

FAMILY STRUCTURE IN THE SIBERIAN JAY AS REVEALED BY MICROSATELLITE ANALYSES

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Abstract. The Siberian Jay (*Perisoreus infaustus*) lives in resident, territorial family groups outside the breeding season, but does not breed cooperatively. Thereby it offers an opportunity to study the evolution of territorial group living, without confounding effects of reproductive cooperation. During a long-term study in Finland 1974–2000, we observed Siberian Jay group composition in autumn. Using microsatellite analysis based on feather or blood samples we clarified kin relations within the groups. We found that out of 311 groups that included at least one more individual than the territory holders, 74% were nuclear families, including breeding birds and 1–3 retained offspring. However, 26% of the groups were not families, but consisted of pairs accompanied only by individuals that were not their offspring. According to extensive pedigrees we found that 70% of the 82 immatures associated with a nonparent pair were not related to either territory holder. Of these 82 immatures, 91% were associated with pairs that had no offspring on their own, suggesting that they were failed breeders or newly established pairs. The composition of groups was mostly unchanged during the observation period within each season, regardless of kinship. Previous studies have reported apparent nepotism between parents and retained offspring in the Siberian Jay, and a high degree of aggression toward nonoffspring, so we did not expect to find such high frequency and remarkable within-season stability of nonfamily groups. These observations suggest that there are important fitness benefits to gain from territoriality and group living, regardless of kinship.

Key words: delayed dispersal, family structure, microsatellite analyses, offspring retention, *Perisoreus infaustus*, Siberian Jay.

Estructura Familiar en *Perisoreus infaustus* Determinada Mediante Análisis de Microsatélites

Resumen. Los individuos de la especie *Perisoreus infaustus* viven en grupos familiares residentes que son territoriales durante la época reproductiva, pero no exhiben cría cooperativa. Así, esta especie ofrece la oportunidad de estudiar la evolución del sistema de vida en grupos territoriales sin los efectos de la cooperación reproductiva. Observamos la composición de grupos de *P. infaustus* en el otoño durante un estudio a largo plazo en Finlandia (1974–2000), y con base en muestras de plumas o sangre, clarificamos las relaciones de parentesco al interior de los grupos mediante análisis de microsatélites. Encontramos que de 311 grupos que incluían al menos un individuo adicional a los dueños del territorio, el 74% eran núcleos familiares, incluyendo aves reproductivas y 1–3 crías. Sin embargo, el 26% de los grupos no correspondían a familias, sino que consistían de parejas acompañadas sólo por individuos que no eran sus crías. Utilizando pedigrís detallados, encontramos que el 70% de los 82 inmaduros asociados con una pareja no parental no estaban relacionados con ninguno de los dueños del territorio. De esos 82 inmaduros, el 91% estuvieron asociados con parejas que no tenían crías propias, lo que sugiere que habían tenido intentos de reproducción fallidos o que se habían establecido recientemente. La composición de los grupos se mantuvo casi constante durante el período de observación de cada estación, independientemente del grado de parentesco. Estudios previos habían reportado un aparente nepotismo entre parentales y sus crías y un alto grado de agresividad hacia individuos que no eran sus crías en *P. infaustus*, por lo que no esperábamos una frecuencia tan alta de grupos no familiares, ni la marcada estabilidad de éstos. Estas observaciones sugieren que la territorialidad y la vida en grupo proveen beneficios importantes de adecuación biológica, independientemente del grado de parentesco.

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INTRODUCTION

Vertebrates do not commonly live in family groups outside the breeding season. Only 112 species of birds and 63 species of mammals (excluding primates) form multigenerational family groups (Emlen 1995, 1997), and almost all these species (96% and 90% respectively) exhibit some kind of cooperative breeding. Conversely, cooperative breeding is nearly restricted to family-dwelling species; only 12% of cooperatively breeding birds and 5% of mammals do not live in family groups. There are only a few exceptional species that provide an opportunity to study the evolution of these two types of social behaviors disconnected from each other (Hatchwell and Komdeur 2000).

One well-studied, family-living species that was thought not to have any kind of helping behavior, the Gray Jay, (*Perisoreus canadensis*, Strickland and Ouellet 1993), has been found to exhibit a new form of reproductive cooperation: retained offspring from preceding years provision fledged siblings, but not nestlings (Waite and Strickland 1997). In the present study we provide a comprehensive description of group structure in its Eurasian congener, the Siberian Jay (*Perisoreus infaustus*). This species is strongly philopatric, with closely related males holding neighboring territories (Ekman, Eggers et al. 2001). This feature is commonly associated with cooperative breeding (Brown 1987, Zack 1990). Nevertheless, cooperative breeding has not been recorded despite concerted searches for it (Ekman et al. 1994). The Siberian Jay thus seems to be an exception to the rule that group living is connected to cooperative breeding.

In two previous papers (Lillandt et al. 2001, 2002) we developed methods for parentage determination based on microsatellite analysis of feather or blood samples, collected during our 25-year population study on the Siberian Jay. Here we use these methods to examine genetic relationships within Siberian Jay groups that we have observed in late summer and autumn during 1974–2000. Using these data we address two main questions: (1) To what extent are groups observed in autumn nuclear families, consisting of parents and retained offspring? (2) Are non-offspring immatures that join groups relatives of the territory holders? We present data on the status of every individual as well as the composition and within-season changes in composition

of groups. This detailed information about group structure forms a basis for further studies on group dynamics and dispersal in this species.

METHODS

STUDY SPECIES

The Siberian Jay is a highly sedentary omnivorous inhabitant of the Eurasian taiga. It is a long-lived bird (up to 20 years) that forms life-long, monogamous pair bonds and lives on permanent, large, all-purpose territories (normally 1–4 km² in our study area), mainly in old-growth coniferous forests (Edenius and Meyer 2002). In winter the species is thought to be highly dependent upon food stored in trees throughout the territory (Cramp et al. 1994). These caches are strictly individual (Ekman et al. 1996). Pair members very rarely give up their territory or partner once established, but widowed birds commonly establish new pair-bonds (B-GL, pers. obs.).

The breeding biology of the Siberian Jay has been described thoroughly by Blomgren (1964, 1971), Lindgren (1975), and Kokhanov (1982). Breeding activities begin in March, when the ground is still covered by a thick layer of snow. The 3–5 young fledge in May, and some of them stay with their parents until the next breeding season. During late summer and autumn the family moves around its territory, storing food in the tree crowns for use in the winter. Nonoffspring immatures or adults commonly join the groups, but these strangers encounter aggressive behavior from other group members (Ekman et al. 1994, Sklepkovych 1997). Although supernumerary birds are frequently found in the territories even during the breeding season, and are occasionally seen at the nest (Carlson 1946, Matero 1996), true helping has never been recorded (Blomgren 1964, 1971, Lindgren 1975, Ekman et al. 1994). Immatures may disperse at any time of the year. Dispersal distances are normally short, especially among males, and thus neighboring males often are close relatives (Ekman, Eggers et al. 2001).

STUDY AREA

We studied Siberian Jay behavior and population dynamics from 1974 to 2000 mainly in Kristinestad and Närpes in western Finland (62°22'N, 21°30'E), close to the Gulf of Bothnia. The study area is near the southwestern border of the species' breeding range in Finland, where the jay

population density is lower than at northern latitudes (Kemppainen 2002, Helle and Lillandt 1997). The study began in a 120-km² forest, delimited by 100–1500-m-wide agricultural fields or peatlands (for details see Lillandt 1993). The number of jay territories in this area varied between seven and 17 during the 27 years of the study. Between 1985 and 1992 the study area was enlarged into neighboring forests, and since 1992 a 70-km² eastern study area (3–5 jay territories) and a 155-km² northern area (15–32 territories) was monitored annually. All three main study areas are quite well delimited by open fields. In 1998 we again expanded the study area to a total of 1000 km² of forest within a total land area of about 1500 km² (58, 78 and 81 territories during 1998, 1999 and 2000, respectively).

The landscape is a typical lowland (0–30 m elevation), where the forests are dominated by conifers such as Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*), with some broad-leaved trees, mainly birch (*Betula* spp.). Human settlements are confined to agricultural areas, while the forests are mainly uninhabited. The forests are, however, affected by forestry practices such as forest thinning, clearcutting, planting, draining, and road building. Because of ownership, forestry treatment areas are mostly small (0.5–2 ha), and every Siberian Jay territory (1–4 km²) consists of many different kinds of forest stands, from clearcut areas to mature forest (up to 100 years old). At least one-fourth of the study area is covered by peatlands, extensive pure pine forests, or young, mixed, or fragmented forests in which no Siberian Jay territories have been found despite regular monitoring. Most of these areas without jays are found along the edges of the studied forest areas, close to human settlements.

POPULATION MONITORING

Most of the data presented in this paper were collected during late summer and autumn (July–October), when food-hoarding jays could easily be attracted to feeding stations in their territories. Feeding stations consisted of bags made from wire netting, containing different kinds of lard or boiled potatoes. We distributed feeding stations in relation to jay density, with feeders placed at 0.25–1.0 feeders km⁻². This variation was due to the fact that territories are smaller in high-density areas. Thanks to a dense network of forestry roads it was possible to reach almost

every one of the 40–483 feeding stations used each year by car; this enabled us to monitor these large numbers of feeding stations 1–5 times each year. However, especially in the years 1978, 1980, and 1983–1987, the monitoring effort was lower, and a number of jay groups escaped attention in these years (Lillandt 1993). We removed feeding stations as soon as every bird was banded or identified (below). Because we fed the birds only during a few weeks in the autumn, when the forest was already full of food for this omnivorous species, we find it unlikely that the feeders affected the behavior or population dynamics of the jays.

The annual monitoring of the jays at feeding stations was facilitated by using playbacks of the birds' own calls, even though the birds are not very reactive to the sounds of conspecifics. At the feeding stations, unbanded birds were caught in baited traps or mist nets. Every bird was given a unique combination, consisting of a numbered aluminum band and 2–3 color bands, for later identification by binoculars or a telescope. Caught birds were also weighed and measured (wing length; beak length, depth, and width; tarsus length; and tail length). We used these morphological measurements to sex the birds (males are slightly larger than females). Sex determination based on morphology of adult birds was correct in 97% of cases ($n = 144$, 1974–1995) when compared to sexing by molecular techniques (B-GL, unpubl. data). In this paper we do not categorize immatures by sex, except for those few individuals that had established a pair bond in their first autumn, because the groups included immatures of both sexes in approximately equal numbers.

Our data set for the years 1974–2000 consists of 616 group-years; that is, the number of annual group observations summarized over the study period. Because of missing information about the status of at least some group members, observations from 53 group-years were discarded, leaving a total of 563 group-years. The typical Siberian Jay group is a nuclear family (sensu Emlen 1997), consisting of a territory-holding pair followed by 1–2 offspring, but in many cases 1–2 nonoffspring birds join territory-holding pairs. Because of the complex group structure we evaluate the status of individuals and the composition of groups separately.

TABLE 1. Results of parentage determinations in 442 immature and 171 adult Siberian Jays. Allelic profiles were compared to observed parent pairs in the studied populations in Finland, 1974–2000. The parentage determination system was validated within groups with known parent-offspring relationships. Parentage assignment presumed that no allelic mismatches between the offspring and the parent pair occurred on nine scored microsatellite loci (Lillandt et al. 2001, 2002). Individuals were divided into three groups: (1) immatures that completely matched the territory holders with which they associated in the autumn; (2) immatures that did not match the territory holders or that had no potential parents in the same territory; and (3) individuals banded as adults.

	Matched no sampled pair	Matched only one pair	Matched two pairs	Total
Immatures observed with matching parents				
Both parents sampled		270	16 ^a	286
Only one parent sampled	21 ^b			21
Neither potential parent sampled	9 ^c			9
Immatures observed after leaving natal territory	39	84	3 ^d	126
Individuals banded as adults	125	42 ^e		171

^a In 11 cases the allelic data were complete (nine microsatellite loci); the other 5 cases were based upon 3–8 loci.

^b All 21 birds matched the only sampled parent; four were banded as nestlings.

^c Four individuals were banded as nestlings.

^d In two cases the allelic data were complete; one was typed on only four loci.

^e In seeking parentage of individuals banded as adults, we included potential parent pairs that were alive 1–2 years before the individual was banded. In four additional cases we found matching parent pairs that lived 3–8 years before the tested individual was banded; in these cases the parentage was not regarded as confirmed.

AGEING, PARENTAGE DETERMINATION, AND PEDIGREES

To evaluate the status of individuals and composition of groups we needed information on the age and relatedness within groups and local populations. The birds were divided into two age categories by the shape of their outermost rectrices: immatures (<1 year) and adults (>1 year, Svensson 1992). In order to check age later on, we collected one rectrix (generally the left outermost) from most birds from 1976 onward. From 1997 on, we collected blood samples ($n = 357$) from every banded individual. These collections made possible extensive parentage determinations spanning the whole 27-year study period. In total, we had samples from 613 of the 735 jays banded in this study. In addition, 28 individuals escaped capture and banding, and an undetermined, low number of individuals escaped observation altogether because of insufficient monitoring efforts in some years.

Because we monitored (and banded) the jays mainly in July–October, and the young fledge in May, immatures had several months to move between territories before they were banded. To check for this possibility we performed parentage determination by analyzing nine variable microsatellite loci, using DNA from feather or

blood samples. Technical information on microsatellite acquisition has been given elsewhere (Hansson et al. 2000, Lillandt et al. 2002). The parentage determination system was validated within groups with known parent-offspring relationships, and the determinations for immatures banded from 1976–1998 are described in Lillandt et al. (2001). In the present study we included 144 new immatures banded from 1999–2000 in the data set, whereby the total number of tested immatures is 442 (Table 1).

To get as complete pedigrees as possible we also determined parentage for birds banded as adults. This category, totaling 171 sampled birds, included individuals found in territories when the study started in each area, adult immigrants originating from outside the study area, and individuals that for some reason escaped attention when they were immature. Basically we used the same microsatellite methods to determine parentage (Lillandt et al. 2001, 2002). Because we did not know the hatching year for birds banded as adults, we compared their allelic profile to every pair of jays present during any potential hatching year of the tested individuals. However, when the number of mutually related candidate parents increases by pooling data from

TABLE 2. The social status of Siberian Jays observed in groups in autumn between 1974 and 2000 in Finland. Relatedness was determined by microsatellite typing. The data set consisted of 563 group-years, after excluding 56 group-years because of incomplete DNA sampling. Note that an individual can be included in more than one category during its life. The numbers at the level of individuals are not exactly the sum of numbers of observed group-years (Appendix).

Social status	Immatures	Adults	Age unknown
Solitary	9	13	2
Established territory holder	36	370	
Individual accompanying genetic parent(s)	299	5	
One of the parents replaced with a stepfather/mother	6	3	
Individual accompanying a nonparent pair or solitary adult	82		
With which they were observed also as immatures		7	
With which they were not observed as immatures		8	
Individual accompanying an unrelated same-sex adult		13	

several years, the risk for total matches by chance between a tested individual and a nonparent pair also increases. To avoid the risk of mistakenly regarding an individual as an offspring of a particular pair, we allowed a maximum gap of two years between the banding of the adult and the last living year of its potential parents. For each of 42 banded adults we found one matching parent pair that met this restricted condition. In four cases we found matching parent pairs that lived 3–8 years before the banding of the tested individual; in these cases we regarded the parentage as unconfirmed. No adult individuals completely matched more than one parent pair. The results of parentage determinations for this study are presented in Table 1.

Pedigrees for the studied populations were established by combining data from field observations and microsatellite analyses. Using the pedigrees, we investigated to what degree immatures were related to each of the nonparental territory holders they associated with. The most complete pedigree included eight consecutive generations. In two other populations the pedigrees extended over ca. 10 years. Because Siberian Jays are long lived and there was continuous immigration, the completeness of the pedigrees varied largely between study areas and years during the study. We present means \pm SD for our observations.

RESULTS

STATUS OF INDIVIDUALS

Immatures. A total of 432 immature birds was observed in the 563 group-years (Table 2). In

autumn, 305 of these immatures (71%) were associated with their genetic parents, a widowed parent, or one genetic parent and one step-parent. The remaining 127 immatures were found either solitarily in a territory, established as territory holders, or associated with a nonparent pair or a nonparent same-sex adult bird (Table 2). Because it is not possible to distinguish immatures pairing with an opposite-sex, nonparent bird in the autumn from immatures simply joining such an individual, all these cases were regarded as established pairs.

Adults. Most adult birds ($n = 383$) were members of a breeding pair or were temporarily widowed. In 36 cases adults appeared as supernumerary individuals in different group compositions (Table 2); these cases included 35 individuals. Thirty-one birds delayed breeding during the first years after banding, while four adults were found associated with only a same-sex adult after previously being normally paired. One individual delayed breeding for three years, 11 delayed for two years. The remaining 19 birds either established a territory on their own ($n = 12$) or disappeared the next year.

GROUP STABILITY

Group composition remained mostly unchanged between observations within each season (July–October). In 440 group-years we made at least two reliable observations within the same autumn; the mean time span between first and last observation was 30.2 ± 25.0 days. In 357 group-years (81%) no changes in group composition were observed. In the remaining 83 group-years

TABLE 3. Composition of Siberian Jay groups in Finland during the autumns of 1974–2000. Groups were classified as nuclear families (a breeding pair plus its offspring) or nonfamily groups (territory holders plus birds that are not their offspring). Data compiled from Appendix.

Social status	Number
Nuclear families ($n = 230$ groups)	
Fathers	223
Stepfathers	2
Mothers	220
Stepmothers	6
Immature offspring	305
Adult offspring	8
Nonoffspring immatures	7
Nonoffspring supernumerary adults	5
Nonfamily groups ($n = 81$ groups)	
Territory-holding males	76
Territory-holding females	81
Nonoffspring immatures	74
Nonoffspring supernumerary adults	15

(19%) we recorded the following types of changes: (1) loss of territory holder ($n = 26$); (2) establishment of a new territory holder ($n = 10$); (3) movement of territory holder from one territory to another ($n = 3$); (4) loss of immature from natal territory ($n = 24$); (5) loss of nonoffspring immature ($n = 11$); (6) addition of a new nonoffspring immature to a group ($n = 12$); and (7) loss of a supernumerary adult ($n = 4$). Some groups had more than one type of change in a single season.

GROUP COMPOSITION

We observed 1–5 individuals in each territory during the autumns (mean 2.7 ± 0.8 individuals; $n = 563$). Among these there were 24 solitary birds (4%), which cannot be regarded as groups according to a strict definition. For groups that

changed size within the season we recorded the maximum number of individuals. When classifying the annual observations from each territory according to the number of birds and their age, status, and relatedness to the territory holders no fewer than 45 different composition types were found (Appendix). These belonged to four main categories: (1) solitary birds ($n = 24$); (2) single territory-holding pairs ($n = 228$); (3) nuclear families with offspring and in 12 cases one nonoffspring immature or adult supernumerary bird ($n = 230$); and (4) nonfamily groups consisting of territory-holding pairs or widowed territory holders with only nonoffspring birds ($n = 81$). The composition of categories 3 and 4, which are of special interest for this study, is presented in Table 3.

Altogether 82 immature birds were associated with nonparent pairs in different group composition types. According to pedigrees 57 of these immatures (70%) were not related to either of the territory holders with which they were associated (Table 4). Of these 82 immatures, 75 (91%) were found in groups that included no offspring of the territory-holders. These were probably failed breeders or newly established pairs. Only seven nonoffspring immatures were observed in mixed groups that also included offspring of the territory holders. We identified no cases in which all of the territory holders' own offspring had left their natal territory before nonoffspring immatures joined the pair. Among the immatures that had left their natal territory during their first summer, we had data for 80 individuals on the situation in their natal territory. In 70 cases (88%) dispersing immatures had siblings that remained with their parents, while only 10 dispersers left no siblings behind in their natal territory.

TABLE 4. Relatedness between 82 immature Siberian Jays and the nonparental territory holders with which they associated in the autumn. The origin of the immatures was determined by microsatellite typing and the coefficient of relatedness (r) was calculated from pedigrees (Brown 1987) that were confirmed by microsatellite analyses. The completeness of pedigrees varied greatly between areas and years.

	No. (%) of immatures
Territory holders related to the immature	
$r = 0.25-0.5$	19 (23)
$r = 0.01-0.24$	6 (7)
Territory holders not related to the immature	
Immature with known parents living in another territory	36 (44)
The origin of the immature unknown (probable immigrant)	21 (26)

DISCUSSION

We combined data from 27 years of field observations of Siberian Jays with results from microsatellite analysis (Lillandt et al. 2001, 2002), to reveal patterns of group living outside the breeding season in this apparently pair-breeding species. According to our two main questions we got the following results: (1) A clear majority (74%) of the 311 groups that included any supernumerary birds were nuclear families, but a considerable fraction of groups consisted of established territory holders accompanied by only nonoffspring birds (Table 3). (2) Immatures that had joined groups with territory-holding nonparents were mostly (70%) not relatives to any of these territory holders (Table 4). Taking into account the strong kin-structure of the population (most birds have relatives in nearby territories; Lillandt et al. 2001, B-GL, unpubl. data), the finding that 30% were related to one of the territory holders gives no reason to believe that immatures seek out relatives when they disperse at an early stage from their natal territory.

The “ecological constraints hypothesis” proposes an explanation for the evolution of delayed dispersal and cooperative breeding. Young birds remain on their natal territory and help at their parents’ nests because they are “ecologically constrained” by a shortage of suitable habitat, high dispersal costs, a shortage of breeding partners, or low probability of successful breeding once a territory has been obtained (reviewed by Hatchwell and Komdeur 2000). Delayed dispersal and group living occur without cooperative breeding in the Siberian Jay, so there must be benefits other than indirect fitness consequences of cooperative breeding (Ekman, Baglione et al. 2001). Ekman et al. (1994) showed that Siberian Jay parents selectively tolerate offspring at food in winter, but not nonoffspring. Retained immatures are more successful in terms of foraging success (Sklepkovych 1997), winter survival (Ekman et al. 2000), and, in males, lifetime fitness (Ekman et al. 1999) and territory acquisition (Ekman, Eggers et al. 2001).

Studies of Tufted Titmice (*Baeolophus bicolor*) by Pravosudova et al. (1999, 2000, 2001) reveal a group structure similar to the Siberian Jays we studied. Territory holders were more aggressive toward nonoffspring than toward retained off-

spring in the group, but there were no measurable consequences on the nutritional condition of nonoffspring (Pravosudova et al. 2001). Ptilochronological analysis of feathers grown during normal molt showed that retained offspring were in better nutritional condition than nonoffspring before the winter season. This suggests that retained offspring were originally dominant individuals, and that nonoffspring had been subordinates in the natal territories before dispersing. If this is the case also in the Siberian Jay, retained offspring might do better later in life (Ekman et al. 1999, 2000, Ekman, Eggers et al. 2001), just because they are a selected sample of higher quality individuals.

THE SIBERIAN JAY NONFAMILY

The dispersal process that takes place in summer is poorly studied in the Siberian Jay, but our observations suggest that there are considerable similarities to the sister species Gray Jay. Strickland (1991) reported that dominant Gray Jay immatures expel siblings from the natal territory, whereby almost every pair is accompanied by only one immature in the autumn. In the Siberian Jay two immatures commonly stayed in their natal territory, but there were almost never more than two, despite a mean clutch size of 3.9 ± 0.6 (Lillandt 1993). In our study 19% of the observed immatures had left their natal territory and associated with pairs without offspring in the autumn, thereby forming nonfamily groups. In the population studied by Ekman, Eggers et al. (2001), 42% of the immatures observed in the autumn had left their natal territory.

Why, then, do nonoffspring individuals stay in territories with possibly aggressive territory holders rather than search for a better place? Among several possible answers to this question, there may be severe costs of moving around, as in Western Bluebirds (*Sialia mexicana*, Kraaijeveld and Dickinson 2001), or important benefits from winter group territoriality (e.g., relaxed predation pressure, groups having knowledge about feeding places and shelter, food stores, future possibilities of acquiring a territory and partner). The decision to stay in a nonfamily group may be a result of competition within the larger groups on better territories, suggesting that, as in Tufted Titmice, early-dispersing individuals are losers in the competition with conspecifics (Pravosudova et al. 2001). Further studies are needed in order to resolve the

cost-benefit analysis of the dispersal behavior in the Siberian Jay. We feel that this is a key question that, when solved, could give important insights in dispersal behaviors in species with group territoriality.

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APPENDIX. Group size and composition in 563 Siberian Jay group-years, observed in summer-autumn 1974–2000 in Finland. The relatedness of individuals was determined by microsatellite typing. Only groups with complete DNA samples and observations are included. “Imm.” = immature.

Group composition	Group size					Total (group- years)
	1	2	3	4	5	
Solitary birds (24 individual-years)						
Adult male	4					4
Adult female	9					9
Unbanded bird (not sexed or aged)	2					2
Immature	9					9
Territory-holding pair with no other birds (228 group-years)						
Adult pair		200				200
Adult male paired with immature female		7				7
Adult female paired with immature male		12				12
Territory-holding immature pair		3				3
Two adult females (not parent-offspring)		3				3
Two adult males (not parent-offspring) ^a		3				3
Adults with only immature offspring (206 group-years)						
Adult pair, 1–3 immature offspring			125	72	1	198
Adult male, 1 immature offspring		3				3
Adult female, 1–2 immature offspring		2	3			5
Adults with only adult offspring and mixed groups with immatures and adults (5 group-years)						
Adult pair, 1 adult offspring			1			1
Adult male, 1 adult offspring		1				1
Adult pair, 1 immature offspring, 1 adult offspring				3		3
Mixed groups (11 group-years)						
Adult pair, 1–2 imm. offspring, 1 nonoffspring imm.				5	1	6
Adult pair, 1–2 imm. offspring, 1 nonoffspring retained ^b adult				2	1	3
Adult pair, 1 imm. offspring, 1 nonoffspring adult				2		2
One parent and a new mate, plus offspring (8 group-years)						
Adult male, stepmother, 1–2 imm. offspring			1	1		2
Adult male, stepmother, adult offspring			2			2
Adult male paired with imm. stepmother, imm. offspring			1			1
Adult male paired with imm. stepmother, adult offspring			1			1
Adult female, stepfather, imm. offspring			1			1
Adult female, stepfather, imm. offspring, 1 nonoffspring imm.				1		1
Pair or single adult with only nonoffspring individuals (81 group-years)						
Adult pair, 1–2 nonoffspring imm.			54	3		57
Adult pair, 1–2 nonoffspring imm., 1 nonoffspring adult				1	1	2
Adult female, 1 nonoffspring imm. (same sex)		2				2
Adult pair, 1 nonoffspring imm., 1 retained nonoffspring adult ^b				1		1
Adult pair, 1 retained nonoffspring adult ^b			3			3
Adult female, 1 retained nonoffspring adult ^b female		2				2
Adult pair, 1 nonoffspring adult			5			5
Adult female paired with imm. male, 1 nonoffspring imm.			2			2
Adult female, paired with imm. male, 1 retained nonoffspring adult ^b			1			1
Adult male paired with imm. female, 1 nonoffspring imm.			4			4
Two adult females (not closely related), 1 nonoffspring imm. (same sex)			1			1
Territory-holding imm. pair, 1 nonoffspring imm.			1			1
Total number of groups	24	238	206	91	4	563

^a In two group-years, a third individual was temporarily observed with the two adult males.

^b Formerly observed as a nonoffspring immature in the same territory.