area: mean size 18.12g; n = 49, 2009) insectivorous migratory birds (Fig. 1), that breed in the Northern Hemisphere and overwinter in Southern Hemisphere. In Japan, barn swallows usually breed from the end of March until the end of August. After breeding, they migrate to Southeast Asia and Taiwan, i.e., their wintering grounds, and they return to the breeding grounds the following year. During migration, the majority of annual mortality occurs (Møller, 1994). The annual mortality is about 40-70% for adults and 70-80% for first-years, accordingly most live fewer than four years (Turner & Rose, 1989). They live in close association with human habitation and build nests on or in man-made structures such as barns, bridges, or residential houses. Because swallow nests are easily found and swallows are not overly wary of humans, it is easy to observe their breeding schedule and behavior. Moreover, they are easy to handle and because identification of individuals is important in studying the movement of animals, swallows are ideal for studying bird movements. Therefore, particularly in Europe and North America, many researchers are studying the life history and behavior of swallows, and substantial ecological data have been obtained in this

regard.

In Europe and North America, barn swallows prefer to breed in barns and stables that contain cattle (Møller, 1994; Ambrosini *et al.*, 2002) and mostly live in colonies. In contrast in my study area, barn swallows are mostly solitary breeders and nest on residential houses or stores. They breed together, i.e., in 2-4 breeding pairs, only on large buildings such as the fisheries cooperative building beside the port. Usually, swallows begin to breed when they are one year old, i.e., first-years (Turner & Rose, 1989). Males arrive approximately 0-16 days earlier than females (n = 24, 2010; Ringhofer, unpublished data) and establish a small breeding territory. Adults return to their previous nest sites in successive years, besides unattached males perform a nest showing display, circling over the nest site, singing, and descend to the nest site, to attract females (Turner & Rose, 1989). After establishing breeding pair, they build open cup-shaped new nest or repair an old nest from previous years. Building a nest takes about one week and repairing an old nest takes a few days, depending on the weather (Turner & Rose, 1989). Swallows nests remain for many breeding seasons, and their average life expectancy was seven years in a Belgian study (Møller, 1994). After building a nest, female begins to lay eggs, at the rate of 1 egg per day. The number of eggs per brood is mostly 5 in the first brood (maximum 6) and 4 in the second brood in our study area. The incubation period is approximately 14 days, and is followed by a nestling period of approximately 20 days, that in turn is followed by the fledging period. Swallows usually breed twice in 1 breeding season, i.e., there are 2 broods in 1 breeding season. However, in some cases there is only 1 or even no brood. For example, if the mate of the breeding pair at a nest site arrives late or dies, the beginning of the breeding period at the nest site is delayed. Particularly in my study area, spring storms at the

beginning of the breeding seasons are a cause of delay in the beginning of the breeding period. Moreover, repeated re-nesting caused by the continual predation at the nest site decreases the chance of breeding. During the breeding season, swallows forage near the nest and they mainly feed on aerial insects. In my study area, 81% of swallows foraged within 250 m of their nests ( $n = 308$ , 2009; Ringhofer, unpublished data). To mark individuals, swallow nestlings can be easily captured by hand at the nest sites and adults can be captured with a butterfly net while roosting on or near the nest.

From 2008 to 2010, I conducted field studies at 3 volcanic islands, i.e., Niijima ( $34^{\circ}38'N$ ,  $139^{\circ}26'E$ ;  $23.9 \text{ km}^2$ ), Shikinejima ( $34^{\circ}33'N$ ,  $139^{\circ}22'E$ ;  $3.9 \text{ km}^2$ ), and Kouzushima ( $34^{\circ}21'N$ ,  $139^{\circ}13'E$ ;  $18.9 \text{ km}^2$ ), which are part of the Izu Islands located approximately 47–52 km south of Tokyo, Japan (Fig. 2). Suitable breeding habitat ranges for swallows, i.e., residential areas, are clearly patchy and limited on these islands. There are 2 residential areas on Niijima (Honson,  $7.8 \text{ km}^2$  and Wakagou,  $0.8 \text{ km}^2$ ), 1 in Shikinejima ( $3.2 \text{ km}^2$ ), and 1 on Kouzushima ( $3.2 \text{ km}^2$ ). As the movements of swallows are limited in my study area, I could observe individuals more easily and track the movements of individuals more accurately than in continuous habitats.

## **Scope and outline of this study**

In this study, my purpose was to interpret the dispersal process in barn swallows. By identifying individuals, we observed the dispersal behavior of barn swallows on 3 Islands. The aims of this study were to (1) describe the distribution of the dispersal rate of barn swallows, while examining the differences in dispersal patterns among

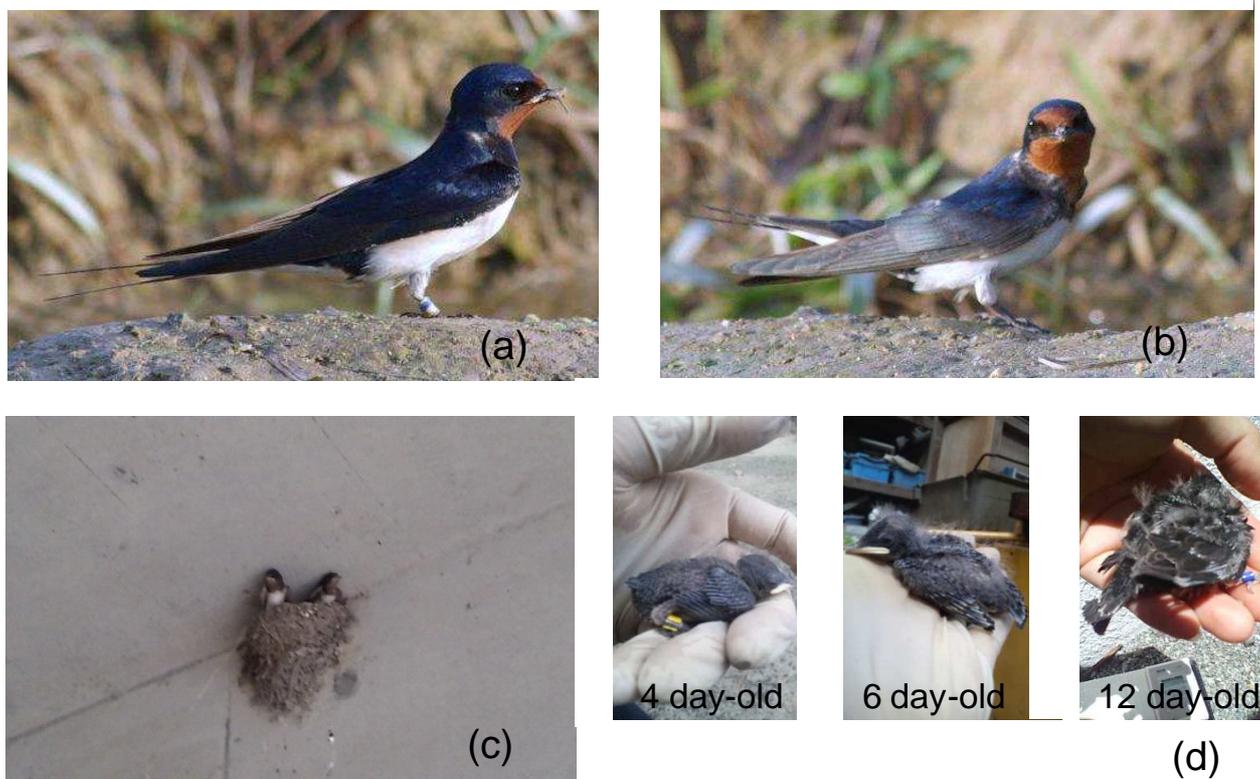
individuals; (2) determine the relative contributions of environmental and social factors to habitat selection during the dispersal process; and (3) assess when and how these factors influence the dispersal process of barn swallows.

In the current chapter, I have explained the general importance of dispersal and the mechanism underlying habitat selection during the dispersal process. In addition, I have accounted for the study species and study area pertaining to this thesis.

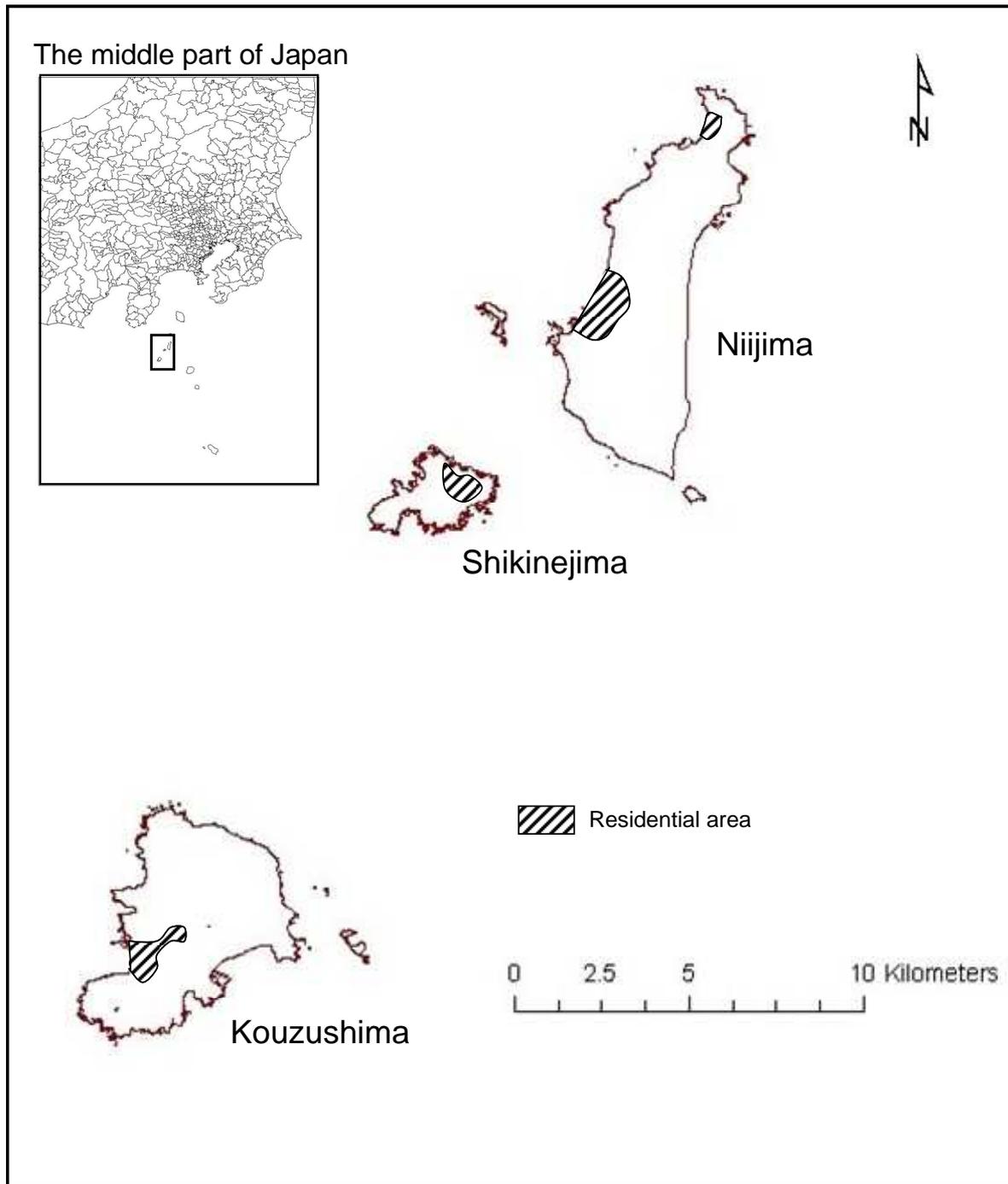
In Chapter 2, I have estimated the dispersal rate with reference to the sex and age of swallows, by using a mark-recapture procedure. For a more accurate estimation of dispersal rate and for comparing the results, I have also used a genetic method for estimating the dispersal rate and distance.

In Chapter 3, I have analyzed the relationships of 2 types of factors (environmental and social factors) with the habitat selection of individuals during the dispersal process. In this analysis, I have considered the decision-making of individuals at several spatial scales.

Finally in Chapter 4, I have summarized the dispersal process of migratory barn swallows breeding on these islands comparing with previous studies. In addition, I suggested 4 significant points to consider while studying dispersal process.



**Fig. 1** The study species, barn swallows. (a) is the male and (b) is the female of barn swallows. Male has longer tail than female. (c) is the nest with fledglings. Nest is made from mud, contains dry grass. (d) is the nestlings of various ages. I determined their age by degree of the growth of wings and body sizes.



**Fig. 2** The study area, Nijima, Shikinejima, and Kouzushima. These islands are part of the Izu Islands located in the Middle East part of Japan. Range of residential areas, i.e., the suitable breeding sites for barn swallows, are indicated with shaded areas.

## Chapter 2

# Estimating the dispersal rate of barn swallows

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### Introduction

Although dispersal behavior is found in a heterogeneous environment, cost and benefit of dispersal differ according to the environmental structure. Even within the same species, the dispersal rate and dispersal strategy may differ in different environments (Clobert, 2001); therefore, to investigate the dispersal process, we must know the dispersal rate of the species in the study area.

Dispersal behavior has often been directly examined in the field by using mark-recapture (or mark-resight) method. In this method, individuals with tags or leg rings and the dispersal distributions are determined by trapping or resighting the individuals. However, using such a direct method in the field is presumed to bias estimates of the dispersal rate (Baker *et al.*, 1995). In this method, not all movements of individuals at various life stages are sampled (Wilson *et al.*, 2004) and the data are based on a restricted sampling area; therefore, long-distance dispersers are missed (Koenig *et al.*, 1996) , and the dispersal rate of individuals in the population or the extent of gene flow cannot be captured. Correcting for this bias is an important step towards obtaining a better estimate of the dispersal rate. For increased accuracy, 2

methods can be considered. First, tracking, such as radio-tracking or satellite-tracking, is an efficient method for increasing the effect size of the study area that is being monitored. In a previous study comparing the estimates of dispersal of the same individuals by using both the mark-recapture method and the radio-tracking method, the dispersal distances using radio-tracking method were longer than using mark-recapture method in both males and females of a mammalian species and an avian species (Koenig *et al.*, 1996). Using radio tracking, it was found that the estimates of dispersal distance increased by approximately 300% in both sexes of mammals, by approximately 500% in male birds and by approximately 750% in female birds. However, the cost of the equipment makes it difficult to increase the amount of data collected. In addition, the equipment is not light enough for use on small animals such as barn swallows (~20g; Møller, 1994).

The second method for determining dispersal is to indirectly measure dispersal and gene flow by using genetic markers. In a previous study comparing the dispersal of the same individuals by using both the mark-recapture and the genetic-marker methods, the means and variance values of the dispersal distance were much larger with the genetic-marker method than that with the mark-recapture method (Koenig *et al.*, 1996). To estimate dispersal distances using genetic markers, we should compare the geographical distance and the genetic data among individuals. In general, close neighbors are genetically more similar than distantly separated individuals, and the correlation of genetic variation between individuals decreases with an increase in the distance among individuals. This phenomenon is called “isolation by distance,” which arises because of geographically restricted gene flow (Wright, 1943). Isolation by distance occurs within subdivided populations when populations exchange genes at a

rate dependent on geographical distance or occurs within continuously distributed populations, when the dispersal of gametes is spatially restricted (Hardy & Vekemans, 1999).

Previous studies of species on island found the genetic structure of populations is influenced by behavioral traits of the species. For example, Galápagos hawks living on the Galápagos Islands avoid flying overwaters and their populations differ greatly among islands (Bollmer *et al.*, 2005, 2006). In contrast, Galápagos doves are strong flyers and frequently move among islands, consequently, the gene flow is high and there is little genetic difference among the populations in different islands (Santiago-Alarcon *et al.*, 2006). Therefore, the movement of individuals such as dispersal, influences gene flow between populations in different sites and determines the genetic structure of populations at certain sites.

The dispersal of barn swallows is studied using mark-recapture method in Denmark, Britain, and Ireland (Turner & Rose, 1989). From a previous study, adults are known to be site faithful and often return to their previous nest site if they successfully bred in the previous year, with only a few swallows changing to other sites (Shields & Crook, 1987). First-years individuals, who do not have previous breeding experiences often returned to within 3 km of their natal sites, most within 30 km (Turner & Rose, 1989). However, because these values of dispersal distance have been obtained based on mark-recapture (or mark-resight) studies, they may be biased. Here, I used the mark-resight method to directly examine the movement of barn swallows among populations and I also used the genetic-marker method to indirectly estimate their movement. Since the indirect genetic-marker method can compensate for estimating dispersal distance on the basis of the direct mark-recapture method (Salonan *et al.*,

2010), it can be used to corroborate or supplement the mark-recapture method (Wilson *et al.*, 2004). In the mark-resight method, I tagged individual barn swallows with leg rings and resighted them at nest sites in the next breeding season to observe breeding and determine the natal dispersal distance. In the genetic-marker method, I calculated pairwise relatedness between individuals by using microsatellite markers and compared the relatedness with geographical distances among individuals. The objective of this chapter is to estimate dispersal distributions in 3 islands (Niijima, Shikinejima, and Kouzushima) and to compare the results of the mark-resight method with the genetic-marker method.

## **Methods**

### **Field method and sample collection**

From 2008 to 2010, I conducted a field study in Niijima, Shikinejima, and Kouzushima. During the breeding seasons in 2009 and 2010, I located and monitored active nests and observed swallows at the nests every day in Niijima, every 4 days in Shikinejima, and twice every 10 days in Kouzushima. Swallow nestlings (2008:  $n = 172$ , approximately 50 % of all the nestlings; 2009:  $n = 398$ , approximately 95 %; 2010:  $n = 244$ , approximately 90 %) and breeding pairs (2009:  $n = 54$ , approximately 65 % of all the breeders; 2010:  $n = 14$ , approximately 25 %) were marked using combinations of colored plastic rings (A. C. HUGHES Ltd.) and individually numbered aluminum rings authorized by the Ministry of the Environment, Japan (Fig. 1a). I simultaneously collected blood samples (20-40 $\mu$ l) from all the swallows. Blood was collected from a

wing vein (Fig. 1b) and preserved in Lysis Buffer (Roche Applied Science). Breeding pairs were caught with butterfly nets at night while they were sleeping at or around the nests during the egg incubation period. Nestlings (the offspring inside the nests before fledging) were caught by hand from each nest during the day. Sixty-one active nests were studied in 2009 (n = 41 in Niijima, n = 7 in Shikinejima, and n = 13 in Kouzushima) and 73 nests in 2010 (n = 47 in Niijima, n = 7 in Shikinejima, and n = 19 in Kouzushima).

#### **Mark-resight method: Direct estimate of the dispersal rate**

I observed the dispersal behavior of barn swallows by resighting the marked individuals at each nest site. During routine observations of nest sites in 2010, I visually checked the combination of colored plastic rings on their legs by using binocular glasses. I noted the birth or breeding sites of the individuals and for adults, I determined the sex on the basis of tail length and throat color.

Using ArcGIS 9.3 (ESRI), I plotted the location of active nest sites for both 2009 and 2010 on a map and calculated the dispersal distance of individuals from their natal sites or previous breeding sites to the new breeding sites.

#### **Genetic-marker method: Indirect estimate of the dispersal rate**

DNA was extracted from the blood samples by using the DNeasy Blood and Tissue Kit (Qiagen). I screened 8 microsatellite loci, and five of these, HrU3, HrU5, HrU6, HrU10 (Primmer et al., 1995, 1996) and Pocc6 (Bensch et al., 1997) were amplified successfully (Table 1). These microsatellite loci were amplified using polymerase chain reaction (PCR). The PCR reaction mixture volume was 5  $\mu$ L, and included 0.5  $\mu$ L DNA,

2.5  $\mu$ L 2 $\times$  QIAGEN Multiplex PCR Master Mix, 0.1  $\mu$ L forward primer, 0.1  $\mu$ L reverse primer, and 1.8  $\mu$ L distilled water. The PCR cycling conditions were as follows: initial denaturation at 95 °C for 15 min; 40 cycles at 94 °C for 30 sec, 57 °C for 90 sec, and 72 °C for 60 sec; and a final extension step at 60 °C for 30 min. The PCR products for all the loci were resolved on a Beckman CEQ 8000 DNA sequencer (Beckman Coulter) and sized using the GenomeLab SNPStart Primer Extension Kit (Beckman Coulter).

I calculated pairwise relatedness (Queller & Goodnight, 1989) within populations by using the program SPAGeDi (Hardy & Vekemans, 2002). Relatedness calculates the genetic similarity of 2 individuals relative to that of the average similarity in the study population. Relatedness values range from -1 to 1, where a value of 1 indicates completely related (identical twins) and 0 or less than 0 indicates unrelated. For example, the relatedness values between parents and offspring is 0.5. SPAGeDi is a computer package primarily designed to characterize the spatial genetic structure of mapped individuals by using genotype data. It can compute relatedness between individuals and analyze how these values are related to their geographical distance. When we define distance intervals for analysis, it compares the mean observed relatedness of each distance interval with the expected value calculated from a defined number of permutations.

In this study, I used 5 microsatellite markers to calculate pairwise relatedness among adults of each sex or among nestlings and examined the relationships between individuals with respect to geographic distances. I considered 3 spatial scales within Niijima: home-range, 250 m; within residential areas, 2.5 km; and between residential areas, 15 km. In addition, I considered 2 more spatial scales within 3 islands: between two Islands, 25 km; and between three islands, 35 km. The home-range scale was

defined as the range of foraging habitat in this study area. Of the foraging swallows observed during the peak of the breeding season (June) in 2009, 85% (n = 308) were located within this range. I performed 1,000 permutations to calculate the expected value of mean relatedness and investigated the difference between this value and the mean observed value.

The DNA samples of 52 adults (29 females and 23 males) in 2009 and 106 nestlings (n = 40 in 2008 and n = 66 in 2009) were used for the analysis. In the samples sets of nestlings, I randomly chose 1 sample from each nest and used it to obtain the genetic information pertaining to nestlings from each nest.

## **Results**

### **Mark-resight method: Direct estimate of the dispersal rate**

During field observation in 2010, I resighted 59 individuals (n = 46 in Niijima, n = 2 in Shikinejima, and n = 11 in Kouzushima) marked in previous years, of which 43 were involved in breeding pairs and were successfully identified (n = 37 in Niijima, n = 0 in Shikinejima, and n = 6 in Kouzushima). These 43 individuals included 18 adults (9 females, 9 males), that is 33 % of the adults marked in the previous year, and 25 first-year individuals (14 females, 11 males), that is 6 % of the nestlings marked in the previous year.

The breeding dispersal distances of all the adults were within 6 km of their previous breeding sites (Fig 2a). Five females and 6 males returned to their previous breeding sites (i.e., they did not disperse). Although the females tended to disperse

farther than the males (females: mean distance, 728.4 m; males: mean distance 628.5 m), there was no significant difference in their dispersal distances (Mann-Whitney *U*- test:  $Z = 0.19$ ,  $P = 0.85$ ).

The first-year individuals dispersed significantly farther than the adults (Fig 2b; Mann-Whitney *U* test:  $Z = 4.63$ ,  $P < 0.0001$ ). From the first-years, one-half of the males stayed on their natal island and dispersed within 3 km of their natal sites. More females than males dispersed more than 21 km, i.e., between Niijima and Kouzushima, (females: mean distance, 9815.7m; males: mean distance 6339.7 m). However, there was no significant difference in their dispersal distances of males and females (Mann-Whitney *U* test:  $Z = 0.87$ ,  $P = 0.39$ ).

### **Genetic-marker method: Indirect estimate of the dispersal rate**

The mean value of relatedness among adults was low in both sexes in all the spatial scales (Fig 3). Among the males, the relatedness slightly differed from the expected value of mean relatedness between residential areas (Fig 3a, two-sided test,  $P = 0.056$ ). The relatedness among females did not differ significantly in all the spatial scales (Fig 3b).

The mean relatedness among nestlings was low and did not differ among individuals in all the spatial scales (Fig4).

## **Discussion**

In the mark-resight method, 33% of the previously marked adults and 6% of the

first-years were resighted the following year. Because this is a relatively high resighting rate for first-year swallows with this method (0.7% in Møller, 1994; 2% in Shields 1984), it is likely that we could obtain more accurate dispersal data. The observational data showed that the dispersal distance of adult males and females was within 6 km and that they stayed near their breeding sites of the previous year. In previous studies, it was suggested that adult barn swallows are site faithful and rarely disperse to a new breeding sites (Shields, 1987; Safran 2004). However, approximately one-half of the adults did not come back to the same breeding sites in my study area. Unlike other study areas, the breeding of swallows were disturbed by other species in my study area. Jungle crows (*Corvus macrorhynchos*) and Japanese rat snakes (*Elaphe climacophora*) prey on swallow nests, and tree sparrows (*Passer montanus*) sometimes break the nests or remove the eggs and pull out the nestlings from the nests. In such situations, breeding pairs tended to change their breeding sites. It is possible that the breeding pairs in my study area were forced to disperse and change their breeding sites, because of disturbance by other species.

The first-years dispersed significantly farther than the adults, having dispersed among the farthest islands (approximately 30km). No first-year individual returned to its natal site. This supports the results of previous studies in that first-years seldom return to their natal sites (Shields, 1984; Brown & Brown, 1999). Previous studies have stated that most first-years dispersed within 3km of their natal sites (Turner & Rose 1989). However, the current study showed that only 50% of the first-year males and 33% of first-year females dispersed within 3km. This might be because of the difference in landscapes between study sites. Since the possible breeding areas in my study area was patchy and limited, I could investigate dispersal distance more accurately than that

in previous studies that had continuous landscapes where the movements of individuals was not limited. In addition, there remains the possibility that swallows in this study area usually do disperse farther than those in previous studies because of the patchy and limited breeding areas.

There were no significant difference in their dispersal distance of males and females both in adults and first-years. Since competition for territory is thought to be intense in male birds and site familiarity is important for them, female birds commonly disperse more than males (Clobert *et al.*, 2001). In this study, it is possible that patchy breeding area bound the dispersal distance of female swallows. In addition, considering that two first-year males dispersed between furthest islands, there remains the possibility that further investigation in larger study area or correcting more data of dispersals may leads the result that females disperse farther than males. Using the mark-resight method, we could investigate the actual dispersal distances of adult and first-year barn swallows. Taken together, the results of this study showed that adults tended to stay near their previous breeding sites within islands, but first-years did not and dispersed a maximum of 27km from their natal sites. However, given that 6 first-year individuals dispersed to the furthest islands, there remains a possibility that the first-year individuals dispersed farther than the range of this study area.

In the genetic-marker method, I calculated the pairwise relatedness among individuals in 5 spatial scales. In adult swallows, both in females and males, relatedness was low and did not significantly differ among individuals throughout all the spatial scales; only slight genetic differences were observed among individuals of different islands. Because males are usually the philopatric sex in birds, it is expected that spatial genetic structuring in the study area is more likely to be observed in males. However,

there was no such a clear trend among males. It is possible that males disperse farther than I expected; however, I could not conclude solely on the basis of genetic data.

The relatedness among nestlings was also low and did not significantly differ throughout all the spatial scales. This result indicates that breeding pairs (i.e., the parents of nestlings) were usually genetically different and that inbreeding did not occur in this group of barn swallows living on these 3 islands. Several reasons for this result can be considered. One possibility is that individuals of either both sexes or 1 sex of the adults or first-year swallows dispersed farther than I expected and may brood freely not only within the study area but also outside the area. Since the genetic structure in a population is influenced by the social behavior of individuals (Clobert *et al.*, 2001), it is also possible that an individual's strict avoidance of inbreeding causes the low relatedness among nestlings. Considering the results that relatedness among adults in both sexes was low and differed throughout this study area, the latter possibility is not very likely. In addition, from the results of the mark-resight method, I know that the dispersal distances of adults were short and those of first-years were significantly longer. It is more likely that the long-distance dispersal of first-years caused the high gene flow and subsequently resulted in low relatedness and little genetic differences in all the barn swallows within this study area. A more definite possibility is that first-year barn swallows may disperse much more than the distance described in previous studies and would disperse over the maximum geographic distance of this study area (approximately 30km).

Long-distance dispersal of first-year individuals carries costs while moving and searching for new breeding sites in an unfamiliar environment (Clobert *et al.*, 2001; Stamps, Krishman & Reid, 2005). Movement between habitats consumes energy and

the risk of mortality increases during searching and after settlement into a new habitat. The time consumed during searching reduces the time for important activities after settlement, such as finding resources or breed mate. Although the energy cost of dispersal does not seem very large for migratory barn swallows, because migrant birds usually have only limited breeding seasons, the time for searching breeding sites would be limited. This leads to questions regarding how these birds can search for breeding sites far from their natal sites. Previous studies found that birds can gather information about the habitat quality of a new breeding site during the previous breeding season (Pärt & Doligez, 2003; Parejo, White & Danchin, 2007). Ormerod, who studied the pre-migratory movements of 3,337 ringed barn swallows in Britain and Ireland, found that the distance that first-years moved at the end of the breeding season was 25–32 km in average (Ormerod, 1991). In addition, I observed 1 newly fledged juvenile of Niijima in Shikinejima and another juvenile in Kouzushima during the breeding season when they were born (Ringhofer, unpublished data). Newly fledged juveniles are supposed to have the ability to fly to other islands over the sea. Therefore, it might be possible for barn swallows to investigate and gather information for selecting a breeding site for the following year in the previous breeding season.

In conclusion, from the 2 methods used to estimate the dispersal rate, I obtained data pertaining to several important issues. From the genetic-marker data, I found that the relatedness of both adults and nestlings was low in all the spatial scales and that the gene flow seemed to be high throughout the 3 islands. From the observational data, I found that first-years dispersed more and farther than adults and they even dispersed among the furthest islands. Combining the results of the 2 methods, I could say that the long-distance dispersal of first-year barn swallows generated the

gene flow in swallows in this study area. These results indicated that first-years freely dispersed among these 3 islands and dispersed farther than that previously observed (Turner & Rose, 1989); furthermore, some of them may have dispersed more than 30 km. Finally, I can quite accurately estimate the dispersal distances of barn swallows in this study area by using observational and genetic data. This study is one of the few studies to combine observational and genetic data to investigate dispersal (Wilson *et al.*, 2004). Arriving at conclusions solely on the basis of a single data type led to misunderstandings about dispersal (Harris *et al.*, 2009), therefore, it is important to use both observational and genetic data to study the dispersal rates of animals.



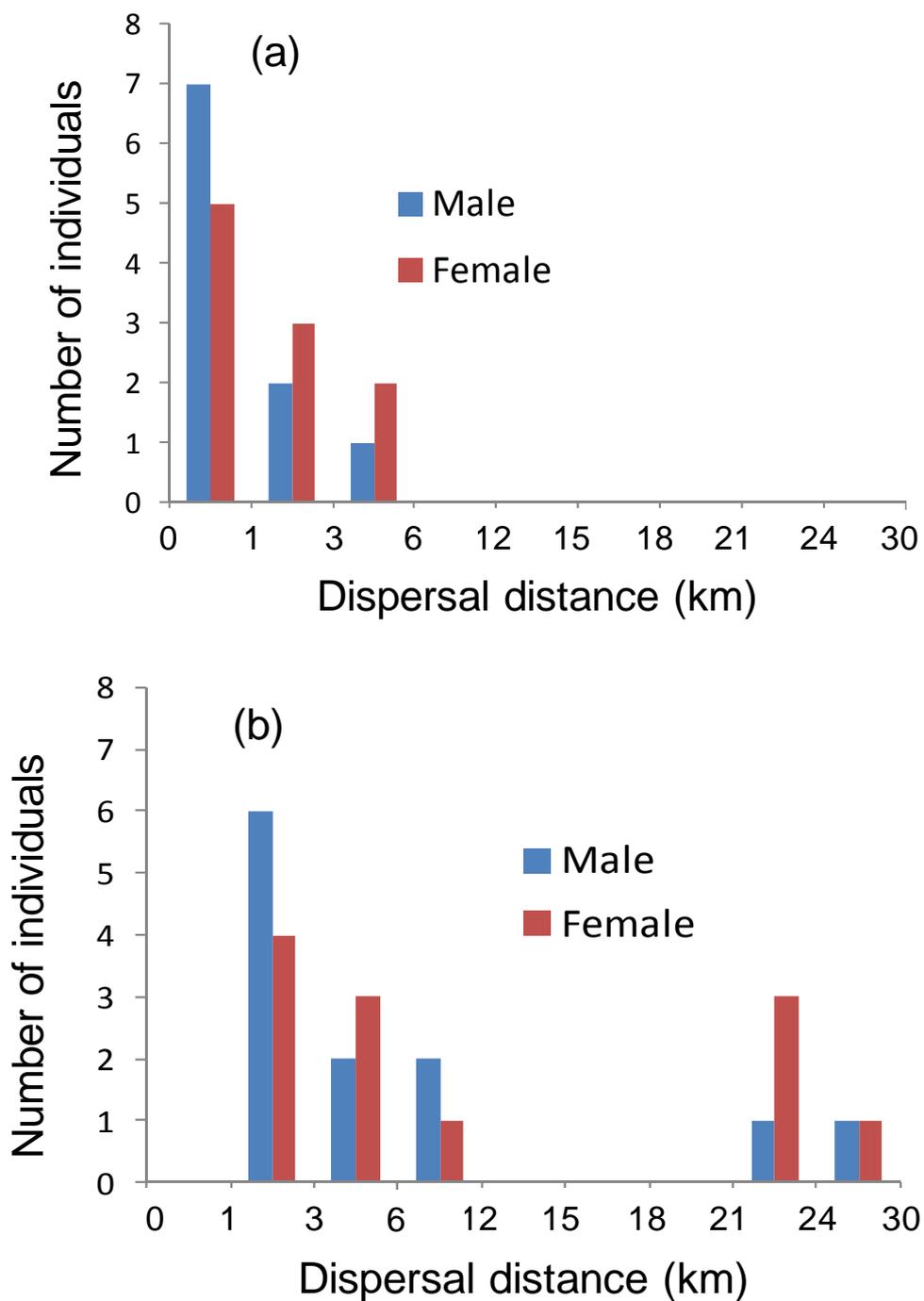
**Fig. 1a** Identifying a swallow by leg rings. Individually numbered aluminum ring on right leg (left picture), and colored plastic rings on both legs (right picture).



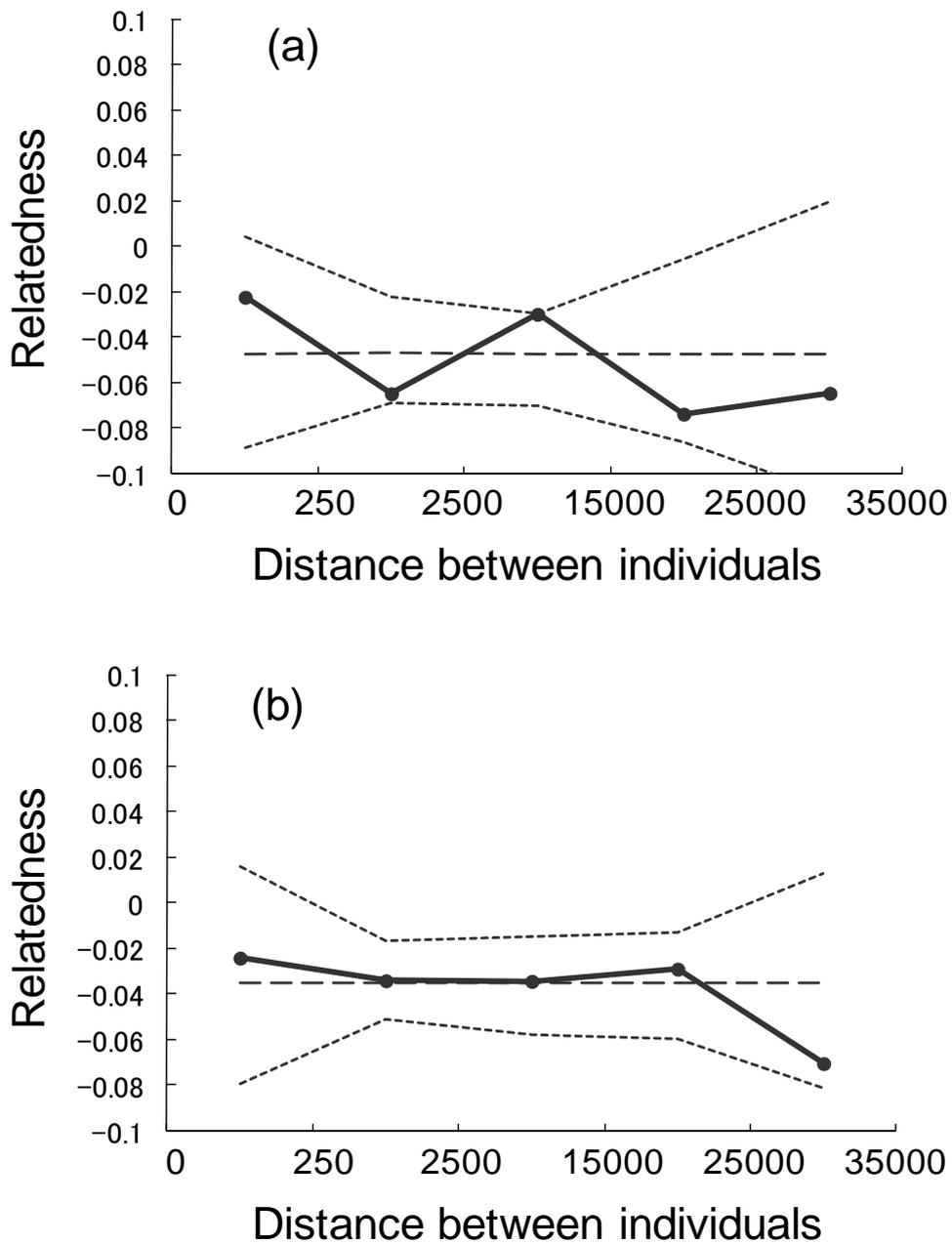
**Fig. 1b** Taking the brood from a swallow from the vein at left wing with a needle.

**Table 1** Primer sequences for barn swallow microsatellite.

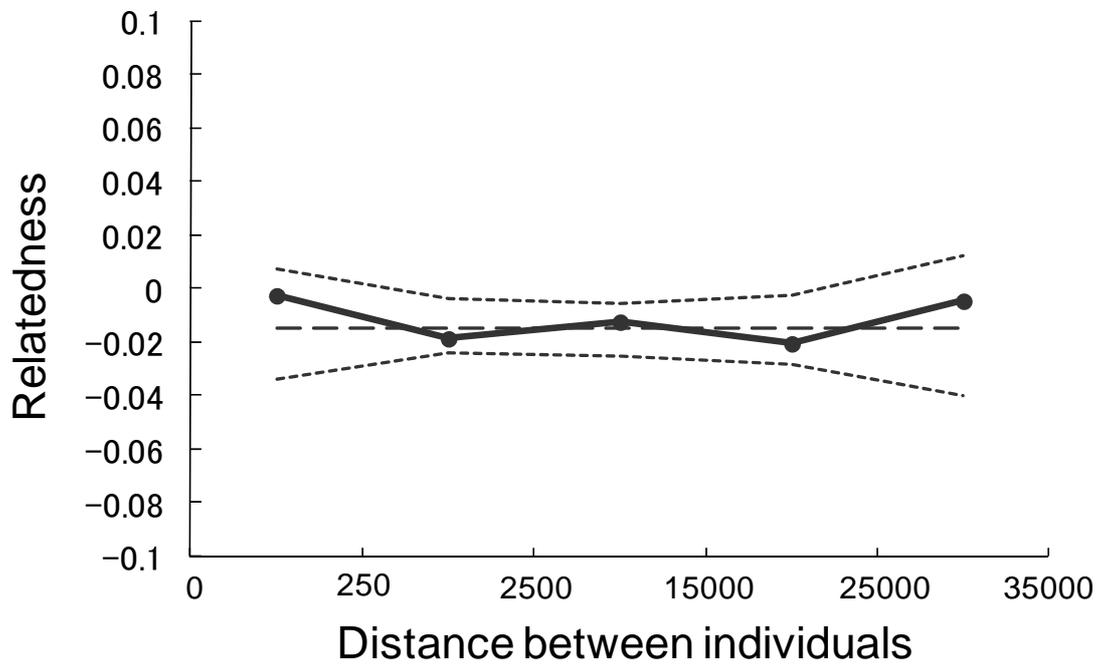
Marker name	Primer sequences
HrU3	A-CACTGGCTCTAGGCTGTCATC B-CTGTCCCATGTCAGGCCAGTC
HrU5	A-TCAACAAGTGTCATTAGGTTC B-AACTTAGATAAGGAAGGTATAT
HrU6	A-GCTGTGTCATTTCTACATGAG B-ACAGGGCAGTGTTACTCTGC
HrU10	A-TGAGTGACTCTGATTTTCAGAT B-GCAGCAATATAAATGTTAAATTC
Pocc6	A-TCACCCTCAAAAACACACACA B-ACTTCTCTCTGAAAAGGGGAGC



**Fig. 2** Observed dispersal distance of barn swallows in 2010. (a) breeding dispersal of adults; (b) natal dispersal distance of first-years.



**Fig. 3** The mean relatedness among adults in five spatial scales. (a) relatedness among males; (b) relatedness among females. Spatial scales are as follows: Home-range: 250m, within residential areas: 2500m, between residential areas: 15000m, between two islands: 25000m, between three islands: 35000m. Dashed line is the expected value with 95% CI (short dashed line above and below this value) calculated from 1000 permutations.



**Fig. 4** The mean relatedness among nestlings in five spatial scales. Spatial scales are as follows: Home-range: 250m, within residential areas: 2500m, between residential areas: 15000m, between two islands: 25000m, between three islands: 35000m. Dashed line is the expected value with 95% CI (short dashed line above and below this value) calculated from 1000 permutations.

# Chapter 3

## Social cues are preferred over resource cues for breeding-site selection in barn swallows

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### Introduction

Habitat selection is a major issue in ecology, because it plays an important role in determining both individual fitness and population dynamics (Pulliam & Danielson, 1991; Fletcher, 2006). Birds are known to gather information about habitat quality before making decisions on habitat selection (Jones 2001; Dale et al. 2006). They select habitats by using a combination of direct resource cues, such as the quality and quantity of safe nest sites or food resources, and indirect social cues, such as the presence or breeding performance of conspecifics (Danchin et al. 2004; Dall et al. 2005).

Since nest predation is the main cause of reproductive failure leading to reduced fitness (Martin 1993), and the risk of predation varies among nest sites (Fontaine and Martin 2006ab), birds are expected to select nest sites that are safe from predation. Social information about habitat quality is easily gathered compared to information on individual experiences in a changing environment (Danchin et al. 2004).

However, it remains unclear how birds assess nest predation risk and how it affects other factors in the decision-making process for breeding-site selection (Eggers et al. 2006; Lima 2009). Additionally, although these factors and their interactions vary

spatially and temporally, only a few studies have simultaneously assessed resource factors and social factors (but see Müller et al. 2005; Betts et al. 2008a). Most studies used individual density as an indicator of habitat preference without obtaining direct estimates of habitat preference (Robertson and Hutto 2006). However, when habitat preference is assessed using the density of individuals alone, the actual effect of predation risk cannot be determined (Chalfoun and Martin 2007). This is because nest predation is related to fine-scale factors, such as nest-site characteristics, whereas density mainly represents large-scale effects, such as food availability (Pulliam 1988; Martin 1998). From the results of chapter 2, swallows seem to disperse long distance, probably over this study area, and there seemed to be less heterogeneity in the landscapes of islands within study area. Therefore, I considered only the fine spatial scale which was suggested to be appropriate for understanding habitat selection (Arlt & Pärt 2007), and would be more important to determine the breeding performance of swallows.

High-quality breeding sites are settled first, and arrival time correlated with habitat preference in migrant birds (Aebischer et al. 1996; Currie et al. 2000). Since high-quality male swallows arrive at the nest sites first (Møller 1994), such nest sites might be preferable. If poor-quality males arrive late, all the good nest sites will probably have been selected and they would not have a real breeding-site selection. However, there are many buildings available for nest sites in my study area, and since there were more buildings without new nests than buildings with new nests, I think that the breeding-site selection of high-quality males does not influence that of other males. Although the date that females lay the first eggs was assumed as an indicator of breeding-site preference in birds (Forsman et al. 2008), it is affected by seasonal climate

variables, such as temperature (Visser et al. 2009), and male quality (Helfenstein et al. 2003). Considering the direct effects of nest-site quality in breeding-site preference, it may be important to use the male arrival date as an indicator of breeding-site preference.

Barn Swallows (*Hirundo rustica*) are migratory, insectivorous, small passerines (Turner and Rose 1989) that breed in close association with human activity and build nests on man-made structures such as barns, bridges, or residential houses. They build open cup-shaped nests and often reuse old nests built by conspecifics in previous breeding seasons (Barclay 1988; Møller 1990).

Here, I analyzed the relationship between predation risk and breeding-site selection in Barn Swallows by using male arrival date as an indicator of breeding-site preference. Several possible resource and social factors were considered as direct and indirect cues. First, I examined the nest-site characteristic related to the occurrence of nest predation. Second, I investigated the cues that are preferentially used in the process for breeding-site selection, including the nest-site characteristic related to predation as one of the direct resource cues.

## **Methods**

### **Nest location and individual monitoring**

During the breeding season, I located and monitored active nests every day in Niijima and twice every 10 days in Kouzushima. Because of fewer active nests in Kouzushima than in Niijima and because I complemented my information with that from building

owners about the breeding schedule of swallows, periodic monitoring on the island seemed sufficient to estimate the breeding schedule. In 2010, the islands had a maximum of 66 active nests (Niijima,  $n = 47$ ; Kouzushima,  $n = 19$ ) where males arrived and became active, namely, including nests where males arrived but failed to breed. I recorded the egg-laying date, clutch size, hatching date, hatching success, fledging date, and fledging success. The arrival dates of males were only recorded in Niijima in 2010. After swallows settled at the nest sites and formed breeding pairs, I monitored the breeding schedule at each nest every 3 days.

Swallows were individually identified by marking nestlings (2008:  $n = 172$ , about 50% of all nestlings; 2009:  $n = 398$ , about 95% of all nestlings; 2010:  $n = 244$ , about 90% of all nestlings) and breeding pairs (2009:  $n = 54$ , about 65% of all breeders; 2010:  $n = 14$ , about 25% of all breeders) by using combinations of colored plastic rings (A.C. Hughes) and individually numbered aluminum rings authorized by the Ministry of Japan Environment Agency. Breeding pairs were caught with butterfly nets while sleeping in the nests at night, and nestlings were caught from the nests by hand during the day.

## **Factors for determining nest-site characteristics related to predation**

### ***Nest predation***

At the study sites, the nests of swallows were predated by jungle crows (*Corvus macrorhynchos*) or Japanese rat snakes (*Elaphe climacophora*). Predator species were determined using field signs such as nest damage, carcasses of nestlings, and broken eggs, in addition to information provided by the building owners where swallows nested. Crows were the main predators in my study area (85% of all predation) and usually

depredated all of the eggs or nestlings simultaneously. Thus, I only analyzed the above datasets to determine nest-site characteristics related to predation.

### *Nest-site characteristics*

Nest-site characteristics, such as concealment, are thought to decrease nest predation rates (Martin 1993). In addition, Barn Swallows build open-cup nests on the walls of buildings, and the building structure is thought to influence the number of fledglings (Fujita 1993). Therefore, I considered building structure and nest location to represent possible nest-site characteristics related to the occurrence of predation. The characteristics may be relatively stable compared to other predation related factors, such as local crow densities. Since stable characteristics are a reliable cue for habitat selection (Schlaepfer et al. 2002), I considered nest-site characteristics as a direct resource cue for breeding-site selection.

In my study area, most nests were located in buildings surrounded by at least three or four walls with an entrance, such as a garage or storage area. Thus, three nest-site characteristics associated with nesting location were evaluated: width (mean value  $\pm$  SD: 403.76  $\pm$  223.36cm) and height (mean value  $\pm$  SD: 275.73  $\pm$  67.78cm) of the entrance that crows could use to approach nests and distance from the entrance to the nests (mean value  $\pm$  SD : 385.37  $\pm$  312.45cm).

In addition to nest-site characteristics, the proximity of people to nests was evaluated to determine predation risk. Birds breeding indoors tended to have lower predation rates than those that bred outdoors (Møller 2010). Furthermore, crows did not approach swallow nests when people were present (Ringhofer, unpublished data). Thus, I assumed that the proximity of people would likely reduce predation. I recorded the daytime presence and flow of people during observations of male arrival dates (see

detailed description in “Breeding-site preference” section). The proximity of people to nest sites (i.e., within 2–4 m) was divided into three levels: (1) no persons present within 30-min (level 1), (2) one person present every 15 min (level 2), and (3) at least one person almost always present every 5 min (level 3).

## **Variables for analyzing breeding-site selection**

### ***Breeding site preference***

I used the arrival date of males as indicators of breeding site preference and conducted observations at each existing nest at the onset of the breeding season (from March 22, 2010) in Niijima. Each nest site was monitored during two 15-min observations per day every 3 days. If a swallow appeared at the nest site at least once during an observation, I changed the observation schedule at that nest to two 1-h observations per day to determine if the male had actually settled at the nest site or was only searching for breeding sites.

To estimate reliable values reflecting breeding site preference, I did not include data sets of individuals that returned to the same nest sites used in the previous year to exclude the effect of site fidelity. I aimed to investigate how swallows select breeding-sites using cues in the current year, and site-faithful males might select nest sites based on cues from the beginning of previous breeding seasons. Also, I did not include data sets of individuals that moved from other nest sites because of breeding failure. Because most Barn Swallows in my study area were solitary breeders, I only used data for the first male that arrived at each nest site. During observations, I identified the age of the breeding individuals (adults or first-years) by visually checking

the combination of colored plastic rings on their legs. Of all the males that arrived, 10 were locally born yearlings (born in Niijima). Two males that successful bred in the previous year moved to other nest sites this year. The 23 males used in my analysis included 7 first-time breeders.

### ***Direct resource cues***

I used nest-site characteristics related to predation (which I detected in my previous analyses on nest predation) and areas of potential foraging habitats as possible direct resource cues influencing breeding-site selection. Foraging habitats were represented by the total area of three types of vegetation, including forest, forest edge, and farmland, where foraging behavior by swallows was mainly observed during the breeding season (71/89 incidents in 2009). I analyzed a vegetation map provided by the Japanese Ministry of the Environment by using Arc GIS 9.3 (ESRI) to measure the areas of the three foraging habitats within a 250-m buffer of each nest site. I used a buffer size of 250 m because 85% ( $n = 308$ ) of foraging swallows observed during the peak of the breeding season (June) in 2009 were located within this range. This supports the results from previous studies on European swallow populations, in which >90% of Barn Swallows foraged within a distance of 500 m from their nests (Møller 1987).

### ***Indirect social cues***

As possible indirect social cues for breeding-site selection, I focused on the number of breeding pairs and breeding success in the previous year. The number of breeding pairs was assumed to represent the presence of conspecifics. I also used this variable to control for the possibility that previous breeding pair density might affect the number of early-arriving individuals in the next year. Breeding success was defined as the number of total fledglings per pair at each nest site during the breeding season and was assumed

to indicate the breeding performance of conspecifics.

### *Number of old nests*

The number of old nests has been suggested to play a crucial role in breeding-site selection of Barn Swallows (Safran 2004). Nest predations were not rare in my study area. Since swallows build nests that remain for several breeding seasons and often reuse old nests (Barclay 1988; Møller 1990), if predation occurred at a nest, the damage to the nest likely remained, unless repaired. To repair damaged nests, swallows must spend more time and energy than that by individuals breeding in old undamaged nests (Barclay 1988; Cavitt et al. 1999). Therefore, I assume that the presence of old or undamaged nests or the extent of damages may be direct resource and/or an indirect social cue for breeding-site selection. If the number of undamaged old nests is related to breeding-site preference only at the finer spatial scale, the nest-site scale (see the “spatial scales for analysis” section below for details), this can be regarded as a direct resource cue, because swallows can benefit from using an undamaged old nest instead of building a new nest. Conversely, if it is related only at the larger spatial scale, the home-range scale, this can be regarded as an indirect social cue, because it is important for swallows to breed near undamaged old nests, which could be indicators of a safe area with little or no predation risk.

Prior to the breeding season, I counted the number of old nests in my study area and categorized the degree of nest damage into four levels: (1) old nests with no or minimal damage to the edge, (2) nests with up to 50% lost, (3) nests with 50–80% lost, and (4) only the imprint of a nest remaining on the walls of buildings. Because swallow nests are broken during predation attacks by crows, I assumed that undamaged old nests (level 1) were nests that had not been recently depredated by crows.

### *Spatial scales for analysis*

When analyzing breeding-site selection, I used indirect social cues, number of old nests, and number of undamaged old nests at two spatial scales. The large spatial scale was within a 250-m buffer of each nest and defined as the foraging-habitat range (i.e., the home-range scale; see “Direct resource cues” section for more details)). The finer spatial scale was the actual nest site, including the building. At the home-range scale, I summarized the values of the cues for all nests within 250 m of each nest site by using ArcGIS.

### **Statistical analysis**

#### *Nest-site characteristics related to predation occurrence*

To examine the nest-site characteristics related to the incidence of predation, I included the occurrence of predation at each nest site (depredated: 1; not depredated: 0) as a response variable in generalized linear models (GLMs) assuming binomial distribution. Since the three nest-site characteristics were intercorrelated, I first used principal component analysis (PCA) based on the correlation matrix to derive two components (Table 1). Principal component I (PCI) primarily represented the narrowness of the entrance, and principal component II (PCII) primarily represented the distance from the entrance to the nest. Then, I used PCI and PCII, proximity of people, and islands (Nijjima or Kouzushima) as explanatory variables. I only analyzed nest-site data sets for which all records of the response and explanatory variables included in the models were available ( $n = 32$ ). I first constructed the initial model by incorporating all the explanatory variables. Then, I conducted a series of stepwise deletion tests, where any nonsignificant explanatory variable was removed. The significance of the terms in the

model was determined by calculating the deviance of the model with and without those terms and comparing the reduction in deviance with the chi-square test.

### ***Breeding-site selection in swallows and predation risk***

I tested whether swallows select breeding sites based on nest-site characteristics related to predation as a direct cue of predation risk or based on social cues that may indirectly indicate predation risk. I used GLMs with quasi-Poisson as the error distribution. The arrival date of males was the response variable representing breeding-site preference. Two types of direct resource cues (i.e., nest-site characteristics related to predation and potential foraging habitats), two types of indirect social cues (i.e., the number of breeding pairs and breeding success in the previous year), number of undamaged old nests, number of old nests, and individual age were used as the explanatory variables. Since the arrival dates were suggested to differ with age in European Barn Swallows (Balbontin et al. 2009), ages of males that arrive first at the nest sites were used. The considered spatial scales were the nest-site and home-range. I only used the data sets for nest sites where all records of the response and explanatory variables included in the models were available ( $n = 23$ ). Since my sample size was limited, I investigated the breeding-site selection of swallows by using minimal variables and did not to include the interactions between variables and the number of old nests for four different categories as explanatory variables. To investigate whether swallows select their breeding-sites based on the degree of damage to the old nests and if they use undamaged old nests more frequently than other old nests, I included the numbers of undamaged old nests and total old nests. I tested the multicollinearity of the explanatory variables based on the value of variance inflation factor (VIF, Montgomery and Peck 1982). Since the VIF was more than 0.1 and less than 10 for all the variables (i.e., in the

tolerance range; Bowerman and O'Connell 1990), all were used as the explanatory variables in the model. I selected the variables by using the same procedure as that used for the analysis of predation occurrence. The significance of the terms in the model was determined using *F* test. All analyses were conducted using R statistical software (The R project for Statistical Computing; <http://www.r-project.org/>).

## **Results**

### **Nest-site characteristics related to predation**

The incidence of nest predation (7/32 nests) was negatively related to the narrowness of the entrances (PCI: from the PCA of nest-site characteristics) to the buildings where swallows nested (Table 2). In contrast, none of the other variables indicated a risk of predation.

### **Breeding-site selection in swallows and predation risk**

The number of undamaged old nests was negatively related to the arrival date of males at the home-range scale (i.e., within 250 m of the nest site), but not at the nest-site scale (Table 3, Fig. 1,  $n = 23$ ). I detected no relationship between male arrival date and nest-site characteristics related to predation (i.e., narrowness of the entrances to the buildings where swallows nested). Other direct resource and indirect social cues were not related at either spatial scale.

## **Discussion**

The incidence of nest predation by Jungle Crows, the main predators of Barn Swallow eggs and nestlings, was reduced if the entrance to the buildings where swallows nested were narrow. Crows appeared to avoid approaching nests that were located in buildings with narrow entrances. Therefore, the narrowness of the entrance may make it more difficult for crows to see inside a building or approach the nests.

In this study, I compared the significance of direct resource and indirect social cues for breeding-site selection in Barn Swallows. My results indicate that when male swallows select their breeding sites, they likely use an indirect social cue, such as number of undamaged old nests.

A previous study on variation in the colony size of Barn Swallows (Safran 2004) suggested that old nests are a cue for settlement decisions by site-unfamiliar individuals. In this study, although I obtained a similar result showing the importance of undamaged old nests for site selection in male swallows, there were some differences. In addition to the number of old nests, I also focused on damages that might have been caused by predation. As described previously, most of the swallows in my study area were patchily distributed on the islands and were solitary breeders, and nest predation by crows was not rare. Thus, I considered possible resources and social cues to determine the breeding-site preference variables of individuals (i.e., male arrival date) rather than the settled number of individuals in breeding sites. As a result, I detected the actual and relative importance of possible cues for individual breeding-site selection in Barn Swallows. My results and those of the previous study (Safran 2004) clearly show that, although there was a slight difference between the study sites, the presence of old

nests at the beginning of the breeding season substantially influences decision-making in Barn Swallows.

The number of undamaged old nests was related to breeding-site selection in males at the home-range scale but not at the finer nest-site scale. Previous studies have suggested that old nests could be used by birds to reduce the costs (i.e., energy or time) of nest building (Cavitt et al. 1999). If swallows were attracted to undamaged old nests only as a means for reducing the cost of nest building and for use as direct resource cues, the presence of undamaged old nests should have also been related to breeding site selection at the nest-site scale. However, my findings did not support this hypothesis. Consequently, swallows likely used undamaged old nests as an indirect social cue that may indirectly predict resource quality and quantity.

A previous study in Europe investigated the effect of the presence of livestock on the number of breeding pairs at two spatial scales and showed that the presence of livestock are more influential at the nesting scale than at the foraging-range scale (Ambrosini and Saino 2010). This result appears to differ from my results in that breeding-site preference was related to the number of undamaged old nests at the home-range scale, but not the nest-site scale. I suspect that this discrepancy could arise from the relatively high level of predation risk at my study sites. Predation on eggs and nestlings, mainly by Jungle Crows, were common at my study sites. As previously explained (see above), because predation is likely to occur in a non-deterministic way and may be related to the home-range of such predators, it is likely to be difficult for swallows to make precise evaluations of predation risk at the nest-site scale (<10 m), while it could be possible at the home-range scale ( $\geq 250$  m). I surmise that a certain number of undamaged nests at the home-range scale might be indicative of a low risk of

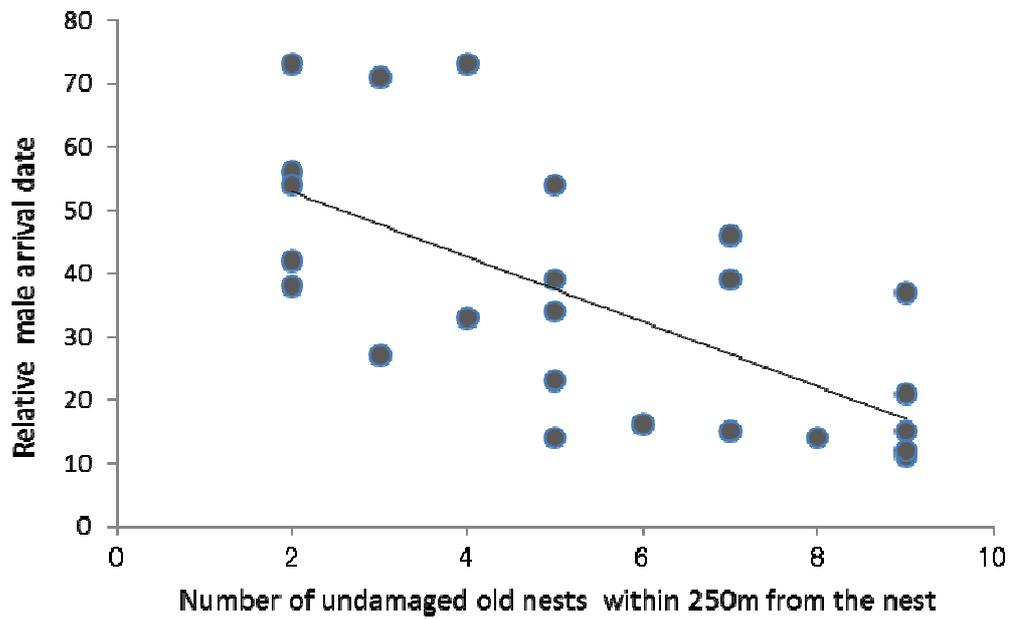
predation by crows.

Among the possible indirect social cues, number of breeding pairs and breeding success in the previous year did not contribute to breeding-site selection. Birds have been shown to gather information about the presence and breeding performance of conspecifics during the breeding season to select a suitable breeding site in the following year (Pärt and Doligez 2003; Parejo et al. 2007; Betts et al. 2008b). However, the number of breeding pairs and breeding success provide information about the presence and breeding performance of conspecifics for a single year only, whereas undamaged old nests may provide information from several years. Thus, in birds that maintain nests over many seasons, such as swallows, an undamaged old nest may be a reliable indirect social cue that represents a low risk of predation. Moreover, a previous study in Europe showed that past ecological conditions are better predictors of the distribution of Barn Swallows than that by the current ecological conditions (Ambrosini et al. 2002b). Although study sites differ, it is likely that swallows select their breeding sites based on reliable cues that provide information from prior years, and thus, their distribution is related to the conditions of past breeding sites.

The use of indirect social cues for breeding-site selection reduces the costs associated with trial and error learning (Danchin et al. 2004). Additionally, breeding performance is higher in individuals using indirect social cues than those using environmental cues (Boulinier and Danchin, 1997). Social factors integrate the effects of environmental factors on breeding-site selection (Doligez et al. 2003). Moreover, indirect social cues are assumed as useful when birds have limited time for habitat sampling because of the seasonal constraints of breeding (Boulinier and Danchin 1997; Valone and Templeton 2002). Since swallows are migratory birds, they likely have

limited habitat-sampling opportunities. Therefore, they may use indirect social cues as reliable cues for breeding-site selection.

In conclusion, the findings of this study show that breeding-site selection in Barn Swallows is based on the cue of undamaged old nests and that nest sites surrounded by undamaged old nests are preferred breeding sites. This investigation is one of the few studies that simultaneously analyzed the relative effects of resource and social cues on breeding-site selection (Müller et al. 2005; Betts et al. 2008a). This study shows the importance of an indirect social cue in the process of breeding site selection in migratory birds. Furthermore, I show that factors affecting breeding-site selection may vary at different spatial scales. Although the nest-site characteristics related to predation did not affect the analysis in terms of predator activity (Schmidt et al. 2006) and memories (Sonerud 1993), swallows might cue on nest-site characteristics in hierarchical breeding-site selection strategies. Further analysis is required to examine whether swallows use a combination of undamaged old nests and nest-site characteristics as cues at different spatial scales.



**Fig. 1** Relationship between the arrival date of males and number of undamaged old nests. Relative male arrival date is expressed as the number of day after the arrival date of the first male swallow at the nest site in our study area (considered as March 10, day1). The line represents the trend of the data

**Table 1.** Results of principal component analysis of three characteristics of nest sites where swallows bred: the height and width of the entrance that crows could use to approach nests and the distance from the entrance to the nests.

	PCI	PCII	Contribution
<b>Loadings</b>			
Height	0.87	-0.03	0.76
Width	0.73	-0.56	0.85
Distance to nest	0.56	0.79	0.93
<b>Eigen.values</b>	1.60	0.94	
<b>Cumulative.prop. (%)</b>	53.17	84.65	

**Table 2.** Results of the generalized linear model analysis of nest-site characteristics related to predation occurrence. Predation incidence is the response variable. PCI is principal component I, and PCII is principal component II from the principal component analysis of three nest-site characteristics associated with nesting location. Residual deviance of initial model = 24.15 on 27 *df*, null deviance = 33.62 on 31 *df*. Residual deviance of final model = 28.6 on 30 *df*, null deviance = 33.62 on 31 *df*. Only nest sites that fulfilled all explanatory variables were used for this analysis ( $n = 32$ ).

Terms	$\Delta D$	P
<b>Initial model</b>		
PCI: Narrowness of the entrance	-5.694	0.017
PCII: Distance from the entrance to the nest	-1.347	0.246
Proximity of people	-0.123	0.726
Island	-2.630	0.105
<b>Final model</b>		
PCI: Narrowness of the entrance	-5.020	0.025

**Table 3.** Results of the generalized linear model analysis of breeding-site preference in swallows. Arrival date of males is the response variable. Adequate spatial scales were considered for each explanatory variable. Residual deviance of initial model = 71.88 on 11 df, null deviance = 254.33 on 22 df. Residual deviance of final model = 141.96 on 21 df, null deviance = 254.33 on 22 df. Only nest sites that fulfilled all explanatory variables were used for this analysis (n = 23).

Terms	$\Delta D$	P
<b>Initial model</b>		
Age of individuals	0.197	0.666
Direct resource cues		
Nest-site characteristics related to predation	0.263	0.618
Areas of foraging sites within 250 m	1.973	0.188
Indirect social cues and old-nest numbers		
Breeding success of previous year at nest site	3.020	0.110
Breeding success of previous year within 250 m	0.025	0.878
Number of previous breeding pairs at nest site	0.132	0.724
Number of previous breeding pairs within 250m	0.002	0.968
Number of undamaged old nests at nest site	0.001	0.979
Number of undamaged old nests within 250 m	1.636	0.227
Number of old nests at nest site	0.498	0.495
Number of old nests within 250 m	0.383	0.549
<b>Final model</b>		
Number of undamaged old nests within 250 m	14.929	0.0001

# Chapter 4

## General discussion

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### Dispersal rate and distance of barn swallows breeding in volcanic ocean islands

Animal dispersal comprises 3 stages; departure, searching, and settlement (Clobert, 2001). During each stage, dispersal carries with it various fitness costs and benefits. The costs include increased mortality during searching and settlement (Laren & Boutin, 1994) and limited time available for other important activities, such as breeding (Jakob *et al.*, 2001). The benefits include avoiding competition between kin or non-kin conspecific individuals, and reducing the chance of inbreeding. These costs and benefits vary among individuals. For example, female birds tends to disperse more than males (Dobson, 1982), and first-years disperse more than adults (Greenwood & Harvey, 1982). Therefore, the dispersal strategy of an individual of a species is determined by a balance of costs and benefits, which varies in space, time, and among individuals.

Based on observational and genetic approaches, I found that there was no significant difference in dispersal distance between female and male barn swallows (Mann–Whitney  $U$  test:  $Z = 0.19$ ,  $P = 0.85$ ) and that first-year swallows dispersed more than adults (Mann–Whitney  $U$  test:  $Z = 4.63$ ,  $P < 0.0001$ ); moreover I found that first-year swallows most likely dispersed beyond the range of my study area, which

included 3 volcanic ocean islands: Nijjima, Shikinejima, and Kouzushima. In my study area, the number of dispersed adults was more and the dispersal distance of adults and first-years was longer than those reported in previous studies (Shields, 1984; Brown & Brown, 1999). Because dispersal rates and distances may differ in different environments and even within the same species (Clobert, 2001), the different environments between study areas might be the cause of these results. In contrast to the landscapes in previous studies, the landscapes in my study area were not continuous; moreover, areas serving as suitable breeding sites for swallows were limited. In addition, the relatively high nest predation rates in my study area might have led adults to change their breeding sites during the breeding seasons. Namely, the patchy landscape in my study area enables to obtain accurate dispersal rate and distance of individuals, but on the other hand, I can't deny that this landscape may be one of the reason that cause the difference between this study and previous studies.

Because 2 approaches were used to gather the data and the landscape of the study area, the data on dispersal distance in this study are likely to be more accurate than those in previous studies. Unlike in my study areas, previous studies of dispersal were observed in a non-fragmented or continuous landscape, where the movements of individuals were not limited. In addition, most previous studies used only the mark-recapture (or mark-resight) method to estimate dispersal rate and distance. In contrast, I used both mark-recapture and genetic-marker methods together. By combining the results of 2 methods, I was more clearly able to demonstrate that first-years dispersed much farther than that described in previous studies; moreover, my study showed that the first-years dispersed over the maximum geographic range of the study area (approximately 30 km). Because it is possible that making conclusions based

on only a single data type can lead to misunderstandings about dispersal (Harris *et al.*, 2009), the errors in the estimated dispersal distances from previous studies could have been the reason for the difference in the dispersal distance observed in previous studies and those observed in my study.

This is one of the few studies that used both observational and genetic methods to investigate dispersal (but see Wilson *et al.*, 2004) and attempted to estimate more accurate dispersal rates and distances of barn swallows breeding in the Izu islands. In addition, estimation of the dispersal distances of barn swallows in this study area was useful for deciding the spatial scales in the analysis of their dispersal process, i.e., breeding site selection.

## **Importance of social cues in breeding site selection of migratory barn swallows**

Birds are known to select habitats by using a combination of resource and social cues that directly and indirectly represent habitat quality (Danchin *et al.*, 2004; Dall *et al.*, 2005). Recently, the use of social cues, in particular, has received increased attention (Danchin *et al.*, 2004; Dall & Giraldeau, 2005, and references therein). Social cues include the presence or breeding performance of conspecifics. The use of social cues for selecting habitat reduces the time needed to search for a suitable habitat and enhances the value of the information obtained about habitat quality (Nordell & Valone 1998; Danchin *et al.*, 2004). In addition, breeding performance is higher in individuals using indirect social cues than those using environmental cues (Boulinier and Danchin, 1997).

Therefore, social cues may be more useful to migratory birds, which have relatively limited time for habitat sampling because of the seasonal constraints of breeding, than to resident birds (Boulinier & Danchin, 1997; Valone & Templeton, 2002).

Barn swallows are migratory birds. In a previous study on the colony size of barn swallows, old nests were suggested to be an important cue for site-unfamiliar individuals (Safran, 2004). However, from the results of this study, Safran did not declare the old nests as the social cues and conclude that immigrant swallows cued on old nests only to reuse them. These results agreed with those of another study (Cavitt, Pearse & Miller, 1999). In contrast, I analyzed the breeding site selection of barn swallows by considering a combination of resource and social cues, and my results suggested that the number of undamaged old nests served as an important social cue for the selection of a breeding site. The number of undamaged old nests was related to breeding-site selection in males at the home-range scale but not at the finer nest-site scale. In addition, I compared the effects of old nests (both damaged and undamaged old nests) and undamaged old nests and found that the number of undamaged old nests influenced breeding site selection more than old nests (Ringhofer, unpublished data). These results indicated that undamaged old nests were not a resource cue but a significant social cue that influenced breeding site selection more than other social cues, such as breeding success and number of breeding pairs in the previous year.

Several factors could explain the difference between previous study and my study. Since nest predation is the main determinant of breeding success in birds (Martin, 1993; Fontaine & Martin, 2006), it would appear that predation is strongly correlated with habitat quality; therefore, birds would avoid nest sites having a high predation risk while selecting breeding sites. Moreover, they might use resource cues for selecting

breeding sites. However, there were some cases in which birds could not gather enough information about habitat quality during settlement based on only resource cues (Boulinier & Danchin, 1997). When it was impossible to obtain information on habitat quality based on resource cues alone, animals used social cues to aid in their search (Smith & Peacock, 1990; Muller *et al.*, 1997). Social factors integrate the effects of environmental factors on breeding-site selection (Doligez *et al.* 2003). In my study area, unlike the area used in previous study, swallow nests were often predated and destroyed by jungle crows, and the breeding attempts were, at times, disturbed by tree sparrows. Therefore, it was likely that swallows in my study area used information on the number of undamaged old nests because it provided faster and more accurate information about the habitat quality. In addition, in contrast to the findings of previous study, barn swallows in my study would usually select an initial nest site with old nests; moreover, they did not breed in colonies at stables but rather solitarily on buildings in residential areas. In addition, there were enough buildings, (i.e., potential nest sites), indicating that this was not a limiting factor for breeding site selection (Ringhofer, unpublished data).

The differences in nesting patterns of barn swallows or landscapes between Safran's study site and my study site and the high rate of predation in my study site might be the factors responsible for the differences in these results. This would support the results of previous studies, which showed that even among the same species the dispersal pattern was different among populations living under different environmental conditions (Mennechez *et al.*, 2004). In addition, other studies hypothesized that social cues are important for habitat selection of migratory birds (Boulinier & Danchin, 1997; Valone & Templeton, 2002). The finding of my study that social cues (specifically, the quality of safe nest sites) were preferred for breeding site selection by migratory barn

swallows provide additional support for this hypothesis.

### **Spatial scales of breeding site selection of barn swallows**

As cited previously, a social cue at the home-range scale was related to breeding site selection of barn swallows in my study area; however no cues at the nest-site scale showed such a relationship. One previous study hypothesized that larger scale factors provide a context for, and may constrain, the effects at the nest-site scale (Thompson, 2007). Another study assumed that at the nest-site scale, because effects of 1 factor would be altered by the effects of various factors (Pärt, 2001), it might be difficult to detect the effect of that 1 factor. It might be possible that swallows in my study area selected breeding sites in a hierarchical manner, with first cueing on the number of undamaged old nests at the home-range scale and then cueing on some other factors at the nest-site scale. However, because I analyzed breeding site selection by combining the factors at 2 spatial scales and my result showed the effect of the factor at the home-range scale was significant, the effects of the factors at nest-site scale might be insignificant or even absent. Thus, I can state that barn swallows breeding in my study area selected their breeding sites largely based on a reliable cue at the home-range scale, namely, the number of undamaged old nests.

Previous studies on breeding patch selection of migratory species described that when spatial autocorrelation of patch quality is low, random strategy (i.e., random selection) outweighs prospecting strategy (i.e., selection based on social cues) (Boulinier & Danchin, 1997). They also described that prospecting strategy outweighs random selection when the level of temporal autocorrelation of patch quality is

relatively high. Therefore, it is possible that the results of my study might have been influenced by a high spatio-temporal autocorrelation of factors related to habitat quality (e. g., predation) within a 250 m area (home-range area of swallows) and low temporal autocorrelation of factors at a finer spatial scale such as nest site. In addition, because the breeding season of barn swallows is limited and the natal dispersal distance is extensive, it is likely that the birds do not have much time to gather information on habitat quality. Therefore, their lack of knowledge (Lima & Zoller, 1996) and limited availability of cues to access habitat quality (Orians & Wittenberger, 1991) at the time of breeding site selection can also be as factors that influence the results of my study.

Finally, the results of breeding site selection analysis in barn swallows indicate that the effect of cues differ at different spatial scales, even when the cues are same. These results showed that when dispersal and breeding-site selection at multiple spatial scales is analyzed, the strategy of breeding site selection can be more accurately understood.

## **Individual behavior and dynamics at the group level**

In this study, I learned that barn swallows do not select their breeding sites randomly but follow decision-making “rules” based on a cue that indirectly represents habitat quality. From this, I could predict how swallows respond to changes in habitat quality and understand the distribution of swallows within this study area. I also learned that swallows use social cues for selecting breeding sites. Because social factors, those that act as cues for individuals, are affected by activity of other conspecific individuals in

the group, it can be said that the breeding-site selection and distribution (i.e., the dynamics of the group) of swallows have a recursive relationship. By estimating the dispersal rate and distance with observational and genetic methods, I understood that natal dispersal distance was extensive and the relatedness was low over a large range because of the high gene flow within the group. These results suggested that dispersal behavior of individuals influenced the genetic structure of the group breeding in my study area, which is in accordance with suggestions in previous studies (Greenwood & Harvey 1982; Hanski, 1999; Clobert *et al.*, 2001).

Although the relationship between individual behavior and population dynamics has been emphasized 30 years ago (Łomnicki, 1980; Sutherland, 1996), studies to combine these 2 levels of phenomena have not yet been developed. The results of this study may account for the relationship between individual behavior and population dynamics and its importance. Considering the relationship between individual level and population level phenomena provides essential information for ecological studies (Sutherland, 1996, Smith, Reynolds, and Sutherland, 2000), such as to help understand and predict population patterns or plan and implement a management plan. In addition, previous study have proposed that habitat selection can be linked to population limiting factors across spatial scales (Rettie & Meisser, 2000). It was hypothesized that individuals select habitat in an attempt to overcome major limitations at each level (e.g., individual or population level). In my study, analyzing the results at 2 ecologically important spatial scales and the number of undamaged old nests, which is supposed to represent a low risk of predation, gave more information on breeding site selection of barn swallows. Considering the hypothesis above and because predation influences individual fitness, it is possible that predation acts as a limiting factor of the

populations in my study area.

## **Future perspectives**

According to the results of my study, I suggest considering 4 points while studying the dispersal process of animals. First, the ecological information of the species at the study site should be investigated. For example, the dispersal rate and distance of species and the relationship with other species should be studied. In addition, while estimating the dispersal rate and distance, both observational and genetic data should be used to avoid misconceptions about dispersals. Second, based on ecological information, several spatial scales should be determined to analyze the effects of various factors at those spatial scales on habitat selection and to determine the true roles of cues. Third, to avoid misconceptions about the effects of cues on breeding site selection, both resource and social cues, which are directly and indirectly related to habitat quality, should be considered during analysis and the relative effects of these factors should be investigated. Finally, to understand habitat selection of a species, the relationship between individual behavior and population dynamics should be considered. In my study, I analyzed breeding site selection of birds at 2 spatial scales by considering hierarchical decision making of individuals, and my results showed the significance of social cues. I believe that these facts emphasize the importance of the relationship between individual behavior and population dynamics.

One further direction for this study will be to investigate when individual of barn swallows gather information about habitat quality. I can already suggest the types of cues that barn swallows will use, but I cannot provide insight on when the individuals

gather the information. To study this, the following experiments would be useful; (1) move the damaged or undamaged old nests to other places or artificially damage the undamaged old nests after the breeding season and (2) investigate breeding site preferences of individuals in the next breeding season and breeding selection at their selected nest sites. From such experiments, I will be able to understand when individual swallows gather information related to habitat quality at various spatial scales. In addition, because of the extensive dispersal distance of first-years, I would need to expand my study area and gather dispersal data over several years. These protocols would enable me to capture more accurate and complete data on the dispersal process and enable me to examine the phenomena at larger spatial scales, such as the recursive relationship between individual behavior and population and the cycle of population dynamics.

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## References

- Aebischer, A., Perrin, N., Krieg, M., Studer, J. & Meyer, D. R. 1996. The role of territory choice, mate choice and arrival date on breeding success in the Savi's warbler *Locustella luscinioides*. *Journal of Avian Biology*, 27, 143-152.
- Ambrosini, R. & Saino, N. 2010. Environmental effects at two nested spatial scales on habitat choice and breeding performance of barn swallow. *Evolutionary Ecology*, 24, 491-508.
- Ambrosini, R., Bolzern, A. M., Canova, L., Arieni, S., Moller, A. P. & Saino, N. 2002a. The distribution and colony size of barn swallows in relation to agricultural land use. *Journal of Applied Ecology*, 39, 524-534.
- Ambrosini, R., Bolzern, A. M., Canova, L. & Saino, N. 2002a. Latency in response of barn swallow *Hirundo rustica* populations to changes in breeding habitat conditions. *Ecology Letter*, 5, 640-647.
- Anderson, D. P., Turner, M. G., Forester, J. D., Zhu, J., Boyce, M. S., Beyer, H. & Stowell, L. 2005. Scale-dependent summer resource selection by reintroduced elk in Wisconsin, USA. *Journal of Wildlife Management*, 69, 298-310.
- Arlt, D. & Pärt, T. 2007. Nonideal breeding habitat selection: A mismatch between preference and fitness. *Ecology*, 88, 792-801.
- Baker, A. J., Daugherty, C. H., Colbourne, R. & McLennan, J. L. 1995. Flightless brown kiwis of New Zealand possess extremely subdivided population structure and cryptic species like small mammals. *Proceedings of the National Academy of Sciences of the United States of America*, 92, 8254-8258.
- Barclay, R. M. R. 1988. Variation in the costs, benefits, and frequency of nest reuse by barn swallows (*Hirundo rustica*). *Auk*, 105, 53-60.

- Bensch, S., Price, T. & Kohn, J. 1997. Isolation and characterization of microsatellite loci in a *Phylloscopus* warbler. *Molecular Ecology*, 6, 91-92.
- Betts, M. G., Rodenhouse, N. L., Sillett, T. S., Doran, P. J. & Holmes, R. T. 2008a. Dynamic occupancy models reveal within-breeding season movement up a habitat quality gradient by a migratory songbird. *Ecography*, 31, 592-600.
- Betts, M. G., Hadley, A. S., Rodenhouse, N. & Nocera, J. J. 2008b. Social information trumps vegetation structure in breeding site selection by migrant songbird. *Proceedings Of The Royal Society Of London Series B-Biological Sciences*, 275, 2257-2263.
- Bollmer, J. L., Kimball, R. T., Whiteman, N. K., Sarasola, J. H. & Parker, P. G. 2006. Phylogeography of the Galapagos hawk (*Buteo galapagoensis*): A recent arrival to the Galapagos Islands. *Molecular Phylogenetics and Evolution*, 39, 237-247.
- Bollmer, J. L., Whiteman, N. K., Cannon, M. D., Bednarz, J. C., De Vries, T. & Parker, P. G. 2005. Population genetics of the Galapagos Hawk (*Buteo galapagoensis*): Genetic monomorphism within isolated populations. *Auk*, 122, 1210-1224.
- Boulinier, T. & Danchin, E. 1997. The use of conspecific reproductive success for breeding patch selection in terrestrial migratory species. *Evolutionary Ecology*, 11, 505-517.
- Bowerman, B. L. & O'Connell, R. T. 1990. *Linear statistical models: and applied approach*, 2<sup>nd</sup> edition, Duxbury, Belmont.
- Bowler, D. E. & Benton, T. G. 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biological Reviews*, 80, 205-225.
- Brown, C. R. & Brown, M. 1999. Barn swallow: *Hirundo rustica*. *Birds of North*

*America*, 1-31.

- Cavitt, J. F., Pearse, A. T. & Miller, T. A. 1999. Brown Thrasher nest reuse: A time saving resource, protection from search-strategy predators, or cues for nest-site selection? *Condor*, 101, 859-862.
- Chalfoun, A. D. & Martin, T. E. 2007. Assessments of habitat preferences and quality depend on spatial scale and metrics of fitness. *Journal of Applied Ecology*, 44, 983-992.
- Clobert, J., Danchin, E., Dhondt, A. A. & Nichols, J. D. 2001. *Dispersal*. Oxford University Press, Oxford.
- Cody, M. L. 1985. An introduction to habitat selection in birds. Cody, M. L. (Ed.). *Physiological Ecology: Habitat Selection in Birds*. Academic Press Inc., London. 3-56.
- Currie, D., Thompson, D. B. A. & Burke, T. 2000. Patterns of territory settlement and consequences for breeding success in the Northern Wheatear *Oenanthe oenanthe*. *Ibis*, 142, 389-398.
- Dale, S., Steifetten, O., Osiejuk, T. S., Losak, K. & Cygan, J. P. 2006. How do birds search for breeding areas at the landscape level? Interpatch movements of male ortolan buntings. *Ecography*, 29, 886-898.
- Dall, S. R. X., Giraldeau, L. A., Olsson, O., McNamara, J. M. & Stephens, D. W. 2005. Information and its use by animals in evolutionary ecology. *Trends in Ecology & Evolution*, 20, 187-193.
- Danchin, E., Giraldeau, L. A., Valone, T. J. & Wagner, R. H. 2004. Public information: From nosy neighbors to cultural evolution. *Science*, 305, 487-491.
- Dobson, F. S. 1982. Competition for mates and predominant juvenile male dispersal in

- mammals. *Animal Behaviour*, 30, 1183-1192.
- Doligez, B., Cadet, C., Danchin, E. & Boulinier, T. 2003. When to use public information for breeding habitat selection? The role of environmental predictability and density dependence. *Animal Behaviour*, 66, 973-988.
- Eggers, S., Griesser, M., Nystrand, M. & Ekman, J. 2006. Predation risk induces changes in nest-site selection and clutch size in the Siberian jay. *Proceedings of the Royal Society B-Biological Sciences*, 273, 701-706.
- Fletcher, R. J. 2006. Emergent properties of conspecific attraction in fragmented landscapes. *American Naturalist*, 168, 207-219.
- Fletcher, R. J., Jr. & Miller, C. W. 2008. The type and timing of social information alters offspring production. *Biology Letters*, 4, 482-485.
- Fontaine, J. J. & Martin, T. E. 2006a. Habitat selection responses of parents to offspring predation risk: An experimental test. *American Naturalist*, 168, 811-818.
- Fontaine, J. J. & Martin, T. E. 2006b. Parent birds assess nest predation risk and adjust their reproductive strategies. *Ecology Letters*, 9, 428-434.
- Forsman, J. T., Hjernquist, M. B., Taipale, J. & Gustafsson, L. 2008. Competitor density cues for habitat quality facilitating habitat selection and investment decisions. *Behavioral Ecology*, 19, 539-545.
- Fujita, G. (1993). Nest site selection and reproductive success in barn swallows. *Strix*, 12, 35-39 (in Japanese).
- Goudet, J., Perrin, N. & Waser, P. 2002. Tests for sex-biased dispersal using bi-parentally inherited genetic markers. *Molecular Ecology*, 11, 1103-1114.
- Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour*, 28, 1140-1162.

- Greenwood, P. J. & Harvey, P. H. 1982. The natal and breeding dispersal of birds. *Annual Review of Ecology and Systematics*, 13, 1-21.
- Hanski, I. 1999. Habitat connectivity, habitat continuity, and metapopulations in dynamic landscapes. *Oikos*, 87, 209-219.
- Hardy, O. J. & Vekemans, X. 1999. Isolation by distance in a continuous population: reconciliation between spatial autocorrelation analysis and population genetics models. *Heredity*, 83, 145-154.
- Hardy, O. J. & Vekemans, X. 2002. SPAGeDi: a versatile computer program to analyse spatial genetic structure at the individual or population levels. *Molecular Ecology Notes*, 2, 618-620.
- Harris, T. R., Caillaud, D., Chapman, C. A. & Vigilant, L. 2009. Neither genetic nor observational data alone are sufficient for understanding sex-biased dispersal in a social-group-living species. *Molecular Ecology*, 18, 1777-1790.
- Helfenstein, F., Wagner, R. H., Danchin, E. & Rossi, J. M. 2003. Functions of courtship feeding in black-legged kittiwakes: natural and sexual selection. *Animal Behaviour*, 65, 1027-1033.
- Jakob, E. M., Porter, A. H. & Uetz, G. W. 2001. Site fidelity and the costs of movement among territories: an example from colonial web-building spiders. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, 79, 2094-2100.
- Johnson, C. J., Parker, K. L., Heard, D. C. & Gillingham, M. P. 2002. A multiscale behavioral approach to understanding the movements of woodland caribou. *Ecological Applications*, 12, 1840-1860.
- Johnson, K. A. 1980. Spatial and temporal use of habitat by red necked pademelon, *thylagale thetis* (Marsu-pialia: Macropodidae). *Australian Wildlife Research*, 7,

- 157-166.
- Jones, J. 2001. Habitat selection studies in avian ecology: A critical review. *Auk*, 118, 557-562.
- Koenig, W. D., VanVuren, D. & Hooge, P. N. 1996. Detectability, philopatry, and the distribution of dispersal distances in vertebrates. *Trends in Ecology & Evolution*, 11, 514-517.
- Larsen, K. W. & Boutin, S. 1994. Movements, survival, and settlement of red squirrel (*Tamiasciurus hudsonius*) offspring. *Ecology*, 75, 214-223.
- Leonard, T. D., Taylor, P. D. & Warkentin, I. G. 2008. Landscape structure and spatial scale affect space use by songbirds in naturally patchy and harvested boreal forests. *Condor*, 110, 467-481.
- Lima, S. L. 2009. Predators and the breeding bird: behavioral and reproductive flexibility under the risk of predation. *Biological Reviews*, 84, 485-513.
- Lima, S. L. & Zollner, P. A. 1996. Towards a behavioral ecology of ecological landscapes. *Trends in Ecology & Evolution*, 11, 131-135.
- Lomnicki, A. 1980. Regulation of population density due to individual differences and patchy environment. *Oikos*, 35, 185-193.
- Lomnicki, A. & Sedziwy, S. 1988. Resource partitioning and population stability under exploitation competition. *Journal of Theoretical Biology*, 132, 119-120.
- Martin, T. E. 1993. Nest predation and nest sites: new perspectives on old patterns. *Bioscience*, 43, 523-532.
- Martin, T. E. 1998. Are microhabitat preferences of coexisting species under selection and adaptive? *Ecology*, 79, 656-670.
- Massot, M., Clobert, J., Lorenzon, P. & Rossi, J. M. 2002. Condition-dependent

- dispersal and ontogeny of the dispersal behaviour: an experimental approach. *Journal of Animal Ecology*, 71, 253-261.
- Mayor, S. J., Schneider, D. C., Schaefer, J. A. & Mahoney, S. P. 2009. Habitat selection at multiple scales. *Ecoscience*, 16, 238-247.
- Mennechez, G., Petit, S., Schtickzelle, N. & Baguette, M. 2004. Modelling mortality and dispersal: consequences of parameter generalisation on metapopulation dynamics. *Oikos*, 106, 243-252.
- Møller, A. P. 1987. Advantages and disadvantages of coloniality in the swallow *Hirundo rustica*. *Animal Behavior*, 35, 819-823.
- Møller, A. P. 1990. Effects of parasitism by haematophagous mite on reproduction in barn swallow. *Ecology*, 79, 656-670.
- Møller, A. P. 1994. *Sexual selection and the barn swallow*. Oxford University Press, Oxford.
- Møller, A. P. 2010. The fitness benefit of association with humans: elevated success of birds breeding indoors. *Behavioral Ecology*, 21, 913-918
- Montgomery, D. C. & Peck, E. A. 1982. *Introduction to linear regression analysis*. Wiley, New York.
- Mosnier, A., Ouellet, J. P., Sirois, L. & Fournier, N. 2003. Habitat selection and home-range dynamics of the Gaspé caribou: a hierarchical analysis. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, 81, 1174-1184.
- Müller, M., Pasinelli, G., Schiegg, K., Spaar, R. & Jenni, L. 2005. Ecological and social effects on reproduction and local recruitment in the red-backed shrike.

- Oecologia, 143, 37-50.
- Nordell, S. E. & Valone, T. J. 1998. Mate choice copying as public information. Ecology Letters, 1, 74-76.
- O'Neill, R. V., Johnson, A. R. & King, A. W. 1989. A hierarchical framework for the analysis of scale. Landscape Ecology, 3, 193-205.
- Oatway, M. L. & Morris, D. W. 2007. Do animals select habitat at small or large scales? An experiment with meadow voles (*Microtus pennsylvanicus*). Canadian Journal of Zoology-Revue Canadienne De Zoologie, 85, 479-487.
- Orians, G. H. & Wittenberger, J. F. 1991. Spatial and temporal scales in habitat selection. American Naturalist, 137, S29-S49.
- Ormerod, S. J. 1991. Pre-migratory and migratory movements of Swallows *Hirundo rustica* in Britain and Ireland. Bird Study, 38, 170-178.
- Parejo, D., White, J. & Danchin, E. 2007. Settlement decisions in blue tits: difference in the use of social information according to age and individual success. Naturwissenschaften, 94, 749-757.
- Pärt, T. & Doligez, B. 2003. Gathering public information for habitat selection: prospecting birds cue on parental activity. Proceedings of the Royal Society of London Series B-Biological Sciences, 270, 1809-1813.
- Poizat, G. & Pont, D. 1996. Multi-scale approach to species-habitat relationships: Juvenile fish in a large river section. Freshwater Biology, 36, 611-622.
- Primmer, C. R., Moller, A. P. & Ellegren, H. 1995. Resolving genetic relationships with microsatellite markers: a parentage testing system for swallow *Hirundo rustica*. Molecular Ecology, 4, 493-498.

- Primmer, C. R., Moller, A. P. & Ellegren, H. 1996. New microsatellites from the pied flycatcher *Ficedula hypoleuca* and the swallow *Hirundo rustica* genomes. *Hereditas*, 124, 281-283
- Pulliam, H. R. 1988. Sources, sinks, and population regulation. *American Naturalist*, 132, 652-661.
- Pulliam, H. R. & Danielson, B. J. 1991. Sources, sinks, and habitat selection: a landscape perspective on population-dynamics. *American Naturalist*, 137, S50-S66.
- Queller, D. C. & Goodnight, K. F. 1989. Estimating relatedness using genetic-markers. *Evolution*, 43, 258-275.
- Rauter, C. M., Reyer, H. U. & Bollmann, K. 2002. Selection through predation, snowfall and microclimate on nest-site preferences in the Water Pipit *Anthus spinoletta*. *Ibis*, 144, 433-444.
- Rettie, W. J. & Messier, F. 2000. Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. *Ecography*, 23, 466-478.
- Robertson, B. A. & Hutto, R. L. 2006. A framework for understanding ecological traps and an evaluation of existing evidence. *Ecology*, 87, 1075-1085.
- Ronce, O. 2007. How does it feel to be like a rolling stone? Ten questions about dispersal evolution. *Annual Review of Ecology Evolution and Systematics*, 38, 231-253.
- Safran, R. J. 2004. Adaptive site selection rules and variation in group size of barn swallows: Individual decisions predict population patterns. *American Naturalist*, 164, 121-131.
- Santiago-Alarcon, D., Tanksley, S. M. & Parker, P. G. 2006. Morphological variation

- and genetic structure of Galapagos Dove (*Zenaida galapagoensis*) populations: Issues in conservation for the Galapagos bird fauna. *Wilson Journal of Ornithology*, 118, 194-207.
- Schmidt, K. A., Ostfeld, R. S. & Smyth, K. N. 2006. Spatial heterogeneity in predator activity, nest survivorship, and nest-site selection in two forest thrushes. *Oecologia*, 148, 22-29.
- Schlaepfer, M. A., Runge, M. C. & Sherman, P. W. 2002. Ecological and evolutionary traps. *Trends in Ecology & Evolution*, 17, 474-480.
- Shields, W. M. 1984. Factors affecting nest and site fidelity in Adirondack barn swallows (*Hirundo rustica*). *The Auk*, 101, 780-789.
- Shields, W. M. & Crook, J. R. 1987. Barn swallow coloniality: a net cost for group breeding in the Adirondacks? *Ecology*, 68, 1373-1386.
- Smith, C., Reynolds, J. D. & Sutherland, W. J. 2000. Population consequences of reproductive decisions. *Proceedings of the Royal Society of London Series B-Biological Sciences*, 267, 1327-1334.
- Sonerud, G. A. 1993. Reduced predation by nest box relocation: differential effect on Tengmalm owl nests and artificial nests. *Ornis Scandinavica*, 24, 249-253.
- Sutherland, W. J. 1996. *From individual behaviour to population ecology*. Oxford University Press, Oxford.
- Thompson, F. R., III. 2007. Factors affecting nest predation on forest songbirds in North America. *Ibis*, 149, 98-109.
- Turner, M. G., O'Neill, R. V., Gardner, R. H. & Milne, B. T. 1989. Effects of changing spatial scale on the analysis of landscape pattern. *Landscape Ecology*, 3, 153-162.

- Turner, A. T. & Roce, C. 1989. *Swallows and martins an identification guide and handbook*. Houghton Mifflin, Boston.
- Valone, T. J. & Templeton, J. J. 2002. Public information for the assessment of quality: a widespread social phenomenon. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, 357, 1549-1557.
- Visser, M. E., Holleman, L. J. M. & Caro, S.P. 2009. Temperature has a causal effect on avian timing of reproduction. *Proceedings of the Royal Society of London Series B-Biological Sciences*, 276, 2323-2331.
- Wheatley, M. & Johnson, C. 2009. Factors limiting our understanding of ecological scale. *Ecological Complexity*, 6, 150-159.
- Wilson, A. J., Hutchings, J. A. & Ferguson, M. M. 2004. Dispersal in a stream dwelling salmonid: Inferences from tagging and microsatellite studies. *Conservation Genetics*, 5, 25-37.
- Wright, S. 1994. Isolation by distance. *Genetics*, 28, 114–138.