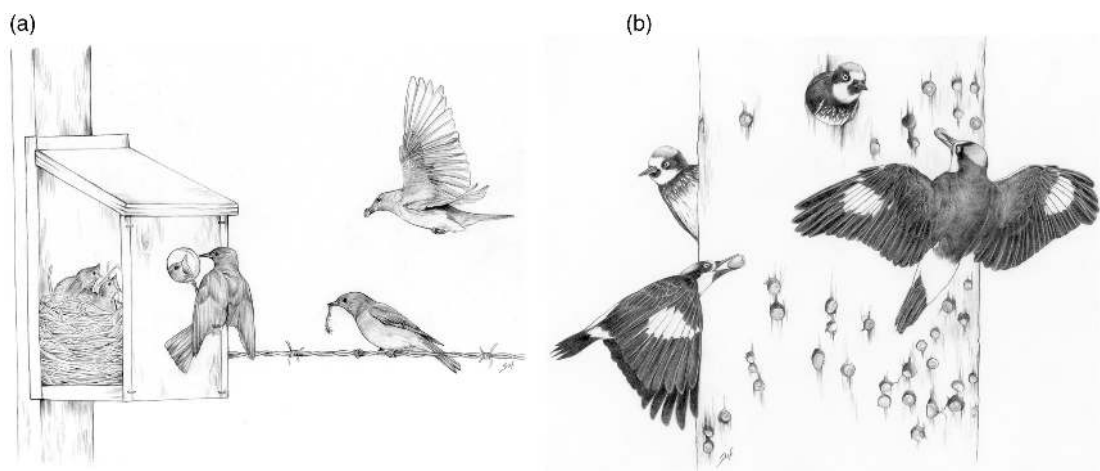


Introduction

Janis L. Dickinson and Walter D. Koenig



Cooperative breeding was described by naturalists as early as the nineteenth century (Boland and Cockburn 2002) and refers to breeding associations with three or more individuals collectively raising young in a single brood or litter. Breeding in groups was little more than a biological curiosity, however, until nearly 30 years after Skutch (1935) first introduced “helpers at the nest” to refer to individuals that forgo breeding to help raise young that are not their own. In the 1960s, evolutionary studies of animal social behavior were quickly transformed by the realization that selection acts mainly on individuals and only rarely on groups (Williams 1966). This insight spawned the field of behavioral ecology,

and, in particular, kin selection and inclusive fitness theory (Hamilton 1963, 1964), which provided a firm theoretical basis for understanding the paradox of helping and other forms of cooperative breeding that appeared to involve a sacrifice in personal reproduction. This book provides examples of studies that test specific predictions based on individual selection and inclusive fitness theory, using a combination of experimental and observational studies designed to measure the socioecological drivers and fitness consequences of giving up at least a share of personal reproduction to help others breed. Relatively quickly after Hamilton’s seminal papers, cooperative breeders became subjects of several

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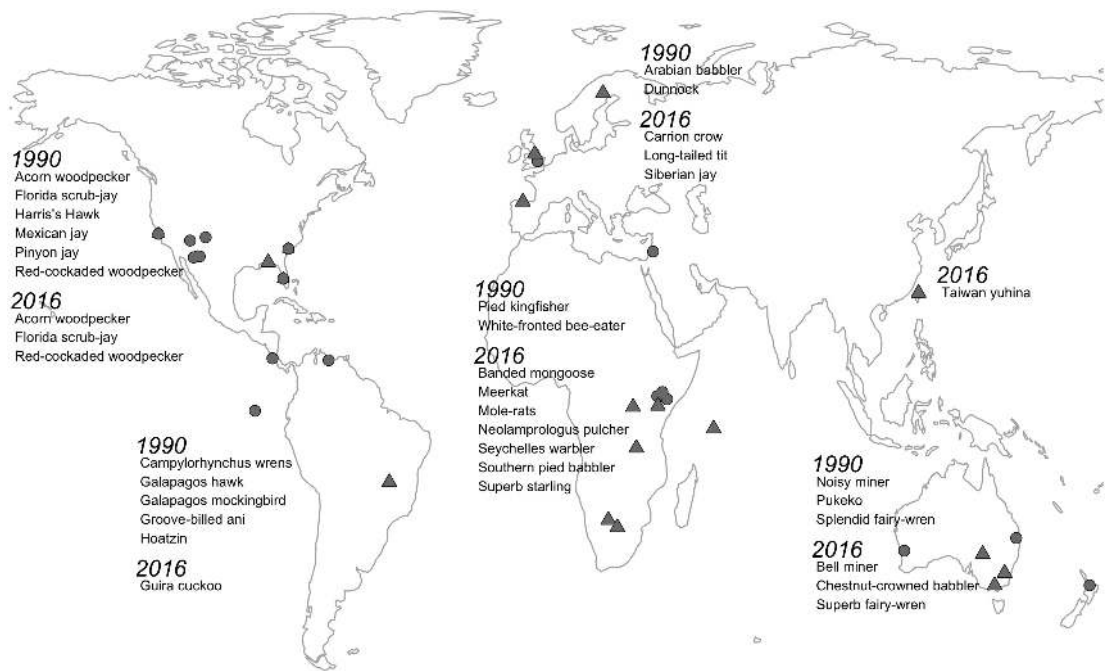


Figure I.1. The geographic distribution of studies represented in Stacey and Koenig (1990; circles) and this book (2016; triangles).

long-term studies, many of which were summarized species by species in Stacey and Koenig (1990) and topic by topic in Koenig and Dickinson (2004). This latter volume reviewed theory and evidence by summarizing the literature across a range of relevant topics. The book we introduce here returns to the earlier model, examining advances based on population studies of vertebrate species across the globe (Figure I.1) with the goal of exploring the ways in which new theory and empirical evidence have altered our perspective on cooperation over the last 25 years. We believe that new insights usually come from exploring the diversity and complexity of animal societies within the context of theory; our hope is that having summaries of these studies all in one place will generate new thinking, while helping to foster generalities and illuminate holes in current thinking.

The chapters in this book include contributions from both new and more senior researchers; three chapters are updates of studies summarized earlier in Stacey

and Koenig (1990), demonstrating the added value that comes with increased longevity of studies in this field. The remaining studies highlight the many advances that have been made with the addition of new, and often exceptional, study systems and experimental approaches.

Results from such studies indicate that what we know today about cooperative breeding may not be representative of the different kinds of systems that are out there, making it difficult to draw general conclusions. Within the complexity that has been uncovered, however, are both consistent patterns and new gems of ideas that help push the field forward. It is only in bringing together and synthesizing the evidence that already exists that a story begins to emerge for each species, allowing us to get a sense of what matters in a system, what the important design features are, and how natural selection has shaped them variously among species. We have particularly enjoyed seeing the insights that emerge when researchers have the opportunity to tell

the whole story in one place, rather than piecemeal in technical publications.

What has happened since the last collection of long-term studies was published in 1990? While reproductive skew theory had already been around for a while (Vehrencamp 1983), it really took hold, generating an array of models and ideas that improved understanding of the extent of reproductive sharing in animal societies and the complexities surrounding measuring and modeling reproductive division of labor (Magrath et al. 2004). Although the original insights provided by reproductive skew theory have proven problematic for most cooperatively breeding vertebrates (Haydock and Koenig 2002; Magrath et al. 2004), the interplay between empirical studies and theory continues to produce new generalizations and understanding of how and why reproductive sharing varies across taxa.

Study systems chosen as exceptions appear early in the book, beginning with a species that exhibits delayed dispersal in the absence of cooperative breeding (Chapter 1), as well as two cases of cooperative breeders that have fluid systems of helping that become possible when localized dispersal of offspring leads to breeding in kin neighborhoods (Chapters 2 and 3). Chapters 2 through 13 focus on cooperatively breeding birds in which relatedness and kin selection are generally critical to the evolution of cooperative behaviors, although beyond that they encompass a wide range of social organizations ranging from socially and genetically monogamous pairs with helpers (Chapters 4, 5, and 7) to species with helpers in which extra-pair matings are common (Chapters 2, 8, and 12), species organized into complex and in some cases multileveled groups (Chapters 9, 10, and 11), and cooperatively polygamous groups with helpers (Chapters 6, 12, and 13). In addition to these are chapters covering species of vertebrates in which individuals cooperating with one another are apparently *not* related, with the idea that these can provide strong, complementary tests of alternative hypotheses for the evolution of cooperation (Chapters 14 and 15).

Great strides have been made in understanding cooperation in non-avian vertebrates, including fishes (Chapter 16) and mammals (Chapters 17, 18, and 19), with several of these studies combining field research

with field and laboratory experiments to test important hypotheses concerning the evolution of helping behavior that are difficult to address in the field alone. In bringing these newer studies together with the three landmark, older studies, which were largely focused on such classic ecological constraints as habitat and cavities (Chapters 4, 5, and 13), it becomes possible to assess current understanding of cooperative breeding in vertebrates and to develop the broad perspective needed to foster new thinking. Significantly, the 19 studies summarized here include some of the most extensive and detailed population studies of wild living vertebrates ever undertaken.

Perhaps the most important technical advance since the 1990 volume is the widespread availability of molecular tools to assess parentage, especially the advent of hypervariable microsatellites, which allow study-wide parentage assignment. While Nick Davies' (1990) dunnock (*Prunella modularis*) chapter was the only study to integrate molecular parentage assignment in the previous book, molecular tools are commonly used today, allowing for assessment of such critical measures as relatedness, incest, inbreeding, reproductive skew, and, of course, inclusive fitness.

Since Hamilton (1963, 1964), the primary body of theory informing studies of social behavior has been inclusive fitness theory, which compares the direct fitness benefits of producing offspring with the indirect fitness benefits of helping relatives produce additional offspring over what they might otherwise produce, weighted by relatedness (Brown 1980). The minimal predictions of inclusive fitness theory are that helpers should prefer, or at least be more likely to aid, relatives over nonrelatives, that the inclusive fitness advantages of helping should be greater than what helpers (as individuals) might otherwise achieve (i.e., Hamilton's rule, which infers that helping must be better than actual outside options), and that if breeding is the better option, helpers should breed independently when they have the opportunity to do so.

The studies presented here provide a breadth of evidence supporting the importance of indirect fitness benefits, which often, but not always, act in concert with limitations on independent breeding to drive decisions to help or cobreed with relatives. In general,

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studies of cooperative breeders indicate that even when indirect fitness benefits are small, they can still be an important driver of helping behavior – because the outside options are even worse. Most of the chapters in this book present strong evidence for the importance of kinship and kin recognition in the behavioral choices that individuals make, especially choices of whether to help and whom to help (Chapters 2, 3, 7, and 11). Explicit tests of Hamilton's rule (Chapters 2 and 3) provide insights that further demonstrate the value of kin selection and inclusive fitness thinking. This large body of evidence supporting the importance of kin selection to helping stands in direct opposition to challenges based on modeling efforts and spotty interpretation of empirical evidence (Nowak et al. 2010).

Unsurprisingly, relatedness and indirect fitness benefits are much less prevalent among same-sex cobreeders in species that exhibit cooperative polygamy, over half of which are thought to involve cobreeding by non-relatives (Riehl 2013). Such partnerships among non-relatives are, of course, driven by direct fitness benefits, rather than indirect fitness benefits arising through collateral kinship (Hartley and Davies 1994). Here we feature two cooperative breeders, both joint-nesting, that exhibit cobreeding by nonkin (Chapters 14 and 15). Despite these examples, studies of species whose cooperative behavior is not based on kinship remain relatively rare, and even ruminating about why unrelated males might help raise offspring of nonkin is intriguing: reciprocity; potential to inherit a mate; experience; high costs of floating or maintaining a territory as an individual?

At a time when funding is challenging to obtain and granting agencies are shying away from the complexity of demographic studies in favor of the “ooh, shiny” payoffs that can arise from short-term, mechanistic questions (Zuk and Balenger 2014), we hope this book inspires renewed interest in long-term studies of social behavior for their value in addressing lifetime fitness consequences of behaviors, their corrective potential (most authors in this book would, we think, agree that their ideas and evidence have changed significantly since they first began their study), their importance to conservation (Chapters 4, 5, and 12), and their capacity to uncover the complexities underlying the

evolution of social behavior. Ideally, long-term studies of social behavior knit together multiple approaches by integrating ecology, life-history theory, behavioral genetics, physiology, and behavior, while forging new connections by measuring the traits, trajectories, and demography of individual agents. Such efforts provide important fodder for new theory and ideas.

Most importantly, in an age when there is a large focus on analyzing existing data, we believe this book illustrates the vital interplay between natural history observations and the development of new ideas, which when situated within a rich domain of accumulated knowledge can be tested rigorously and in ways that advance our understanding of the evolution of social complexity. All of the authors in this book are dedicated naturalists whose propensity to take on the unforgiving commitment of embarking on the long-term study of marked populations of animals is integral to the insights they have had and the discoveries they continue to make.

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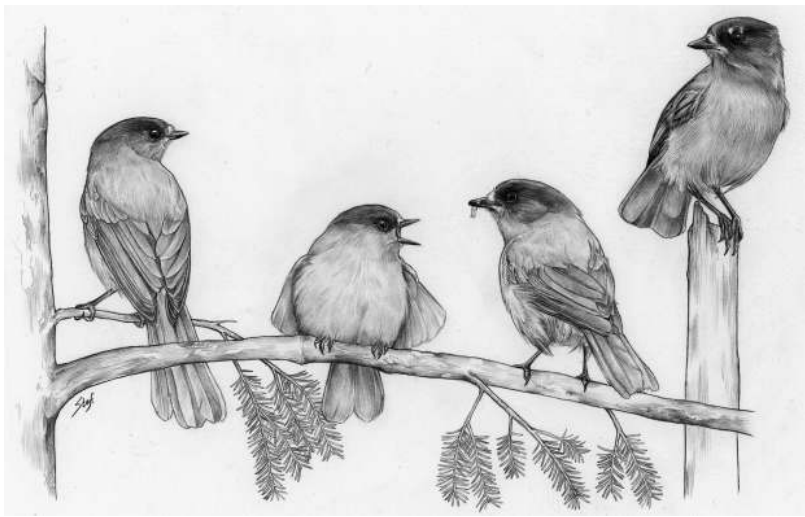
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Siberian jays: Delayed dispersal in the absence of cooperative breeding

Jan Ekman and Michael Griesser



Introduction

In most cases, helping-at-the-nest is associated with delayed dispersal, leading to widespread interest in the selective factors causing offspring to stay and delay breeding on their natal territory. Today, with the identification of a number of species where offspring delay dispersal without ever helping, we have the opportunity to examine a more comprehensive set of fitness benefits of delayed dispersal in cases where it appears to be beneficial even in the absence of helping (Ekman 2006). Here we discuss one such species, the Siberian

jay (*Perisoreus infaustus*), which has been studied extensively as an exceptional case of delayed dispersal in the absence of cooperative breeding.

Our work with the Siberian jay contributes to the field of cooperative breeding by demonstrating how benefits of cooperation other than helping-at-the-nest can select for family-group living. Many studies of the mechanisms facilitating cooperative breeding emphasize the role of offspring as donors of help and breeding parents as recipients of benefits. Given that offspring are an evolutionary asset of the parents, however, parents clearly have an incentive to provide

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care for them in cases where offspring extend their association with parents. Such care could be instrumental in prolonging the time offspring remain in the family, thus facilitating family cohesion. Family-group living evolves as a transactional process, balancing the inclusive fitness costs and benefits among family members. As such, family life involves concession of resources, competition, and cooperation, especially rivalry among siblings (Mock and Parker 1997). Understanding the evolution of delayed dispersal thus requires examination of both cooperative and competitive interactions.

Models explaining why sexually mature offspring remain with their parents on their natal territory have emphasized the role of constraints on access to breeding opportunities and variation in habitat quality (Brown 1969, 1978; Koenig and Pitelka 1981; Emlen 1982). While ecological constraints may explain dispersal decisions within populations, and may account for the delayed onset of independent reproduction, they do not make predictions regarding where offspring will wait prior to gaining breeder status. Thus, we know little about what, in the absence of immediately available breeding opportunities, drives offspring to remain philopatric on their natal territory rather than “floating” – which is generally assumed to involve roaming between territories or groups – or settling in a group of unrelated birds.

We also know relatively little about within-species variation in dispersal timing, as this subject has received much less attention in cooperatively breeding species than the behavior of offspring delaying dispersal. Indeed, variation in dispersal timing, where some offspring disperse while others remain and help, occurs in many, perhaps most, cooperatively breeding species (Riehl 2013), and it has been well documented in a number of thoroughly studied species including southern pied babblers *Turdoides bicolor* (Ridley et al. 2008; Chapter 7) and the Arabian babbler *Turdoides squamiceps* (Zahavi 1990). Models accounting for delayed dispersal based on ecological constraints generally consider independent breeding to be the alternative and do not consider variation in pathways to breeder status among siblings. Given that in the Siberian jay some offspring wait as nonbreeders on the

natal territory while others wait as nonbreeders outside it (Ekman et al. 1994), it is possible to examine the factors that determine how offspring decide between these alternatives and to explore the ultimate fitness consequences of decisions favoring family living and ultimately cooperative breeding.

Study site

Our study site is located outside the village of Arvidsjaur, northern Sweden, about 100 km south of Arctic Circle (Figure 1.1). It is part of the vast continuous taiga biome of northern Scandinavia. Accordingly, the climate is boreal with warm summers and temperatures up to +30°C, cold winters with temperatures down to −40°C (exceptionally to −50°C), and annual precipitation of about 600 mm. The study site is usually snowbound from October until the beginning of May. Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) are the dominant tree species while deciduous trees (birch *Betula pubescens*, aspen *Populus tremula*, willow *Salix* spp.) are less abundant. In wetter locations marshes occur, forming a natural mosaic of forests with marshes.

Our study started in 1989 and the study site was chosen because Siberian jays in this area had been ringed for several decades, nests had been located, and population trends monitored by a local amateur (Lindgren 1975; Griesser and Lagerberg 2012). Our study site consists of two separate areas in continuous habitat (Figure 1.1). The southern area (53 km²; 37 km² when excluding clear-felled areas, plantations, and lakes) is located in intensively managed forests. In this area the primeval forest is interspersed with clear-felled areas and plantations. The northern area is located in a nature reserve (Reivo, 30 km²) with continuous primeval forests unaffected by forestry for over the last 200 years. Managed forests are dominated by the commercially valuable pines, making forests more open as Scots pine has branches in the crown of the tree while spruce often has branches almost down to ground level. This difference in habitat openness strongly influences the breeding success and survival of Siberian jays (see the “Role of vegetation structure”).

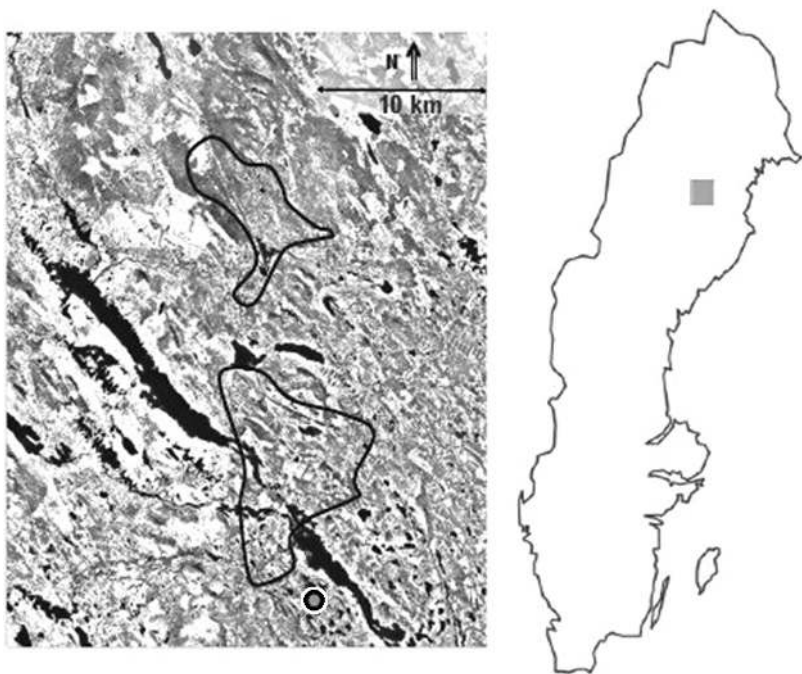


Figure 1.1. Aerial image of the study area (encircled by dark lines). The location of the study site in Sweden is indicated on the map with a black circle; the village of Arvidsjaur is indicated with a gray circle.

Group structure

Siberian jay groups form around a strictly monogamous breeding pair (Gienapp and Merila 2010). Group sizes vary from 2 to 5 individuals (mean: 2.7, range of mean = 2.05–3.43, $N = 20$ years) at the start of the breeding season (March) and between 2 to 6 individuals (mean: 3.25, range of mean = 2.46–3.67) in September, after the breeding season (Figure 1.2). Extra birds consist of a mixture of philopatric offspring and unrelated immigrants (Ekman et al. 1994; Lillandt et al. 2003), with the majority being the latter (66% of nonbreeders in breeding groups, 62% in winter groups; Figure 1.3). Extra birds accompany around 80% of breeders and the most common group composition is a pair of adult breeders accompanied only by immigrants. Most extra birds are first-winter birds or yearlings, with an equal sex ratio among both philopatric and immigrants (Table 1.1).

Groups inhabit territories with ill-defined borders that are partly determined by unsuitable habitats such

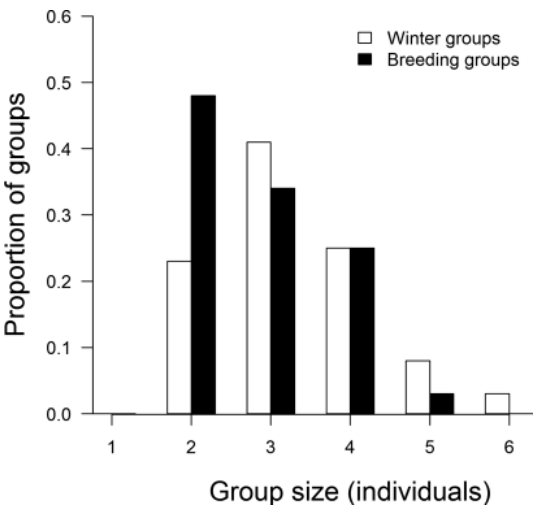


Figure 1.2. Frequency distribution of group sizes ($N = 376$ groups; open symbols: groups during the non-breeding season (“winter”); filled symbols: breeding groups).

Table 1.1. Age and sex-ratio of extra birds in winter (September) groups (N = 270 groups)

Age			
Extra bird category	Number of individuals		Proportion first winter birds
	Juveniles	Older individuals	
Philopatric	143	75	0.65
Immigrant	117	28	0.80

Sex-ratio			
Extra bird category	Number individuals		Sex ratio (males/females)
	Males	Females	
Philopatric	57	59	0.97
Immigrant	70	67	1.04

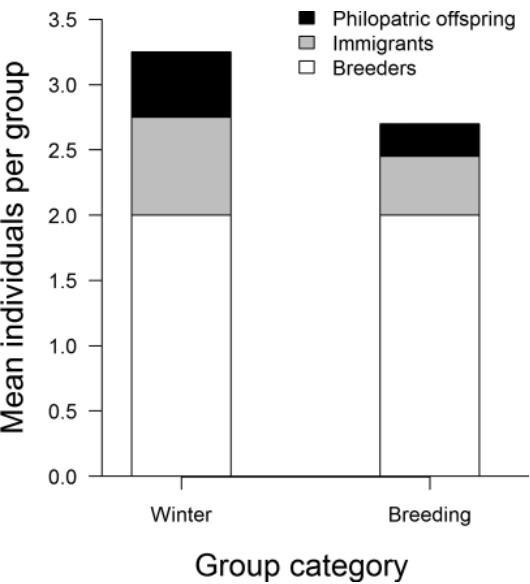


Figure 1.3. The average number of members of each category in winter (assessed in September) and breeding groups (N = 376).

as open bogs, clear-felled areas, and lakes. Territories are stable and many have remained the same over the entire study period. The managed, southern area harbors 35 groups, and the unmanaged, northern area 28 groups, which corresponds to an average territory size

of 1.1 km² in both areas. Once they have settled down to breed, jays rarely shift territories, with shifts having been observed in only 3 of 346 (< 1%) breeding attempts (Griesser et al. 2007). The direction of territory shifts is always from low quality to high quality neighboring territories, which will typically yield higher breeding success (Ekman et al. 2001).

Natal dispersal

Dispersal timing and distance

Siberian jay offspring almost always become breeders by dispersing away from their natal territory, although the timing and distance of dispersal varies considerably (Ekman et al. 2002; Griesser et al. 2014). Offspring only inherit their natal territory if both parents disappear within a short period of time, a rare event that we have witnessed only twice in 20 years. Bimodality in both age and distance is the defining feature of dispersal strategies in the Siberian jay (Ekman et al. 2001, 2002).

One category of offspring (early dispersers) leaves the parental territory between four and eight weeks after fledging (Figure 1.4a). These early dispersers settle as immigrants in groups of unrelated birds without immediately acquiring breeder status or, more rarely, find a vacancy allowing them to become breeders at

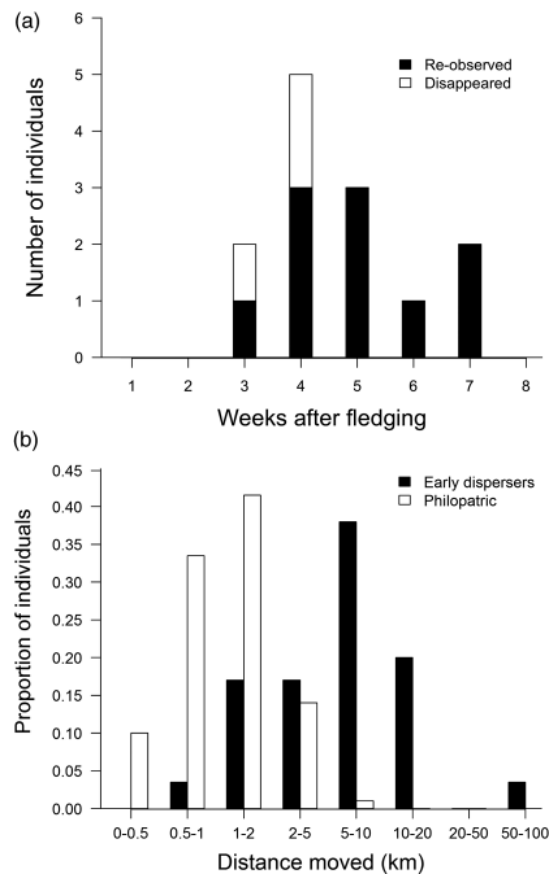


Figure 1.4. (a) The timing of dispersal for early dispersers observed from newly fledged birds with radio transmitters. Filled bars: birds re-observed after dispersal outside the natal territory ($N = 10$). Open bars: birds disappearing without being re-observed ($N = 3$). From Ekman et al. (2002) (b) The frequency distribution of dispersal distances of philopatric offspring ($N = 90$; open symbols) and early dispersers (immigrants; $N = 27$; filled symbols). From Griesser et al. (2014).

the age of one (Table 1.2) (Ekman et al. 1994; Griesser et al. 2008). Out of 31 color-banded fledglings observed daily during the months after fledging (22 of these also carried a radio transmitter) we confirmed 10 early dispersers (seven with radio transmitter and three through re-observation: Figure 1.4a). Three birds disappeared during the same period for which we could not confirm whether they dispersed or died (Ekman

Table 1.2. The increase with age in the fraction of individuals having started to breed

Age (years)	Proportion of population breeding	
	Dispersers	Philopatric
1	0.32	0.21
2	0.78	0.70
3	1	0.87
4	1	0.96
5	1	1

et al. 2002). Out of the seven early-dispersing birds with radio transmitters, six settled permanently in a new territory within two days. The seventh made a temporary stop in a new group before moving to settle permanently with another group a week after dispersing. The mean ($\pm$ standard error [S.E.]) dispersal distance of early dispersers was 9.0 ± 2.6 km, corresponding to having traversed 7.0 ± 2.2 territories ($N = 27$ birds all ringed as nestlings; 12 followed with radio transmitters) (Figure 1.4b). The longest dispersal distance of an untagged disperser was 72 km (Griesser et al. 2014). The majority of early dispersers became breeders either by inheriting breeding position in the group where they initially settled or by filling a vacancy in a neighboring group (Figure 1.5a).

Those offspring that have not dispersed by the age of eight weeks remain on their natal territories at least through the first winter (philopatric offspring). In 75% of successful broods, at most one, and rarely more, offspring delayed dispersal (Figure 1.5b). Philopatric offspring disperse only when they acquire a breeding position except for cases of parent-offspring reproductive conflict, thus making the age of dispersal equal to the age at first reproduction. In contrast to delayed dispersers, philopatric offspring dispersed on average only 1.25 km before settling ($N = 97$; visual re-observations only) (Figure 1.4b) traversing on average 1.2 ± 0.1 territories (Figure 1.6). Philopatric offspring delay dispersal longer and initiate first breeding for later than early dispersers (Table 1.2). Molecular estimates based on 23 microsatellite markers support distance estimates from the direct methods we have described above (Griesser et al. 2014).