

INTRASEXUAL COMPETITION, DISPERSAL, TERRITORIALITY AND THE
MATING SYSTEM OF THE SONG SPARROW ON MANDARTE ISLAND, B.C.

By

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ABSTRACT

I consider the relationship between natal dispersal, the acquisition of breeding resources and the proximate maintenance of the mating system in a population of song sparrows (Melospiza melodia) resident on Mandarte Island, B.C.. The general hypothesis tested was that intrasexual competition for the resources that limit reproduction in each sex is the main factor affecting patterns of natal dispersal, territory turnover and mating system organization. This study reveals differences in the competitive ability of individuals and the consequences of these for natal dispersal, territory acquisition and the ability to monopolize mates.

In this population, natal dispersal, territoriality and the mating system are related through the common mechanism of intrasexual competition for breeding resources. This competition affected reproduction within each sex, and in the opposite sex, raising potential conflicts of interest between mated males and females. I identify correlates of competitive ability, and consider how individuals of each sex maximize the number of young they raised.

All suitable habitat was defended even at low density, resulting in high levels of competition for space. Song sparrows contested for territories year-round. Most settlers were yearlings, but several males were older and had previously

owned a territory. Most floaters settled by evicting owners from all or part of their territories, in contrast to the assumption of most models of dispersal that floaters gain territories only after an owner's death. Relative age and dominance within cohorts affected recruitment and territorial status in the year following hatch in each sex. Differences in age also affected territorial and mating behaviour, particularly in males. Although competitive ability varied with age, differences in competitive ability between males persisted through life.

Approximately 9% of male breeding attempts occurred after a male territory owner had evicted a neighbour and thereby gained access to an additional female. Polygynous males raised more young than monogamous males. Females vigorously defended their territories against female intruders, presumably to prevent polygyny by their mates. Females in polygynous groups often lost the aid of their mate, and raised fewer young, because polygynous males did not aid two females simultaneously. Adding supplemental food altered female time budgets, increased their ability to prevent settlement by female floaters, and increased their reproductive success. This suggests that females are constrained in the amount of time they can spend in territory defence by time spent foraging. The maintenance of monogamy was affected by differences in the abilities of individual males and females to defend their territories against intruders of the same sex.

Dispersal distances were similar among sexes, in contrast to the usual pattern of female-biased dispersal in birds. Given the intense territorial behaviour of males and females, this study supports the hypothesis that biases in dispersal arise when territory establishment is substantially more difficult in one sex than the other. Dispersal on Mandarte was unrelated to inbreeding, common parentage, or reproductive success. However, emigrants from Mandarte were socially subordinate birds that must have outbred if they settled successfully. Female emigrants from local populations in the vicinity of Mandarte may settle more often than males. Dispersal occurred as young birds established ranges in the period following independence, from which they challenged or replaced owners. Adding food during the breeding period reduced dispersal in males and females in late summer and the following spring. Competitive ability probably affects dispersal from the natal population, the likelihood of settlement, and the time of settlement for those birds that remain in the natal population.

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CHAPTER 1. INTRASEXUAL COMPETITION, DISPERSAL AND MATING SYSTEMS IN BIRDS

INTRODUCTION

In this thesis, I consider the relationship between natal dispersal, the acquisition of breeding resources and the proximate maintenance of the mating system. I studied a population of song sparrows (Melospiza melodia) resident on Mandarte Island, B.C., Canada. I focus on the roles of (a) intrasexual competition and (b) individual variation in competitive ability on: territory acquisition and defence, natal dispersal, and the mating system. These topics are of considerable current interest because recent studies (reviewed below) suggest strong links between them. Despite this, no study has simultaneously investigated these topics within a single, well-known vertebrate population.

Early models of territoriality, natal dispersal and mating systems focused primarily on the aggressive behaviour of males. The major factor thought to affect female behaviour was the choice of high quality mates. If competition between females affects natal dispersal, territory turnover and the organization of mating systems, we must assess its importance relative to female choice of mates or territories. The main goal of this thesis is therefore to assess the intensity of competition between individuals of each sex, and to determine if it has a

major effect on the patterns of natal dispersal, territory turnover, and mating system observed in the study population of song sparrows.

In this chapter, I first review briefly the topic of natal dispersal and its relationship to theories of the ecology and evolution of social organization. Second, I review current theories of the organization of mating systems, and I show how competition for resources that limit reproduction might affect the spacing behaviour of both males and females. Third, I describe how intrasexual competition, demography and the organization of mating systems affect patterns of natal dispersal. Finally, I describe the topics and hypotheses addressed in subsequent chapters of this thesis.

Natal Dispersal

Natal dispersal is the permanent movement of an organism from the natal site, as distinct from breeding dispersal, which refers to movements between breeding sites (Lidicker 1975; Greenwood 1980). The frequency and extent of natal dispersal is typically correlated with other life-history traits such as fecundity, survival and mating system (Hamilton & May 1977; Comins et al. 1980; Greenwood 1980; Greenwood & Harvey 1982; Dobson 1982; Waser & Jones 1983). Patterns of dispersal are intimately related to a species' social organization because they affect the frequency and type of interactions between

individuals. The causes of dispersal and its evolutionary consequences have therefore been of general and long-standing interest among biologists (Wright 1940; Miller 1947; Mayr 1963; Wilson 1975; Bradbury & Vehrencamp 1983; Brown 1987).

Dispersal piqued the curiosity of population geneticists several decades ago (e.g. Wright 1940; Miller 1947), because it is the means by which genes flow between populations. In the absence of strong selection, a reduction in gene flow was recognized as a prerequisite to population differentiation and speciation. Recent models of dispersal have incorporated the inclusive fitness of individuals, habitat structure and quality, and the level of competition for resources within populations (e.g. Hamilton & May 1977; Horn 1978, 1983; Comins et al. 1980).

Population biologists began extensive research on dispersal in the late 1950's because of its presumed role in population regulation (Errington 1956; Lidicker 1962). At this time, the factors causing dispersal began to be actively discussed (e.g. Howard 1960; Sadleir 1965). Howard (1960) postulated that a heritable tendency to disperse would be favored because dispersers would colonize vacant habitat, extend the species' range and reduce inbreeding in natal populations. Lidicker (1962) added that dispersal could prevent populations from over-exploiting local resources.

The view that dispersal is an advantageous property of populations and species was championed by Wynne-Edwards (1962), who considered dispersal to be an altruistic exodus of surplus individuals. In contrast, Murray (1967) viewed dispersal as a means of maximizing individual reproductive potential, within the limits of individual ability. He suggested that dispersal is selected for whenever intense local competition makes settlement unlikely, and he offered a model based on behavioural dominance and differential access to breeding resources that was consistent with the patterns of natal dispersal observed in nature.

These authors and others stimulated much research into the relationship between dispersal, population dynamics and social structure (reviews in Lidicker 1975; Gaines & McClenaghan 1980; Waser & Jones 1983), but individual variation in dispersal behaviour was not given close attention (e.g. Brown 1975; Wilson 1975; but see Myers & Krebs 1971). However, the latter topic has recently sparked much interest among researchers investigating relationships between behaviour and the ecology and evolution of social systems (Bekoff 1977; Horn 1978, 1983; Greenwood 1980; Shields 1982, Dobson 1982; Waser & Jones 1983).

In studies of this sort, the main questions addressed are: (1) what are the causes and consequences of variation in dispersal behaviour to the individual? (2) how are social organization and dispersal related? (3) what are the

consequences of such relationships for the evolution of species? To answer these questions within a species, one must first understand some of the major factors that contribute to the success of individuals within populations. Second, one must assess the strength of interactions between individual behaviour and the physical and social environment (Bradbury & Vehrencamp 1983; Woolfenden & Fitzpatrick 1984; Brown 1987). I now explore some of these interactions by considering relationships between individual differences in behaviour, the environment, and the mating system.

Reproductive Competition and Mating Systems

The theory of mating systems is founded on the observation that females commit more energy to each gamete than males (Orians 1969; Trivers 1972). Thus, female reproductive success is often limited by access to resources, while male reproductive success is more likely to be limited by access to fertile females. Trivers (1972) argued that selection therefore favors competitive mate acquisition by males and careful mate choice by females (see also Orians 1969; Selander 1972; Halliday 1978; Wittenberger 1979; Greenwood 1980).

Male reproductive competition is widespread and well-documented (e.g. insects, Parker 1978; fish, Farr 1977; anurans, Arak 1983; mammals, Clutton-Brock et al. 1982; birds, Wiley 1974). Current theory suggests that, as a consequence of such

competition, mature males are often larger, more aggressive and brightly colored, and more endowed with weaponry than females (Selander 1972; Wittenberger 1979; Payne 1984). Females, however, also compete for resources crucial to reproduction. (e.g. insects, Whitham 1986; fish, Schroder 1981; mammals, Hogdon & Larsen 1973, birds, Davies & Houston 1986). Because competition in females is usually much less overt than in males, it remains poorly understood in general (Wittenberger 1979; Oring 1982; Wasser 1983). Reproductive competition among males includes defence of resources required by females, direct defence of females or advertisement for females. In contrast, females typically compete through defence of breeding sites, but rarely by defending males or by advertisement (Wittenberger 1979; Oring 1982; Arak 1983; Petrie 1983).

Ecological factors (e.g. temporal and spatial distribution of food, breeding sites) determine the form of most mating systems (Orians 1969; Emlen & Oring 1977; Wittenberger 1979). This is because the distribution of resources affects the ability of individuals to defend them from conspecifics (Brown 1964; Brown & Orians 1970). Females respond primarily to resource distribution, while males respond either to female distribution or to the distribution of resources that females require (Bradbury & Vehrencamp 1977; Parker 1978; Wittenberger 1979).

When resources are seasonally predictable and clumped in

space, males can maximize exclusive access to females by defending resources that females require (resource defence; Crook 1965; Verner & Willson 1966). The extent to which defending males exclude other males determines the level of polygyny in the population (Orlans 1969; Emlen & Oring 1977). In contrast, when resources are either thinly dispersed or seasonally unpredictable, males must either accompany and defend females during fertile periods (female defence; Clutton-Brock & Harvey 1976; Bradbury & Vehrencamp 1977), or advertise their suitability (lek breeding; Wiley 1974; Emlen 1976).

Females should also defend limiting resources against conspecifics when defence increases: (1) the quality or number of offspring produced, (2) their relative reproductive success (by interfering with reproduction in other females), or (3) reduces the probability of having to share male parental care (Wittenberger 1979; Oring 1982; Wasser 1983; Hannon 1984; Davies & Houston 1986).

In monogamous species, the role of male competition is probably relaxed compared to polygynous and promiscuous species (Selander 1972; Wittenberger & Tilson 1980; Oring 1982). Males may respond either to the distribution of females, or to the distribution of the resources that females require. Females respond to the distribution of resources that affect reproductive success. In this case, either sex or both might defend resources (e.g. Davies & Houston 1986). This could

affect patterns of natal dispersal if the costs or benefits of resource defence depended on proximity to the natal site (Murray 1967; Greenwood 1980; Dobson 1982).

Monogamy is generally rare among vertebrates, except in birds where it is common (Lack 1968; Kleiman 1977; Moller 1986). Wittenberger & Tilson (1980) concluded that most birds were monogamous because males either cannot defend enough resources to attract additional mates or cannot defend more than one female. However, recent work shows that female territorial behaviour in birds reduces polygyny and sometimes enforces monogamy on males by preventing some females from access to territories (Hannon 1983, 1984; Davies 1985; Hurley & Robertson 1985; Stutchbury & Robertson 1985). Further, when male parental care increases reproductive success but cannot be shared among females, females can double the number of young they raise by insuring exclusive access to male aid (e.g. Smith et al. 1982; Davies & Houston 1986). This should select for increased female aggression. In practice, however, female territoriality is difficult to detect because in most monogamous birds defence of a territory by a male is equivalent to defence of a female (Smith et al. 1982).

Mating Systems, Demography and Dispersal

If the factors that affect success in resource defence are similar in males and females, dispersal may be more a

consequence of sex-specific demography than of differences in mating strategy (Murray 1967; Waser & Jones 1983). In contrast, Greenwood (1980) and Greenwood & Harvey (1982) argued that sex-biases in dispersal in monogamous birds are caused by the relative importance of resource defence to males and females, and the costs of inbreeding depression. They believe that males are the main defenders of breeding resources, and that females choose where to settle rather than having their choice forced by intrasexual competition. Making the additional assumption that males remaining near the natal site are more likely to acquire a territory and breed, they concluded that the cost of inbreeding depression would outweigh the cost of dispersal in females, but not in males.

This hypothesis clearly depends on the structure of the mating system and on which sex is primarily responsible for resource defence, which are not yet well-understood for most species. The advantage of remaining near the natal site is also poorly known. Few previous studies have simultaneously investigated intrasexual competition for resources, natal dispersal and the organization of the mating system. This is my overall goal in this thesis.

Goals of the Study

Four characteristics make the song sparrow population on Mandarte Island particularly suitable for a study of intrasexual

competition for resources, natal dispersal and the organization of the mating system: (1) nearly all birds that breed in the population are hatched there, and thus can be observed in detail from hatching to the time they settle on a breeding territory, (2) the lifetime production of independent young for all recruits can be determined, (3) the size of the population allows well-controlled experiments with a sufficient number of experimental subjects, and (4) the natural variation in population size allows observations over a wide range of densities (Fig. 1.1).

In Chapter 2, I first describe the natural history of the song sparrow, the study site, and the methods employed in this study. Further, I have consolidated all methods referred to in subsequent chapters to minimize redundancy. Each technique used is described under a heading that identifies the topic (e.g. Estimating Dominance, Statistical Analyses). I list these in the table of contents to facilitate their location. The methods described in chapter 2 are presented roughly in the order that they are employed in consecutive chapters of the thesis.

In Chapter 3, I consider patterns of territory acquisition and loss by male song sparrows over the 5 years of the study. I also test two assumptions of popular models of dispersal in territorial animals. These are: (1) previous ownership is the main factor affecting the outcome of contests over territories,

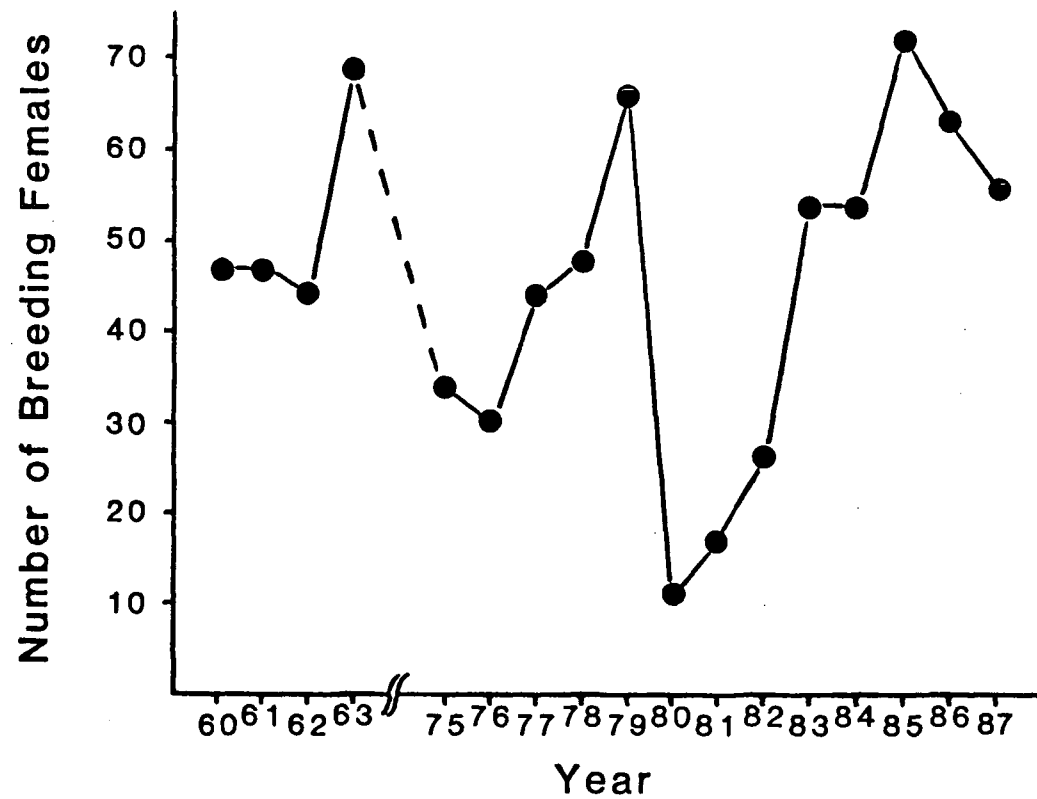


Figure 1.1. The number of females breeding on Mandarte Island during 17 years (Tompa 1964; Smith 1988; this study).

and (2) that mortality of territory owners is the primary mechanism by which habitat becomes available for settlement by non-territorial animals (referred to as 'floaters', after Brown 1969 and Smith 1978). I discuss these results with regard to (a) competition for local territories versus dispersal to unoccupied sites elsewhere, (b) the temporal pattern of territory turnovers, and (c) the role of age in territory defence.

In Chapter 4, I test several hypothesis about the role of surplus, non-territorial floaters in the territorial system of the song sparrow. To do this, I describe aggressive interactions between territorial and non-territorial male song sparrows, and I investigate several factors that might affect the tendency of floaters to localize on the territories of particular males. Finally, I test the hypothesis that the ability to defend territories against challenges by floating male song sparrows is related to the age of the territorial male.

In Chapter 5, I examine the aggressive and territorial behaviour of female song sparrows, and its relation to female singing behaviour. Using observations on the frequency of song by females, and on the situations in which song is most often observed, I test the hypothesis that song is an aberrant behaviour of females that is unimportant in the context of breeding or territorial behaviour. These results are discussed

in light of recent hypothesis about the role of androgens in territorial behaviour.

In Chapter 6, I present observational data to test the hypothesis that the mated status of individual males and females depends on their ability to participate in territory defence. I then present an experimental test of the effects of resource abundance on the time budgets, territorial behaviour and reproductive success of males and females. I first hypothesized that female song sparrows freed from foraging demands would spend more time in activities directly related to territory defence. Second, if female song sparrows defend exclusive access to their mate, or to the resources contained within their territory, I expected that females with extra food would be more able to prevent settlement by surplus, non-territorial females.

In Chapter 7, I investigate patterns of natal dispersal in 5 cohorts of young with regard to population density, kinship, resource distribution and subsequent reproductive success. In this chapter I review and test several hypothesis put forward in the literature to explain individual variation in dispersal distance. I also present results on the effect of food addition on the natal dispersal of young raised on fed and control territories, and on the level of subsequent competition for experimental territories after supplemental feeding had ceased. In Chapter 8, I conclude the thesis by briefly discussing the

roles of intra-sexual competition in dispersal, territoriality and the organization of mating systems.

Chapters 3-7 of this thesis were written as a series of papers. Because of this, the main development of each topic and the statements of relevant hypotheses are dealt with in the introductions of each of these chapters.

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CHAPTER 2. STUDY SPECIES, STUDY SITE AND METHODS

Study Species

The song sparrow is a timid, secretive inhabitant of shrublands that border watercourses, damp meadows and coastline (Nice 1937, Marshall 1948a,b). It breeds throughout North America from central Mexico north to the treeline (Marshall 1948a). Song sparrows are mainly ground-feeding granivores in winter, and therefore either migrants, partial migrants or year-round residents depending on snow cover (Nice 1937). In spring and summer, song sparrows feed primarily on insects and leaf and flower buds, and feed mainly insects to their young (Nice 1937; Johnston 1956b, Tompa 1964).

The song sparrow is a primarily monogamous passerine that often mates for life, and lives mostly within a small (ca. 0.05-1.0 ha) multi-purpose territory (Nice 1937; Johnston 1956a; Tompa 1964). The low frequency of natural polygyny (ca. 3%) can be increased by removing males during the breeding period (Smith et al. 1982), or in migratory populations by experimentally increasing testosterone levels in males (Wingfield 1984). Song sparrows mature at 1 year of age, often fledge more than one brood per year (max=4) of up to five young and typically breed for from 1-3 seasons (max=8, Nice 1937; Smith 1988).

Juveniles gain independence at 25-30 days of age and often join other young in loose flocks. Territorial behaviour among young birds appears after the post-juvenile molt (Tompa 1964). Dominance hierarchies form among young birds during the late summer and fall, and social status in these flocks determines which young remain in the population and eventually settle (Arcese & Smith 1985). Among juveniles, males often dominate females at feeders, and young hatched early in the spring are generally dominant to those hatched later (Arcese & Smith 1985). Offspring do not resemble parents in dominance status (P.Bets unpublished). Some juveniles move within restricted ranges from early fall to the following spring. The degree of localization among juveniles varies, but many gain territories in these areas from fall through spring (Tompa 1964; own observations).

Juveniles that fail to settle by the time breeding commences become highly secretive and live on the territories of breeders (Smith et al. 1982). Females, however, rarely remain unsettled after breeding commences, although many unsettled females sometimes remain in the population until egg-laying begins, but disappear thereafter (own observations). In most years, a small number of male territory owners remains unmated (Smith et al. 1980).

The pair resides on the territory year-round, except where the species is migratory, but territorial behaviour peaks during

the autumn and spring (Nice 1937; Johnston 1956b; Tompa 1964). Males are more visibly territorial than females, but females also fight, especially in late winter and spring (Nice 1937; Tompa 1964; Smith et al. 1980; own observations). Few birds change territories within or between seasons, though females may do so more than males (Nice 1937; but see Weatherhead & Boak 1986).

Mandarte and Halibut Islands

Mandarte Island is located in the Haro Strait, approximately 25 km ENE of Victoria, B.C., Canada. This small (6 ha), long and narrow island (ca. 700 by 90 m) is covered by a thin layer of soil that supports a dense cover of grasses and herbs that remain green throughout most of the year. A depression along the axis of the island supports a dense growth of shrubs that cover approximately 1.5 ha of the island's land area. This shrub area, along with the surrounding meadows and intertidal areas, are the habitats used for feeding and breeding by song sparrows. A few large conifers, and several smaller broad-leaved trees (e.g. Prunus spp., Quercus garryana) grow in clusters throughout the island. Canopy height varies from 1-5 m.

Halibut Island, situated about 1.3 km S of Mandarte, is the closest island with a resident song sparrow population. Halibut supports a small population of song sparrows (ca. 10

pairs; Tompa 1963) and is about half the size of Mandarte in land area. Halibut is less suitable as a habitat for song sparrows than is Mandarte because it is covered primarily by coniferous forest. However, patches of dense shrub that border the forest provide song sparrow habitat which closely resembles that found on Mandarte.

Study Population

The song sparrow population on Mandarte Island has been intensively studied since 1974. Tompa (1964) also studied this population from 1960 to 1964, and he provides a detailed description of the habitat and the biology of the song sparrows that are resident there year-round. The general field methods used since 1974 are described in Smith & Zach (1979), Smith (1981, 1988) and Arcese & Smith (1985). Some data presented here were collected in these previous studies.

In brief, most adults are territorial year-round. Yearlings begin to acquire territories in their first summer, but many remain non-territorial until the beginning of their first breeding season (Chap. 3, 4, 6, 7). The defended habitat is composed primarily of dense shrub (e.g. Symphoricarpos albus, Rosa nutkana), and is used for nesting and feeding. Observations of individual birds can be made relatively easily. As a result, virtually all song sparrow nests are found during incubation, and all young are banded as nestlings with a unique

combination of colored, plastic rings and a numbered aluminum ring.

Census Technique

I visited the island at least monthly for 2-5 days from September to February, and lived semi-permanently on the island from March through August, from September 1981 through 1986. During this time, the locations of all birds sighted were recorded on maps drawn from an aerial photograph, and special attention was paid to conflicts over territories.

From 1 January 1982 to 10 March 1987, intensive censuses of the population were made by myself and up to 2 helpers. During a census, the entire island was searched by walking on all trails, around all shrub patches and along the entire shoreline. I routinely crawled through particularly dense shrub patches. While searching, all birds sighted were followed until identified or lost. When no birds were evident in an area, I sat motionless for up to several minutes listening for song sparrow sounds and watching for motion. Many extremely timid birds (e.g. female floaters) were identified and observed in this way. Playbacks of taped song were sometimes used to locate birds in winter. Because shrub patches cover less than one-third of the 6 ha island, and are well-divided by trails, the entire island was relatively easily censused.

Determination of Territorial Status

Song sparrows on Mandarte Island are resident year-round. Territories of shrubs and adjacent grassland or intertidal areas are defended by song, threat postures, pursuits and fights throughout the year by most adults and a few yearlings. Non-territorial floaters live secretively on the territories of other males, but are relatively easily observed outside of the breeding period. Territorial behaviour is most pronounced in autumn, late winter and spring, but song and territorial aggression occur throughout the year.

I used the presence or absence of several behaviours to determine the territorial status of males and females. I considered birds to be territorial if they sang, perched prominently and unchallenged, and/or consistently evicted other birds from an area of shrubland for at least a day. Territory holders rarely allowed floaters of the same sex to sing or perch prominently in the shrub for more than brief periods. However, floaters occasionally remained for longer periods when owners were off the territory feeding or bathing.

The postures and vocalizations of floaters and territory holders differed strikingly: floaters frequently gave 'tsip' calls (Nice 1943:274), always held their wings flat upon their backs and usually raised their crest feathers when sitting prominently in a shrub or when approached by a territory holder.

Territory owners rarely gave tsip calls, but frequently gave 'tchunks', 'caterwauls' and 'threat notes' (Nice 1943:274). Male owners frequently sang, but females rarely did so (Chap. 5). Owners raised their crests only when alarmed (e.g. in presence of a hawk) and typically held their wings erect along the length of their body. The only exceptions to this occurred when floaters tried to evict territory owners by perching prominently and singing in their territory. Further descriptions of the behaviours of floaters and of transitions in territorial status are given in Chapters 3-6.

Mapping Territory Boundaries

Territory size was measured during the last 2 weeks of April by plotting on maps traced from a low-level aerial photograph the singing posts, movements and points of boundary disputes between all birds. Territory boundaries for males and females were drawn by connecting these points. Boundaries could be most accurately estimated from March to August, when observations were made nearly continuously. Home-ranges of floaters were determined by plotting sightings on maps and connecting the points to form minimum convex polygons.

Assessment of Reproduction

Territories were visited at least every 5 days throughout the breeding period each year. At each visit, males and

females were observed for 20-60 min, or until the stage in the nesting cycle was determined. Regular nest checks revealed when nest failure occurred or the number of young that hatched. Most nests were found during incubation or earlier. After hatching, nestlings were weighed and color-banded at about day 6. The number of fledglings was determined by nest checks and by observing parents feeding newly-fledged young (Smith 1978; Smith & Merkt 1980). The number of young reaching independence was determined from resightings and captures in mist nets during intensive censuses of the sparrow population on the island throughout the summer and fall.

Age of Birds

As there is little immigration to the population (Tompa 1964, Chap. 7), nearly all individuals observed in this study were color-marked and of known age. Because few individuals of either sex survive beyond 4 years, all birds 4 or older were pooled in analyses involving age.

Estimating Intrusion Pressure

Observations on rates of intrusion were made between 1 March and 31 August in 1984 and 1985. I recorded intrusion pressure on the territories of 57 males from 1-6 years of age during 80 h of observation in 1984. In 1985, I recorded intrusion pressure on the territories of 75 males of the same

range of ages during 214 h of observation. An intrusion was recorded whenever a floater was observed trespassing on the territory of the focal male. Forty-one territorial males were observed in both years. All observations were made during 578 periods (15 to 80 min) from 0600 to 2100 hours.

Initial results showed that the number of intrusions, but not the intrusion rate, varied significantly with the length of the observation period. I therefore standardized statistically for each bird's observation period length by regressing the number of intrusions on period length. I then used the log-transformed residuals (hereafter called standard intrusion pressure, SIP) as the y-variate in later analyses. This method proved superior to using rates because the transformed residuals were normally distributed, while rates were not normally distributed even after transformation (Gilbert 1973; Sokal & Rohlf 1981). The slopes and y-intercepts of the yearly regressions were similar (all $P > 0.10$). Territory tenure was measured as the number of days that a male defended a territory during 1 March to 31 August.

Types of Territory Turnovers

I defined 5 types of turnover in territory ownership (males only):

(1) Insertions occurred when floaters settled on the border between two territories or when floaters settled primarily

within one territory.

(2) Take-overs by floaters occurred when floaters acquired the entire territory of an owner.

(3) Replacements by floaters occurred when floaters began defending a territory that was known to have been unoccupied for at least one day.

(4) Take-overs by neighbours occurred when a territory owner expanded its territory to include most (>75%) of a neighbour's territory, and either evicted the owner or forced it to remain in a small portion of its former territory.

(5) Replacements by neighbours, as for floaters, occurred when a neighbour annexed an undefended portion of shrub after the disappearance of an owner.

In all cases, turnovers were scored as take-overs only if a conflict had been observed either previous to or during the observation of a change in ownership. In a few cases, no conflict was observed and the territory was known to have been occupied when last watched: these cases were scored as replacements. These took place in winter when visits to the island were less frequent and the overall number of turnovers that occurred was small. The actual number of take-overs is therefore slightly underestimated. The dates of turnovers were known by observation or estimated as either the date that the owner was last seen (take-overs) or the date when a replacement was first observed (replacements).

Fates of Males

I determined the fates of former male owners for each turnover recorded. Owners either: (1) remained territorial on a portion of their previous territory; (2) dispersed to a nearby territory; (3) became a non-territorial floater; or (4) disappeared from the population. Because floaters are secretive and difficult to observe, some males that apparently disappeared from the population probably survived undetected as floaters. Thus, the number of males that became floaters after being evicted from their territories is probably underestimated.

Seasonal Patterns of Territory Turnover

To examine the seasonal pattern of territory turnover, data were pooled into 6 2-month periods. These are: Jan.-Feb., a period of increasing pre-breeding territorial activity; Mar.-Apr., the first two months of breeding; May-June, peak of the breeding period; July-Aug., end of breeding and the period of post-nuptial molt; Sept.-Oct., autumn period of territorial behaviour; and Nov.-Dec., mid-winter period with only low levels of territorial behaviour. Pooling observations in this way minimized error because I was very confident of the 2-month period within which turnovers occurred.

Recording Song

During the springs of 1984 and 1985, P.K. Stoddard and S.M. Hiebert recorded songs from three females during a study of song repertoire function in males. One of these females was recorded while singing spontaneously. The others sang in response to a playback of songs recorded from a male on a non-adjointing territory. The playback speaker was placed in the center of each female's territory. Songs were recorded on a Uher 4000 tape recorder with a 41 cm parabolic microphone. After recordings were band-pass filtered to reduce ambient noise, sonagrams were made on a Kay 6061B Sona-graph with a 150 Hz plug-in filter.

Definitions of Mated Status

I refer to females as 'monogamous' if they: (1) occupied a territory that was overlapped by a single male, and (2) received aid raising their young from a male whose territory did not overlap completely that of an additional female. During the incubation stage, male aid was defined as alarm calling when a predator or human entered the territory or approached the nest. After hatching, only females whose territorial male fed her young were defined as monogamous.

When a male's territory overlapped the majority of the areas utilized by two or more females, males were defined as

polygynous. The resident females were defined as either 'aided' or 'unaided' using the same criteria as for monogamous females. Several females were left unaided after their original mate was replaced by a floater. These females were pooled with unaided females in polygynous groups for analyses of the effect of male aid on reproductive success.

Food Addition Experiment

In 1985, I placed a single small feeder in the centers of 15 territories located in 2 blocks of 7 and 8 contiguous territories. I chose this arrangement to minimize the number of neighbouring pairs with potential access to adjacent feeders, and to maximize the similarity of fed and control territories in habitat structure. Territory owners used the feeders immediately after I installed them, and continued to use them throughout the experiment to feed themselves, and their nestlings and fledglings. A few neighbours and floaters also used the feeders, but their visits probably often went unseen. A detailed account of the effects of this experiment on reproduction is given in Arcese & Smith (1988).

Supplemental food consisted of moistened, pelleted dog chow (Ralston-Purina Inc., 21% crude protein), vitamin solution, mealworms (Tenebrio sp.) and millet seed. Food was provided twice daily from 28 February, 5 weeks before the onset of laying, to 24 July, after the last young had left their nests.

My helpers and I were absent from Mandarte during 9 of 35 days before laying, 7 of 87 days during the laying and rearing period and 5 of 24 days after the last clutch was initiated. Before leaving, all feeders were heaped with food.

Time Budgets

I recorded the activities of 13 fed and 14 control females, and 14 males of each type, during 2 half-hour periods on different days (55 h total). Control territories were chosen to match closely in habitat structure the territories with added food. Observations were made between 7 March and 15 April, 1985, from 1-6 weeks prior to commencement of incubation by the focal females. To reduce variation due to time of day and weather, birds were observed only between 700 and 1100 h, when temperatures exceeded 4 C, and when wind was light or absent. Observations were made while standing on a 3 m ladder placed so that territories could be observed with little disturbance to the birds. I waited 5 min after mounting the ladder before beginning my observations. Birds ignored me soon after my arrival because song sparrows on Mandarte Island are accustomed to observers.

I recorded the behavior of the focal bird every 7.5 s, when prompted by an electronic metronome. Seven types of behavior were defined:

- (1) feeding (searching for, capturing and consuming food),

(2) preen/loaf (sitting low in shrubs or on the ground, usually with feathers fluffed and wings tucked onto the back, or sunning and preening on a prominent perch [e.g. Nice 1943:48]),

(3) alert (sitting prominently, usually above the shrub canopy, with feathers sleeked and wings held erect along the length of the body),

(4) defense/chase (threatening and/or evicting non-territorial intruders, aggressive posturing opposite neighbour on or near a shared border),

(5) display (for females: copulation solicitation, puff-wave display, song, chatter and/or caterwaul; for males: song, puff-sing-wave, pounce, chatter and/or caterwaul [Nice 1943:274; Chap. 5]),

(6) nest building (females only; grass pulling and carrying),

(7) out of sight (either on or off the territory).

The proportion of time spent in each activity was estimated as the number of periods for which the behavior was recorded, divided by the total number of periods (480). Most behaviors that I recorded lasted several seconds or longer. Thus, my method was sufficient for the goals of this study (Tacha et al. 1985). I also recorded all territorial intrusions that elicited chases from one or both of the focal pair.

Dispersal Distance

Natal dispersal distance was estimated as the straight-line distance between the approximate centers of the natal territory and the territory of first settlement. To estimate the number of territories traversed, I divided the length of the utilized portion of the island (650 m) by the number of territorial females that produced the cohort. I then converted distance moved in meters into territory equivalents by division. This method gives only a rough, minimum estimate of the number of territories traversed by natal dispersers on Mandarte because some young that settled close to their natal site were observed to have visited large portions of the island before settling.

I estimated the distance traveled by fed and control young by late August, 1985, as the furthest distance from the natal territory at which young were observed. Several young birds were involved in feeding or site dominance experiments from 1983 to 1985. These birds are included in analyses presented here because removing them had no effect on the results.

Estimating Dominance

Dominance was estimated by observing aggressive interactions at 4 evenly spaced feeders, and calculating the proportion of total interactions won by each individual (Ketterson 1979; Kikkawa 1981; Arcese & Smith 1985).

Observations were made primarily from mid-July to late September, from 1982-84. Winners and losers of encounters were recorded only when the outcome was clear. For all 3 cohorts, 8378 aggressive encounters were recorded.

This method of estimating dominance predicts the probability of winning encounters most accurately when the number of previous encounters observed is large (Arcese & Ludwig 1986). I therefore conducted correlation analyses using both weighted and unweighted dominance estimates, and excluded birds observed in fewer than 5 encounters (Arcese & Ludwig 1986). Birds observed in fewer than 5 encounters were included as subordinates in frequency analyses (Kikkawa 1981; Arcese & Smith 1985).

Relatedness

Parentage was assumed from the behaviour of territorial pairs. However, 3 extra-pair copulations were observed in a total of about 100, suggesting that the association of males and females on the same territory may not always predict parentage correctly.

A pedigree of the population based on assumed matings was constructed beginning with the 1981 cohort, for which relatedness was partly known. The pedigrees of all young that settled with a mate were traced, and those that shared common

relatives were noted. Pairs with complete pedigrees and no common relatives among parents or grand-parents were considered to be not closely related. Matings were classed as mildly inbred when they took place with grandparents, uncles, aunts or cousins, and closely inbred when between sibs or parents and their offspring (Shields 1982).

Statistical Analyses

Data were analyzed using standard techniques (Siegel 1956; Gilbert 1973; Sokal & Rohlf 1981). I transformed data (e.g. by the angular or logarithmic transformation) if graphical analyses showed that they were not approximately normally distributed (Sokal & Rohlf 1981). In all analyses of variables in which I employed parametric techniques, I also carried out non-parametric tests for comparison. In these cases, only the results of the parametric tests are given, unless the two techniques gave contrasting results. When transformation did not improve the distribution of the data (e.g. as in the case of number of young produced), only non-parametric tests were employed. However, I sometimes used correlation coefficients as descriptive statistics of non-significant relationships. In some cases, the unit of data was the nesting attempt rather than the individual because males and females frequently participated in more than one type of mating association within seasons and between years. Birds that were known or presumed to have had access to the feeders in 1985 were excluded from comparisons of

reproductive success.

I used G-tests with the Williams correction and Fisher's exact probability tests to analyze most frequency data (Sokal & Rohlf 1981). In a few cases, chi-squared statistics were used when expected values were small but adjacent cells could not be combined because of the hypothesis being tested. In these cases, I adjusted chi-square by the continuity correction to give a more conservative test (Sokal & Rohlf 1981). Statistical comparisons are 2-tailed except where I made prior predictions about the outcome of tests. In analyses where I made repeated comparisons of related data, I revised the significance level according to the Bonferroni inequality. This states that only probabilities less than or equal to the initial level of significance (i.e. $P=0.05$) divided by the number of tests conducted should be considered statistically significant (Miller 1981).

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CHAPTER 3. TERRITORY ACQUISITION AND LOSS IN MALE SONG SPARROWS

INTRODUCTION

In many species, reproductive success depends on the successful acquisition of a territory (e.g. Wiley 1973; Clutton-Brock et al. 1982; Smith 1988). This fact has spawned several studies of the morphological (e.g. Searcy 1979; Hannon & Roland 1984) and behavioural characters associated with territory acquisition (e.g. Knapton & Krebs 1974; Arcese & Smith 1985). However, few studies have considered how individuals acquire their first territory, expand a current one or regain lost territories (e.g. Smith 1978; Yasukawa 1979; Picman 1987).

Models of dispersal and territory acquisition usually assume that individuals gain territories only after the death of owners or by colonizing vacant habitats (e.g. Murray 1967; Fretwell & Lucas 1970; Waser 1985). In several bird populations, however, individuals do not always wait until owners die before attempting to become territorial. Instead, non-territorial individuals (floaters, Brown 1969; Smith 1978) sometimes challenge and evict territory holders that are not able to vigorously defend themselves (e.g. Crook & Shields 1985; Freed 1987; Chap. 4). Further, individuals that lose their territories may not simply become part of a 'doomed

surplus' of non-breeders (Errington 1956), but could join the floating population, challenge territory owners and possibly regain a territory and reproduce.

Because this view of territorial dynamics is relatively new, and may contradict some assumptions of current models, it is important to know what conditions favour this type of territorial system and how often it occurs in the wild. This requires detailed descriptions of the territorial dynamics in a population over several years.

In this chapter, I present the results of a 5-year study of the timing and mode of territory acquisition and loss by male song sparrows, and the fates of deposed territory owners. In the song sparrow population resident on Mandarte Island, B.C., most adults are territorial year-round, and contests for territory ownership occur throughout the year between floaters and owners, and between settled neighbours. Three questions are addressed here. (1) How and when are territories acquired? (2) Who occupies vacant territories after an owner dies? And (3) what are the fates of males that lose their territories? I also speculate on factors that affect the level of competition for territories, the resources that are defended by males and the extent to which this population may be representative of others.

RESULTS

Types of Territory Turnovers

The leading cause of turnovers was the insertion of floaters among established territory owners (107 of 292 total turnovers or 37%). In 33 of these 107 insertions, the floater took some area from 2 or more territory owners, while in the remaining 74 a portion of a territory was taken from only one owner. Overall, floaters acquired territories in 71% (206 of 292) of all turnovers, of which at least 76% (156 of 206) involved the aggressive acquisition of a territory. Clearly, many floating male song sparrows actively sought territories, rather than waiting for owners to die.

In 86 of 292 turnovers recorded (30%), neighbours acquired an adjacent territory. Forty-two of these 86 turnovers were the outcome of aggressive encounters. The remaining 44 occurred as replacements. Thus, territory owners also frequently acquired additional shrubland by evicting other males from all or part of their territory.

The Role of Age

The outcomes of contests for ownership between established neighbours showed that the ages of the owners involved played a role in determining which owner won (Table 3.1). For example,

males 4 or more years old lost most or all of their territories in all 13 contests involving this age-class ($P < 0.001$, binomial test). Figure 3.1a shows that the probability of wresting a territory from a neighbour declined sharply after a male reached 2 years of age ($G = 23.63$, $df = 3$, $P < 0.001$). There was a similar, but non-significant, relationship between the ages of new versus old owners of territories after replacements of neighbours, when no conflicts involving the missing male had been observed ($G = 3.60$, $df = 3$, $P > 0.10$; Fig. 3.1b). Pooling these data showed that 2- and 3-year-old males were significantly more likely to acquire adjacent territories from neighbours than were 1- and 4-year-old males regardless of the tactic used to gain the territory ($G = 15.24$, $df = 3$, $P < 0.005$).

Yearling and older floaters were equally likely to acquire territories by insertion, takeover or replacement ($G = 0.30$, $df = 2$, $P > 0.98$, Table 3.2). Overall, however, yearlings accounted for the majority of turnovers that involved floaters (161 of 206 or 78%) because few birds remained non-territorial after their first spring.

Seasonal Variation in Turnovers

The number of turnovers per 2-month period varied seasonally, and the pattern of variation was similar over 5 years (Fig. 3.2). Eighty-three percent of turnovers occurred from January through June, the months prior to and during the

Table 3.1. The ages of owners that won and lost territories as a result of takeovers by neighbours.

Loser Age (years)	Winner Age (years)			
	1	2	3	4+
1	9	4	2	0
2	2	6	0	0
3	4	5	0	0
4+	4	5	4	0

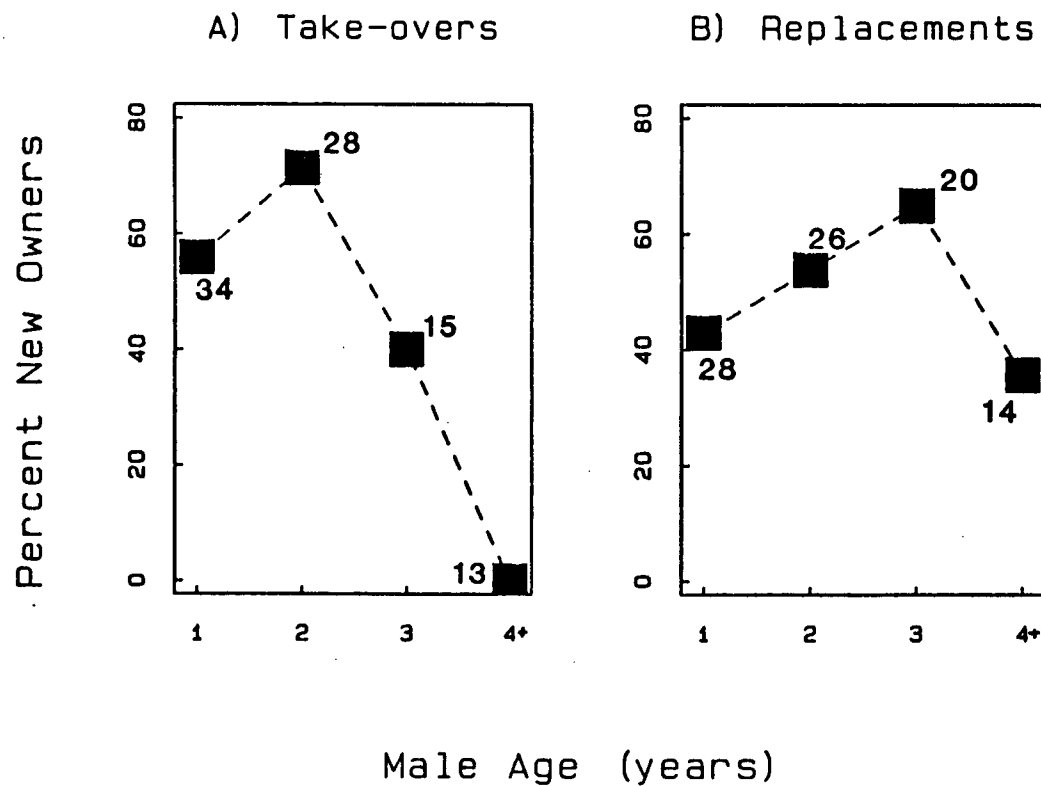


Figure 3.1. The relationship between male age and the outcome of naturally occurring territory turnovers between neighbours. Boxes depict the total number of males of each age that gained territories, divided by the total number of each age (indicated) that were involved in takeovers (A) or replacements (B).

Table 3.2. Type of turnover in relation to the age of the settling floater.

Floater age	Type of turnover		
	Insertion	Take-over	Replacement
Yearling	85	37	39
2+ years	22	12	11

breeding period. In 2 years, (1983,1985) turnovers were also common during the period of autumn territoriality from September through October (Tompa 1964). Birds least often acquired territories from November through December.

There was, however, a significant difference in the seasonal frequency of turnovers involving neighbours or floaters when the data for all 5 years were pooled into 6 2-month periods ($G = 14.19$, $df=5$, $P<0.02$). Floaters acquired territories most frequently during the 4-month period from January through April, but neighbours rarely expanded their territories outside of the breeding period (March-June; Fig. 3.2). For all three types of turnovers involving floaters, the median proportion of yearly turnovers peaked prior to or at the beginning of breeding. Takeovers and replacements by neighbours peaked during breeding. These peaks contributed to significant differences in the seasonal occurrence of each type of turnover (all $P<0.01$, Kruskal-Wallis ANOVA's, $N=5$ years for each of 6 2-month periods).

Turnovers were rare in winter even though many song sparrows sometimes left their territories for a portion of the day to feed on seeds (e.g. Sorbus and Rubus spp.) deposited at a starling (Sturnus vulgaris) roost on the island. To test if the distribution of this food source on the island influenced territory occupancy, I compared the frequency that I observed owners off their territory at least once during a census for

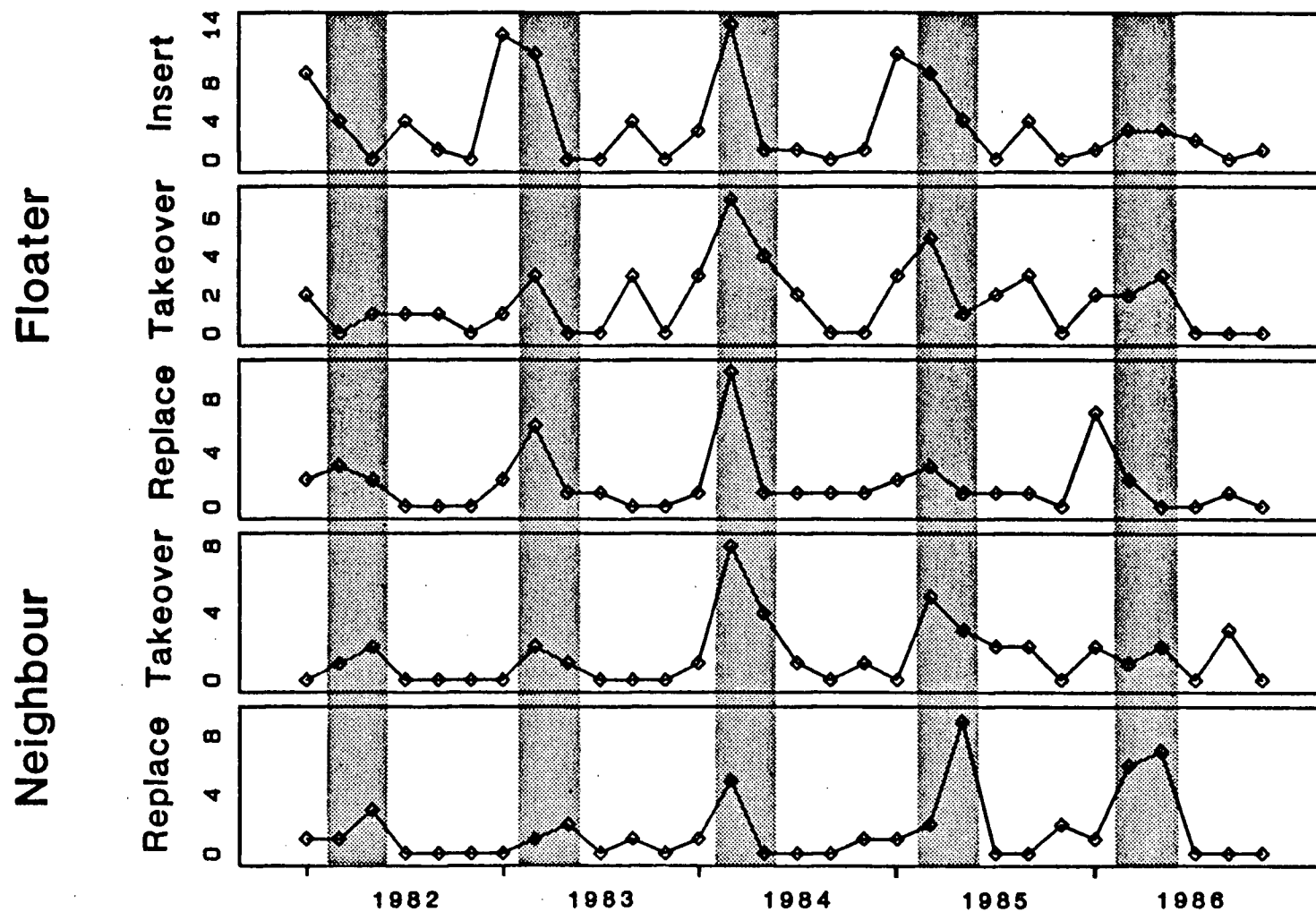


Figure 3.2. The number of turnovers of each type recorded during 6 bi-monthly periods from 1982-6 (see Methods). Shaded regions represent the main breeding period from March through June each year.

birds that owned territories within the starling roost to those birds that owned territories elsewhere on the island. As expected if food distribution were important to the ability of owners to remain on their territories, virtually no 'roost owners' were observed off-territory even during mid-winter, when 20-78% of all other territory holders left their territories for some portion of the day (Table 3.3). Further, nearly all birds observed off-territory were seen in the starling roost feeding on seeds and sprouting cotyledons. However, I found no evidence that the rate of territory turnover differed between these two groups.

Territory Takeover and Polygyny

Male territory owners frequently gained potential access to adjacent territorial females when they annexed their neighbour's territory (63 of 86 cases or 73%). In 24 of 63 such cases, the encroaching male was previously unmated, but in the remaining 39 cases (45% of all neighbour turnovers) males became polygynous. No floaters simultaneously gained ownership of areas that encompassed more than one female's territory.

Fates of Deposed Territory Owners

In 39% (113 of 292) of all turnovers the original owners remained territorial on portions of their former territories. Ten males (3%) moved to a nearby territory just prior to

Table 3.3. The number of territorial males observed off their territory for a portion of the day at least once within the census period in relation to territory location from September to February, 1985-6.

Location	On/Off	Month					
		Sept.	Oct.	Nov.	Dec.	Jan.	Feb.
Roost	On	5	6	4	8	9	7
Territories	Off	0	0	0	0	0	0
Other	On	26	33	16	5	24	41
Territories	Off	0	1	4	18	19	3

replacement or after an insertion, and in 72 cases (25%) males became non-territorial floaters (8 males lost territories and subsequently floated twice and 2 males did so 3 times). Males disappeared after 98 of 292 turnovers (34%). Eighty-three of these were replacements and 15 were takeovers. In some cases, former territory owners that became floaters disappeared from the population within a few days of territory loss, and some were known to be in poor physical condition or have serious injuries (e.g. broken leg, useless or missing foot; see Chap. 4).

Time Spent Floating by Deposed Owners

The length of time spent floating by males that lost their territories varied from 1 day to over 2 years, although only 2 cases exceeded a year. The distribution of days spent floating for birds that regained a territory (range=1-784 days, median=160, N=36) did not differ statistically from that for birds that disappeared from the population without regaining a territory (range=1-517 days, median=75, N=32; Dmax=0.24, $P>0.10$, Kolmogorov-Smirnov test).

Frequency of Regaining a Territory

Thirty-six of 68 males (53%) that lost their territory and were known to have become a floater later regained one, but 69% of these 36 males gained territories without females. However,

several of these males subsequently gained mates, and overall, 27 of the 36 males (40%) that regained a territory subsequently bred. Ten of 36 males (28%) regained their former territory, 15 of 36 (42%) settled on an adjacent territory and the 11 remaining males (30%) settled 2 or more territories distant.

The frequency with which males regained a territory after having lost one and floated appeared to depend on age (Fig. 3.3). However, because of the small number of birds involved, this pattern was not statistically significant ($G = 4.55$, $df=3$, $P>0.1$). The frequency with which males regained a territory might be expected to depend of age if adult survival also depended on age. I therefore re-calculated the expected probability of regaining a territory based on the observed survival rates of males of different age (Nol & Smith 1987). Although 1- and 4-year-old males each did more poorly, and 2- and 3-year-old males each did better than expected by their probabilities of survival (Fig. 3.3), these differences were also not statistically significant ($G = 3.11$, $df=3$, $P>0.1$). Two- and 3-year-old males spent on average 2 months less as floaters after losing a territory than did 1- or 4-year-old males, but this difference was also not statistically significant ($H=4.07$, $df=3$, $P>0.1$, Kruskal-Wallis ANOVA).

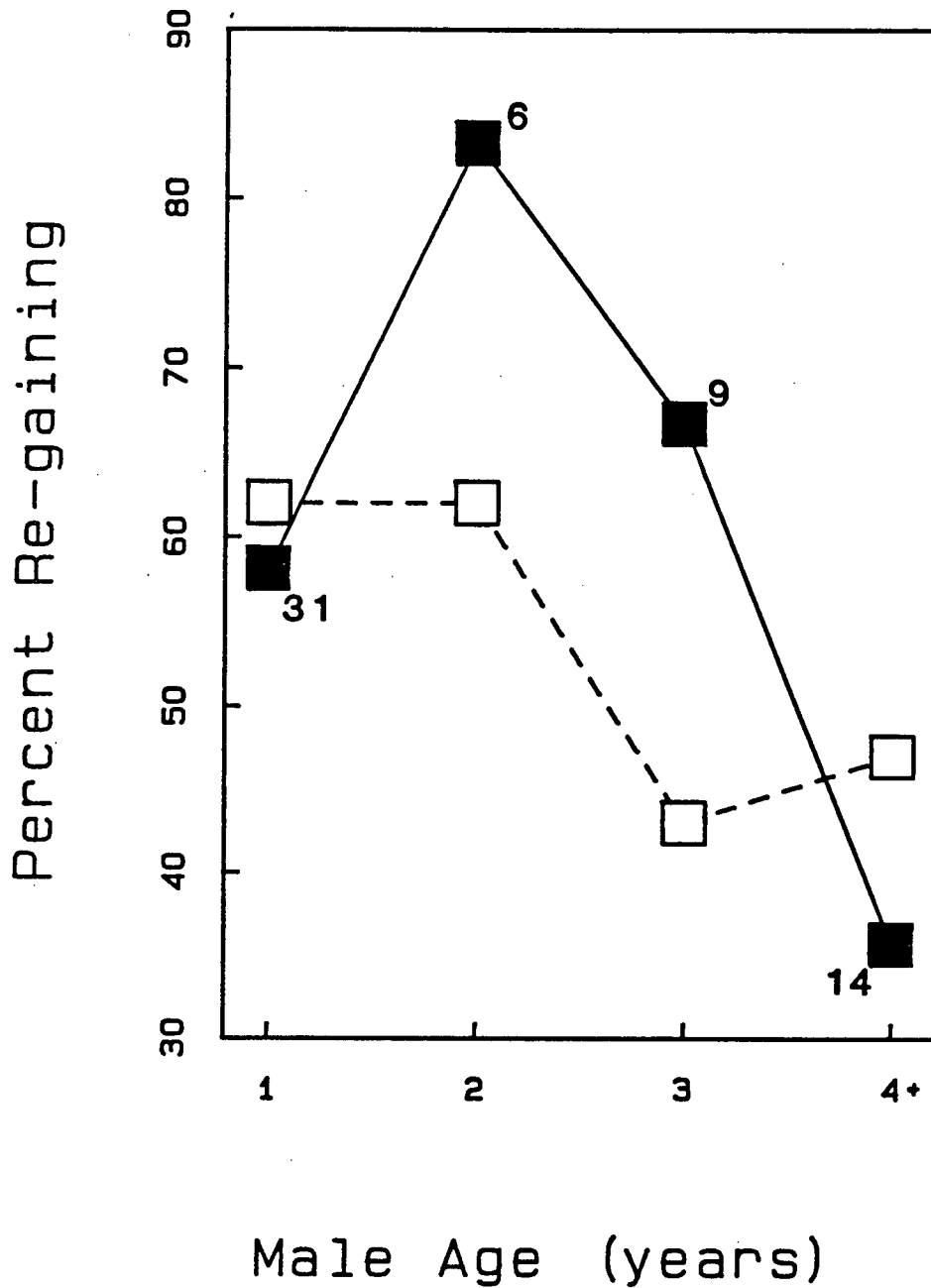


Figure 3.3. The percent of males that regained a territory after losing one in relation to their age at the time of loss (solid boxes), and the expected survival rates to the following breeding season for males the same age (open boxes; Nol & Smith 1987).

Repeat Floaters

All males on Mandarte spend the early part of their life as floaters. However, many males also do not acquire territories before breeding begins and remain unmated for part or all of the following breeding period. These males might remain as floaters because they are inherently less able to defend territories than are males that have acquired a territory. If so, such males might also become floaters later in life more often than males that had acquired a territory by the beginning of breeding in their first year of life.

To test this, I considered males from 4 cohorts (1982-5) that owned a territory at some time in their lives, but had died by August 1987. These males were classed as floaters or as territory owners in late March of their first breeding season, and by whether or not they floated after owning a territory. Only 7 of 39 (18%) territory owners in early life were observed as floaters later. In contrast, 18 of the 39 (46%) yearling floaters that eventually acquired a territory, also became floaters later in life ($G = 7.15$, $df=1$, $P<0.01$).

Summer Survival of Floaters and Owners

The survival of yearlings by the end of breeding was unrelated to their territorial status on 1 March, as their first breeding season commenced, except in 1985 when yearlings that

began the breeding season as floaters survived better than yearling territory owners (Table 3.4). In 3 of the 4 cohorts for which I was had such data, territory owners survived from 6-22% better than did floaters, but when pooled over all cohorts there was no difference in survival (Table 3.4). In contrast, both the annual survival and lifetime reproductive success of yearling territory owners was significantly higher than that of yearling floaters (Smith & Arcese ms).

DISCUSSION

During 5 years, non-territorial male song sparrows most frequently gained breeding territories by evicting resident owners from all or part of their territories. This result contrasts with the assumptions of most current models of dispersal and habitat settlement in territorial animals. (e.g. Murray 1967; Fretwell & Lucas 1970; Waser 1985; but see Buechner 1987). These assumptions are that: (1) previous ownership is the main factor that determines the outcome of contests over territories and (2) mortality of territory owners is the primary mechanism by which habitat becomes available for settlement. I now consider factors that affect the level of competition for local territories versus dispersal to unoccupied sites, the temporal pattern of territory turnovers and the role of age in territory defence.

Table 3.4. The fates of yearling males in 4 cohorts at the end of breeding (31 July) in relation to territorial status at the commencement of their first breeding season (1 March).

Territorial status					
Cohort	Beginning of season		End of season		Percent Survival
	Owner/Floater	Owner	Floater	Absent	
1982	Owner	22	0	4	84.6
	Floater	5	1	2	62.5
1983	Owner	14	0	3	82.4
	Floater	10	16	8	76.5
1984	Owner	10	1	2	84.6
	Floater	7	11	5	78.3
1985	Owner	1	1	4	33.3*
	Floater	9	1	1	90.9
Total	Owner	47	2	13	75.8
	Floater	31	29	16	78.9

* $G_w=6.45$, $df=2$, $P<0.05$

Factors Affecting the Mode of Territory Acquisition

Three factors that could extend length of the period of competition for a locally limiting supply of territories or other breeding resources are: (1) year-round residence and territory defence, (2) an extended breeding period, and (3) a surplus of potential breeders.

In resident, seasonally breeding populations the distribution and abundance of resources will determine if territory defence is economical (Brown & Orians 1970). Resource defence outside the breeding period could improve survival by ensuring access to food and cover, and enhance future reproductive success by promoting access to high-quality breeding sites. On Mandarte, male song sparrows sometimes leave their territories to feed in winter (Table 3.3), but they remain vigorously territorial when challenged on their territories year-round. I suggest that because competition for territories is strong on Mandarte Island, that males gain territories opportunistically, and that once settled, defend them throughout the non-breeding period to ensure access to a breeding site in upcoming seasons.

When year-round defence is the norm and habitat is limited, queues for ownership based on competitive ability may form and result in the most able individuals gaining the best sites, settling first or both (Brown 1969; Popp & De Vore 1979; Chap.

7). Smith (1978) described such a system in the rufous-collared sparrow, Zonotrichia capensis, and a similar situation exists in song sparrows on Mandarte Island (Arcese & Smith 1985; Chap. 4 & 7).

When unoccupied sites are very scarce, the most able floaters should seek out and challenge territory holders whose ability is poorly matched to the quality of the territory that they defend. This could occur when vigour declines because of injury or old age, or if less vigorous birds sometimes acquire superior sites by chance. On Mandarte, floaters do challenge and overthrow those territory holders that are least able to defend themselves: these are typically the youngest and oldest males in the population and those with injuries or handicaps (Table 3.1; Chap. 4).

When breeding seasons are long, floaters that continue to contest for territories may produce more young than those that wait for owners to disappear, especially when the survival of owners in the absence of challenges by floaters is high and the probability of surviving to the next breeding season for floaters is low. These conditions are met on Mandarte: few territories became available after owners disappeared (Fig. 3.2) and the annual survival rate of floaters was lower than for territory holders (Smith & Arcese ms) even though differences in summer survival were small (Table 3.4). Thus, as expected, most floaters gained a territory by evicting owners from all or

part of their former territory, and insertions and takeovers by floaters occurred throughout the breeding period (Fig. 3.2).

The degree of habitat saturation should further influence the tactics of floaters by affecting the probability of settling without engaging in conflicts. During this study, population size more than doubled (36-78 territorial males in April). Because the proportion of males that remain as floaters after breeding commences increases with population size (Smith & Arcese ms), I expected and found that the proportion of floaters that gained territories by takeovers and insertions increased with population size ($R = 0.90$, $N = 5$, $P = 0.05$, Spearman rank correlation, 1-tailed).

Probability of Settlement Elsewhere

Factors that promote local competition for territories would appear to increase the benefits of dispersing in search of unoccupied habitat elsewhere. However, my limited data suggest that breeding opportunities for males elsewhere are few. All 4 males that I observed off Mandarte were floaters. Further, several yearling male immigrants were captured on Mandarte each year, but only 2 immigrant males have settled and bred in 12 years of study (Smith 1988; Chap. 7). This suggests that male song sparrows hatched in the vicinity of Mandarte are unlikely to settle outside of their natal population. This could explain why males contest for local territories even when

the probability of settlement is low.

Mode of Territory Acquisition and Dispersal

In species where the risks of evicting territory owners outweigh the benefits of territorial status, current models of dispersal and habitat settlement may satisfactorily characterize settlement patterns (e.g. Murray 1967; Fretwell & Lucas 1970; Waser 1985). However, in populations like the one described here, the assumptions of these models are not met (Buechner 1987). When floaters form social hierarchies and contest for access to local territories instead of dispersing in search of vacant habitat, time from hatching to settlement, rather than distance moved, may be the most appropriate variable with which to characterize different individuals. Further, floaters probably alter their tactics depending on the level of habitat saturation, the benefits derived by owning a territory, the risks of evicting owners and their own competitive ability. Recent advances in dispersal modelling may allow such variables to be incorporated in the future (e.g. Parker & Sutherland 1986; Buechner 1987).

Occurrence of Aggressive Takeovers

Patterns of territory acquisition and loss in male song sparrows are similar to those described in less detail for rufous-collared sparrows (Smith 1978), red grouse and willow

ptarmigan (Lagopus lagopus, Hannon 1983; Martin 1984; Watson 1985), blue grouse (Dendragapus obscurus, Lewis & Zwickel 1980), European kestrels (Falco tinnunculus, Village 1983), tropical house wrens (Troglodytes aedon, Freed 1987), magpies (Pica pica, Birkhead et al. 1986) and fan-tailed warblers (Cisticola juncidis, Ueda 1986) and others. However, aggressive territory acquisition by floaters of other species generally appears to be less common than in song sparrows (e.g. Picman 1987; Birkhead & Clarkson 1985; but see Ueda 1986). There are at least two explanations for why my results differ from others. First, when species can not be monitored as completely as the song sparrows in this study, many takeovers will be mistaken as replacements, as indeed some were here. Second, there is likely to be considerable variation among species and populations with regard to the modes of territory acquisition. Some reasons for this were summarized above.

Territory Acquisition by Neighbours and Floaters

Floaters usually settled during the 4-month period from January-April (Fig. 3.2), most of which precedes the peak of clutch initiation by females (Smith et al. 1980; Arcese & Smith 1988). In contrast, neighbours rarely expanded their territories outside of the breeding period (March-June; Fig. 3.2). This is expected if neighbours usually expand only after most floaters have settled, or if neighbours expand primarily to gain access to females.

The first explanation is unlikely. Intrusion pressure declined only slightly from spring to summer (Chap. 4) and floaters settled throughout this period, when owners also annexed neighbouring territories (Fig. 3.2). Further, I often observed neighbours trying to prevent floaters from settling in vacant neighbouring territories. In support of the second explanation, however, 45% of males that annexed a neighbouring territory became polygynous at least temporarily. Freed (1987) described a similar situation in tropical house wrens. Male song sparrows that defended more females also produced more young than those that defended a single female (Chap. 6). In contrast, floaters often gained territories outside of the breeding period, when doing so did not ensure reproduction.

Age and Territory Turnover

The reproductive advantages gained by acquiring additional territories and mates suggests that territory holders should compete to replace missing neighbours, and that competitively superior territory owners should evict their less able neighbours. Three studies suggest that competitive ability in song sparrows peaks around age 2-3 on average. Annual survival declines by about 20% after age 2 (Nol & Smith 1987), 1- and 4-year-old males are less able to defend against floaters than are 2- and 3-year-old males (Chap. 4) and 2-year-old males become

polygynous much more often than younger or older males (Chap. 6). As expected by these patterns, middle-aged males were more likely to gain additional territories than 1- or 4-year-old males (Fig. 3.1).

Age is clearly a key factor that affects behaviour and reproductive success in male song sparrows. However, the tendency for males that floated when young to also float after holding a territory, suggests that in addition to age-dependent variation in ability, some males are inherently less able to defend territories than others. In a separate analysis (Chap. 4), males were found to experience consistently higher or lower intrusion pressure than the mean for their age-class across years, even though these means varied substantially. Because any effect of territory quality could be ruled out, this analysis also suggested that inherent differences in ability exist between individuals. As an interesting contrast, heritable factors, such as morphology (Smith & Dhondt 1980), have so far been found to have no measurable effect on behaviour or reproduction in male song sparrows (Arcese & Smith 1985, and P. Bets, unpublished ms cited therein; Schluter & Smith 1986; Smith 1988). I suggest that inherent differences in the ability to defend territories may originate during development.

Routes to Territory Ownership

For male song sparrows on Mandarte Island, the routes to territory ownership can be complex. In song sparrow populations elsewhere, the rate of territory turnover can be high in migratory (Weatherhead & Boak 1986) and non-migratory populations (P.K. Stoddard & M. Beecher personal communication). The existence of floaters in early spring has been experimentally confirmed in a primarily migratory song sparrow population in New York (Wingfield 1985), and in a mainland, resident population near Mandarte Island (Knapton & Krebs 1974). It remains unclear, however, how often floaters exist throughout the breeding period, or what role floaters might play in the territorial system in other populations.

To date, the literature provides few similar examples from temperate-zone species that defend territories year-round (e.g. Birkhead et al. 1986; Eden 1987). However, a recent study of tropical house wrens (Freed 1987) provides some striking parallels to my study. These studies show that year-round territoriality and extended breeding periods are important ecological factors associated with the development of complex, non-territorial 'underworld' systems (Smith 1978). Comparative studies of the song sparrow may illustrate the extent and variation to which underworld systems develop in temperate environments.

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CHAPTER 4. AGE, INTRUSION PRESSURE AND TERRITORY DEFENCE AGAINST FLOATERS IN MALE SONG SPARROWS

INTRODUCTION

The ability to gain and defend territories, mates and other crucial resources has a profound influence on an animal's fitness (Clutton-Brock et al. 1982; Howard 1983; Smith 1988). However, the aggressive behaviour of dominant animals sometimes prevents subordinates from access to such resources (reviews in Brown 1969; Watson & Moss 1970; Patterson 1980; Smith & Arcese 1986). In territorial species, these subordinates often become 'floaters' (after Brown 1969; Smith 1978) that survive in groups outside the main breeding habitat (e.g. Carrick 1963; Birkhead & Clarkson 1985) or reside singly and inconspicuously on the territories of breeders (e.g. Tompa 1964; Smith 1978). Floaters arise in breeding populations when suitable habitats become saturated with dominant territory owners (Brown 1969; Watson & Moss 1970).

When floaters are a consistent feature of the social environment of a species, it may be unprofitable for owners to try to evict them from their territories (Brown 1964, 1969, 1982; Davies & Houston 1981, 1983a, b). In such cases, owners might tolerate floaters or even recruit them onto their territories as 'satellites' (e.g. Van Rhijn 1973; Davies & Houston 1981) or 'helpers' (e.g. Emlen & Vehrencamp 1983; Woolfenden &

Fitzpatrick 1984). Recent studies have shown that subordinate satellites may benefit territory owners by attracting mates (e.g. Van Rhijn 1973; Lill 1976) or by defending the territory (e.g. Davies & Houston 1981, 1983b; Wirtz 1981). Helpers may aid breeding pairs in various ways (see Emlen & Vehrencamp 1983; Wolfenden & Fitzpatrick 1984). In contrast, floaters that do not become helpers or satellites do not assist breeders in raising young or defending the breeding area. These floaters are, however, often capable of breeding when the opportunity to gain a territory arises (e.g. Smith 1978; Hannon 1983; Village 1983).

Several studies suggest that floaters might hinder territory owners (e.g. Tompa 1964; Birkhead & Clarkson 1985). For example, territory owners often spend time and energy chasing floaters from their territories (Myers et al. 1979, 1981; Hixon 1980 and references therein), and owners may reduce the size of their territories at high levels of intrusion pressure (Norton et al. 1981). Floaters can impose a further reproductive cost on owners if they fertilize females that reside on or visit the owner's territory (Howard 1978; Wirtz 1981). In birds, floating females could parasitize the nests of territory owners (Gowaty 1983). Moreover, floaters sometimes acquire territories by evicting territory owners or by usurping parts of their territories (e.g. Tompa 1964; Birkhead & Clarkson 1985). In such cases, floaters could be a serious threat to territory owners, and their relationship with owners

could therefore be important in affecting social organization.

Several factors might affect both intrusion pressure by floaters and an owner's ability to defend against them. For example, floaters might concentrate in high quality habitats to await the deaths of breeders (Smith 1978), or they might intrude selectively on territories with fertile females to seek copulations (Ford 1983). Alternately, floaters might try to gain territories by challenging owners that seem particularly vulnerable to takeover. Territory owners probably also vary in their ability to evict floaters. In the polygynous red deer (Cervus elaphus) for example, middle-aged males defended their harems against challengers most successfully (Clutton-Brock et al. 1982). Some evidence suggests that in birds, territory defence ability increases with age and experience (Yasukawa 1979; Ewald & Rohwer 1980; DeVos 1983). Robinson (1986), however, found that the ability of polygynous male caciques (Cacicus cela), to defend fertile females declined with age. Dhondt (1985) suggested that territorial defence ability also declined among old male great tits (Parus major), but there have been no reports on the factors that affect an owner's ability to defend a territory against floaters.

Because of their generally inconspicuous behaviour, floaters are difficult to study, and their relations with territory owners remain poorly understood. I studied the behaviour of territorial and floating male song sparrows on

Mandarte Island, where the activities of floaters can be observed in unusually complete detail. In this chapter, I specifically address three questions about the effect of intrusions by floaters on territorial males. First, did the density of floaters in particular areas affect intrusion pressure? Second, did floaters selectively intrude on the territories of males: (1) with fertile females, (2) with large territories, or (3) in a particular age-class? Third, did intrusions by floaters affect the reproductive success of territorial males or the number of days that they defended a territory? Further, because intrusion pressure was recorded over successive years, I was able to separate the effects of males and their territories in determining intrusion pressure. Additional observations on the social organization and lifetime reproductive success of floaters are given elsewhere (Chap 3; Smith & Arcese ms). I now give a brief description of the relations between floaters and territory owners in the study population.

Relations Between Owners and Floaters on Mandarte Island

On Mandarte, song sparrows are primarily monogamous, usually live from 1-4 years, and are sexually mature at 1 year of age (Smith 1988). Possession of a territory in the year after hatching has an important effect on lifetime reproductive success (Smith 1988; Smith & Arcese ms). Some males fail to acquire territories before the onset of breeding each year.

These floaters live singly and secretively on the territories of breeders. There they await the deaths of territory holders, or precipitate a takeover by directly challenging them. Floaters are evicted by territorial males on discovery, but floaters that do not sing or perch prominently in territories may go undetected (personal observation). Competition between males for territories is easily observed; it occurs when they fight over vacant areas, when they try to settle between established territories, or when floaters try to overthrow owners. The number of floaters increases with population density, and floaters sometimes comprise over 25% of the male population (Smith & Arcese 1987, ms).

RESULTS

Only rarely were floaters seen by observers when they did not appear to have been detected by territory owners. Floaters typically were extremely secretive and either flew or remained motionless when owners were near. This response appeared to depend upon being detected. Territory owners that detected an intruder usually cocked their heads, craned their necks, vocalized (song, tchunk, puff-sing-wave; Nice 1943) and then chased the intruder. Owners tried to evict floaters whenever they were detected. Intrusion pressure, as measured here, probably represents the territory owners perceived rate of intrusion by floaters, rather than the actual rate, since floaters on Mandarte reside on defended territories, but are

only detected occasionally.

Temporal Patterns of Intrusion

At the beginning of the study period in 1984, floaters comprised 24 of 86 (28%) males present on Mandarte. There were slightly fewer floaters in 1985 (16 of 94, 17%). Standard intrusion pressure (SIP) was not significantly correlated with the time of day in either year (1984: $r=-0.085$, $N=158$, $P>0.10$; and 1985: $r=-0.095$, $N=420$, $P>0.05$). SIP declined slightly as the season progressed in 1984 ($r=-0.130$, $N=158$, $P<0.10$), and in 1985 ($r=-0.197$, $N=420$, $P<0.01$), probably because many floaters gained territories from April-August (Chap. 3). I found no evidence of non-linearity in these relationships (but see Peek 1971).

Floater Density, Territory Size and Female Fertility

Male territories were overlapped by from 0-10 floater home ranges (mean=5.4), but there was no correlation between the number of floater ranges that overlapped a territory and either SIP or tenure in either year (all $P>0.50$). Thus, the density of floaters in an area did not affect the intrusion pressure recorded on particular territories. Similarly, neither SIP nor tenure were related to territory size, nor to whether males had mates (all $P>0.10$). Further, SIP on territories where females were fertile (the nest-building and laying periods) was not

higher than on territories where females were not fertile ($P > 0.40$, 1985 data), even though fertile females use conspicuous vocalizations and postures to solicit copulations (Nice 1943, own observations).

Male Age and Territory Tenure

Male age was related to standard intrusion pressure and to tenure (Fig. 4.1), and the form of the relationships was consistent across years. These relationships were non-linear (Fig. 4.1); 1-year-old and 4-year-old males suffered higher SIP, and held territories for shorter periods, than did 2- and 3-year-olds. Note, however, that while 4-year-old birds were intruded on most in 1984, 1-year-olds were intruded on most in 1985. As expected from these relationships, tenure and SIP were inversely related in 1984 and in 1985 ($r = -0.43$, $N = 57$, and $r = -0.46$, $N = 75$, respectively, both $P < 0.005$). Table 4.1 gives the mean and maximum rates of intrusion observed for each age-class and year.

If the patterns of intrusion and loss of territory resulted primarily from differences in age, then males should experience lower intrusion pressure as 2-year-olds than as 1-year-olds. They should also experience higher intrusion pressure after age 3 (Fig. 4.1). Table 4.2 shows that for 41 birds observed in both years, this pattern was observed, but the difference was statistically significant only for the comparison of 1- and 2-

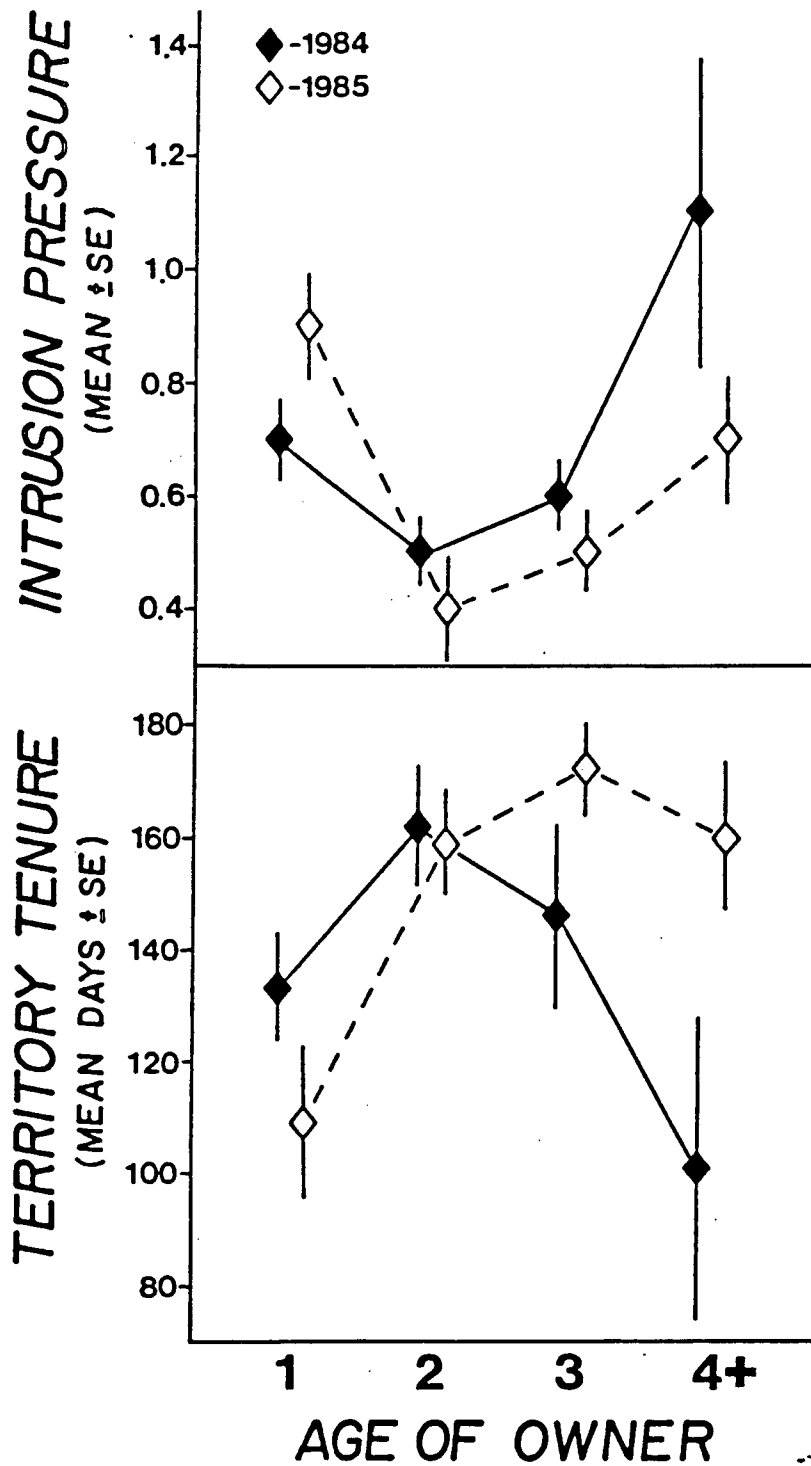


Figure 4.1. The relationships between age of the territorial male and standard intrusion pressure ($F_{2,54}=10.1$, $P<0.001$ and $F_{2,72}=9.5$, $P<0.001$; 1984 and 1985), and between age and territory tenure ($F_{2,75}=3.2$, $P<0.05$ and $F_{2,77}=10.2$, $P<0.001$; 1984 and 1985).

Table 4.1. Mean (SE) and maximum rates of intrusion per hour recorded on territories of different aged males in two years.

Year	Age Class (years)			
	1	2	3	4+
1984				
Mean(SE)	2.5(0.6)	0.9(0.2)	2.3(0.6)	11.7(7.7)
Maximum	8.6	3.9	6.0	42.0
N	22	20	10	5
1985				
Mean(SE)	3.6(0.8)	1.3(0.4)	1.9(0.8)	2.1(0.4)
Maximum	14.4	8.0	15.0	5.14
N	18	26	18	13

year-olds. The failure to observe the predicted increase beyond age 3 is partly explained by the lower rate of intrusion against 4-year-olds in 1985 (Fig. 4.1).

Territory Quality and Male Ability

Variation in intrusion pressure could also result from differences among territories in habitat structure or in their quality as breeding sites. Floaters might be more or less detectable in particular habitats, or they might concentrate in high quality territories. I did not measure these variables; however, I could test if SIP varied predictably for either the same territory across years, or within years for different male owners.

To do this, I compared SIP on 49 territories that remained similar in size and shape across years. I corrected statistically for differences in SIP due to owner age, and these corrected measures were normally distributed. I predicted that SIP on these territories should be positively correlated across years, especially in those that changed owners. However, neither prediction was supported by the data (all territories: $r=0.20$, $N=49$, $P>0.1$; those changing ownership: $r=-0.44$, $N=41$, $P<0.05$).

I then compared SIP for 41 males that were observed in each year, regardless of the resemblance of their territories across

Table 4.2. Changes in standard intrusion pressure for 41 males observed in 2 years.

	Age Class (years)		
	1-2	2-3	3+
Mean change	-0.32*	0.13	0.03
SE	0.09	0.16	0.09
N	13	17	11

* $p < 0.01$, Wilcoxon matched-pairs signed-ranks test.

years, after adjusting for their age-class means. These residuals were normally distributed and positively correlated ($r=0.37$, $N=41$, $P<0.03$, 1-tailed), showing that males varied predictably in SIP across years with respect to the mean of their age-class. In contrast, when I compared SIP on territories with different owners in the same season I found no correlation (Spearman rank= -0.08 , $N=9$, $P>0.50$). These results strongly suggest that intrusion pressure is a consistent attribute of particular males, but not of territories.

Intrusion Pressure and Reproductive Success

Males that held territories for longer periods produced more independent young each season (1984: $r=0.26$, $N=57$, $P=0.05$ and 1985: $r=0.35$, $N=75$, $P<0.01$). Because SIP was negatively related to tenure in both years, I expected negative correlations between intrusion pressure and reproductive success. These correlations were negative, but they were not statistically significant (1984: $r=-0.15$, $N=57$, $P>0.05$ and 1985: $r=-0.19$, $N=75$, $P>0.05$). The average effect of floaters on the seasonal reproductive success of territory owners was therefore small.

Contests over Territory

I observed all or part of 89 contests between floaters and owners over territory during both study periods. Contests, as

I defined them, began with a floater singing on the owner's territory. The large majority of intrusions did not involve singing and were therefore not included by definition. I classified contests broadly into short contests that lasted for less than 1 h and long contests that lasted more than 1 h. There were 29 short and 60 long contests and at least 3 of the long contests lasted up to 2 days. In all long and in several short contests floaters returned from chases repeatedly to sing or perch in the owner's territory. Contests ended when the floater no longer returned to the territory after a chase or when the owner no longer chased the floater.

The length of contests

Of the longer contests (including the 3 lasting longer than a day), 63% (38 of 60) resulted in settlement by a floater. No short contests (0 of 29) resulted in settlement. Thus, floaters that were able to avoid eviction for longer periods were much more likely to be successful ($G = 32.14$, $df = 1$, $P < 0.001$). Of the successful settlement attempts, 53% (20 of 38) resulted in partial acquisition of the owner's territory, and 47% (18 of 38) in total eviction of the owner. Overall, 43% (38 of 89) of contests resulted in settlement by a floater, but this estimate was probably inflated by the fact that long contests were more likely to have been observed.

The number of challengers

I observed from 2-4 floaters on the territory during 9 unusually intense contests. More than one floater often sang during these contests, and defending males seemed to spend much more time chasing than each floater spent evading. In all 9 of these contests the owner lost all or a major part of the territory, compared to 29 losses in 80 (36%) contests when only one floater was observed ($P=0.0005$, Fisher's exact test). The probability of successful settlement thus increased when more than one floater was present. In one case, however, the usurper was not one of the floaters initially observed intruding. Neighbours participated in contests when floaters perched in or flew through their territories, otherwise they did not interfere (but see Tompa 1964).

The replacement of owners by floaters often seemed to take place overnight, with the previous owner simply not appearing on the territory in the morning. In the 18 evictions that I observed part of, only 4 former owners were ever trapped or resighted. Two of these birds acquired a territory the following year; one adjacent and the other 3 territories distant from those lost. I therefore suspect that many former owners died of exposure, starvation, or injury, soon after eviction, rather than entering the floater population (see also Watson 1985). High mortality, resulting from injuries acquired while losing contests, is suspected in several ungulate species

(Clutton-Brook et al. 1982 and references therein).

Case histories

On 4 occasions from 1982-5, I observed the actual transition of ownership, as indicated by the previous owner failing to chase a singing intruder. In one of these cases, the owner suffered a compound fracture of its tibiotarsus when its foot was caught in a shrub while pursuing a floater. This owner continued to sing from low in a shrub, but it no longer chased the floater which thereafter sang throughout the territory. The former owner was not observed again. In a similar case, I observed an owner unsuccessfully attempting to evict a persistent intruder. This bird gained control of the territory soon after my arrival. This deposed owner had also recently suffered a similar compound fracture, though I did not witness its occurrence. In this case, the former owner survived to the following breeding season as a floater and successfully regained a territory adjacent to its previous one.

In a third case, I witnessed a male with a swollen and useless foot being evicted from his territory by a floater that had been repeatedly observed attempting to sing on the territory on previous days. The usurper had taken control of most of the territory by the time of my arrival on the day of takeover. The deposed male was eventually chased from the territory and was not seen again. In the final case, the takeover was

largely completed by the time of my arrival. I observed the former owner singing quietly low in a shrub, while two floaters contested the territory. The former owner remained at his perch with his feathers erect until nightfall and he was not seen thereafter.

Causes of Territory Loss

The role of handicaps

The case histories suggest that handicaps (i.e. a missing or useless foot, leg or eye) play a role in territory loss. However, many of the turnovers summarized above occurred in the absence of an obvious handicap. Further, males occasionally retain territories even when they possess apparent handicaps (personal observation). My observations on the occurrence of handicaps during this study show that only 12.5% (1 of 8) of the males with handicaps held their territory for the remainder of the breeding season, while 79% (109 of 138) of the visibly healthy males did so ($P=0.0005$, Fisher's exact test). Thus, territory loss is sometimes associated with a visible handicap, and these handicaps hinder territorial males. Of all owners that disappeared during the study periods, however, most (29 of 39; 74.4%) appeared to be healthy prior to the loss of their territory.

I do not know what proportion of handicaps result from

conflict with floaters, but my results do show that 46% (18 of 39) of disappearances of territory owners during the study periods were associated with contests with floaters (see also Chap. 3). Floaters may therefore account for a large proportion of all disappearances of territorial males.

Handicaps and age

Of the 8 handicapped males, one was 2-years, 5 were 3-years, and 2 were 4- or more years-old. No territorial 1-year-olds were observed with handicaps. Pooling adjacent age-classes, I found that older birds were more likely to possess handicaps (1 of 90 1- and 2-year-olds versus 7 of 64 3- and 4-year-olds; $P=0.019$, Fisher's exact test).

The weights of owners, evicted males and floaters

Many males that lost their territories to floaters did not possess visible handicaps. However, these apparently healthy males might have been in poor condition. I captured and weighed 6 territorial males before and from 1-6 months after they lost their territories to floaters. These males were significantly heavier before territory loss than after (mean(se): 25.73(0.30)g versus 24.10(0.59)g; $t=-3.16$, $df=5$, $P=0.025$). They were also significantly lighter after territory loss than 50 males that retained their territories (24.10(0.59)g versus 25.53(0.17)g; $t=3.11$, $df=54$, $P<0.005$). In contrast, 10

floaters that had not yet held a territory were identical in weight ($25.47(0.53)\text{g}$) to the 50 territory holders ($25.53(0.17)\text{g}$). Thus, weight loss was peculiar to males that lost their territories, rather than to territory ownership *per se*.

The weight loss of deposed males is not likely to have been a direct result of the contest for the territory, as all 6 males were weighed at least 1 month after being evicted. Further, only one of these males showed signs of a handicap (a well-healed leg fracture) that could have reduced foraging efficiency. Lastly, nearly all captures were made in the late summer and were corrected for time of day (Dhondt & Smith 1980). It is therefore unlikely that seasonal or daily variations in weight affected the results. I suggest that weight loss reflects the poor condition of males that have been evicted by floaters.

Does Ability to Defend a Territory Change with Age?

One hypothesis to account for the relationships that I observed between intrusion pressure, age and territory tenure is that the ability to defend territories depends partly on age, and that floaters detect and try to overthrow the males that are least able to defend themselves (the ability hypothesis). A critical prediction of the ability hypothesis is that the probability of territory loss per intrusion is related to age in

a non-linear way. Thus, 1- and 4-year-old males should have lost their territories more often than expected by differences in intrusion pressure alone. To test this prediction, I compared observed values of tenure with those predicted for each age-class by the regression of tenure on SIP. In both years, 1- and 4-year-olds held territories for shorter, and 2- and 3-year-olds held territories for longer, than expected by differences in intrusion pressure ($G = 6.70$, $df=3$, $P < 0.05$; and $G = 7.32$, $df=3$, $P < 0.05$, 1-tailed tests, 1984 and 1985, respectively). The pooled result was also statistically significant ($G = 9.71$, $df=3$, $P < 0.025$).

DISCUSSION

My results suggest a dramatically different relationship between floaters and territory owners than has yet been described (e.g. Orians 1961; Carrick 1963; Delius 1965; Smith 1978; Watson 1985). Floaters most often intruded conspicuously on the territories of the males that were the least able to defend against them. These were consistently the young, old and handicapped males in the population. In contrast, intrusion pressure was unrelated to territory size, the density of floaters in a particular area, to the fertility of territorial females or even to whether a female was present on a territory. Contrary to the idea that floaters sometimes aid territory owners (e.g. Wirtz 1981; Davies & Houston 1983b), on Mandarte Island at least some floaters are a threat to territory

owners that are not able to vigorously defend their territories. In the discussion following, I contrast my results with those of other studies and I consider further the relationship between age and the ability to defend territories.

Temporal Patterns of Intrusion

Intrusions by floating male song sparrows did not vary predictably with the time of day. In contrast, Kacelnick & Krebs (1983) found that the colonization rate of empty territories by pairs of great tits was highest in the morning. They suggested that the dawn chorus of territorial tits might be a response to daily variation in intrusion pressure. These colonizing birds, however, were probably residents from adjacent, poor-quality habitats rather than being floaters (Krebs 1971; Kacelnick & Krebs 1983). This study considered only intrusions by non-territorial males that resided on the territories of breeders, but were only occasionally detected by them. Daily variation in the song rate of song sparrows (Nice 1943) is therefore probably not a response to intrusions by floaters.

Peek (1971) noted the highest rate of intrusion by floating male red-winged blackbirds (Agelaius phoenicius) during April. Intrusion rate decreased in May, and territorial males that were removed after the peak of breeding were not replaced by floaters (see also Orians 1961). On Mandarte, intrusion pressure

declined slightly from March to July, probably because some floaters settled during this period. However, the replacement of owners by floaters continued throughout the year on Mandarte (Chap. 3, Fig. 3.2), as it did during a study of a resident population of the rufous-collared sparrow (Zonotrichia capensis; Smith 1978). Seasonal variation in intrusion pressure is probably less in species that are territorial year-round versus those that are only seasonally territorial. In species that are territorial year-round, floaters may have to challenge owners opportunistically to assure acquisition of a territory. In seasonally territorial species there may be a smaller advantage to acquiring a territory once the probability of breeding is low (Yasukawa 1979; Chap. 3).

Male Ability, Territory Quality and Intrusion Pressure

Males experienced similar intrusion pressure across years with respect to the means for their age-classes. In contrast, intrusion pressure was not consistent on the same territory between years or for different owners of the same territory within years. Variation in intrusion pressure was therefore unlikely to have resulted from differences in habitat structure or territory quality, but it may reflect the defensive ability of individual males. Intrusion pressure was also unrelated to the number of floater home ranges that overlapped a territory. This shows that floater density did not affect intrusion pressure and it suggests that floaters select and challenge

particular males within their home range. Floaters could do this by concentrating their time in a territory and by making themselves conspicuous there. Conspicuous intrusion, followed by the inevitable chase, might enable floaters to assess and monitor the vigour of territorial males. A strategy of this sort suggests an 'honest' system of assessment (Zahavi 1977), since it would be difficult for owners to conceal weaknesses in their defensive ability.

Males that were evicted from their territories by floaters often disappeared, and they occasionally suffered from visible handicaps that probably contributed to their eviction. Males frequently disappeared or were evicted, however, when they possessed no visible handicap. The loss in weight of males that became floaters after being evicted suggests that these apparently healthy males were also in poor physical condition. Robinson (1986) also found that, among male caciques, weight loss was associated with decreased dominance and ability to defend fertile females.

Intrusion Pressure and Reproductive Success

Intrusion pressure was negatively correlated to tenure, and tenure was positively correlated with the number of young raised to independence in both years. As expected, the relationships between intrusion pressure and seasonal reproductive success were negative in each year, but they were not statistically

significant. Because few birds breed successfully after being evicted by floaters, however, floaters have a potentially detrimental effect on the lifetime reproductive success of individual males.

The Role of Floaters in Territory Turnovers

Smith (1978; personal communication) found that floaters in a population of rufous-collared sparrows did not challenge territory owners, and instead replaced owners only after their presumed death. While some replacements were undoubtedly of this sort on Mandarte, many clearly were not. At least 46% of all disappearances recorded during the study periods were associated with a protracted challenge by one or more floaters. Birkhead & Clarkson (1985) also reported that non-territorial magpies (Pica pica) challenged territory owners by intruding conspicuously on their territories, and that intruders occasionally (4% of 'gatherings') succeeded in acquiring the territory or a portion of it. However, many of the gatherings that they observed (38%) lasted less than 5 minutes. In the 3 contests that involved serious fights between owners and intruders, the intruders evicted the owners (Birkhead & Clarkson 1985). These results suggest that floaters may account for a substantial proportion of turnovers in territory ownership in some species, especially those where floaters are not tolerated on territories as satellites or helpers. This could also be true even in populations where the activities of floaters have

yet to be studied.

The Tactics of Floaters

Subordinate individuals might pursue one of various strategies once they have been prevented from settling in suitable breeding habitats by territory owners (see Introduction). On Mandarte, unsettled birds remained secretively in the main breeding habitat as floaters, and many floaters gained territories by challenging owners that were susceptible to eviction or by replacing owners that disappeared. The eviction of owners was most likely when more than one floater was observed during a contest. In one case, however, replacement was by a floater other than one of the original intruders. Further, floaters that maintained their challenges to owners longer by repeatedly returning to sing on contested territories were more likely to settle.

Two other studies of birds have also identified factors that may affect the severity of contests over territories. Ewald (1985) found that staged contests over feeders between non-breeding hummingbirds (Trochilidae) lasted longer when the contestants were most similar in age and in the level of reward they had previously received. He suggested that hummingbirds adjust the energy expenditure in aggression to their expected energy gain from winning a contest. Krebs (1982) showed that male great tits were more likely to lose their territory the

longer they were held in captivity, and that replacement males fought these released owners harder as their own residence time increased. He proposed that the cost of territory establishment to a replacement decreased with residence time, and that this cost was a key factor in a replacement's decision to escalate or retreat from the contest.

The tactics employed by floaters in contests with owners on Mandarte are probably shaped by two factors. First, floaters reside on only a few territories (ca. 5-10). It is therefore likely that floaters are nearly as familiar with territories as are owners, and have a similar potential ability to exploit them for food. Second, owners rarely regain a territory after losing a contest, and should therefore continue to fight to the limit of their ability. My results suggest some potentially useful tactics: (1) test male vigour by conspicuous intrusion, (2) contest the territory if a weakness is detected, or (3) join contests involving other floaters. The length of contests may be determined by continuous assessment by the floater of the owner's ability to defend the territory, and by the limits of the floater's own ability and available energy.

Are Floaters Pursuing an Alternate Reproductive Strategy?

Ford (1983), Flood (1985) and others have suggested that in birds intrusions by males are frequently directed towards fertile females. Males that intrude primarily to copulate with

receptive females could be pursuing an alternate reproductive strategy to territory defence (Howard 1978; Dunbar 1982). I found no evidence to support this for non-territorial male song sparrows. Intrusions were as common on territories without fertile (laying) females as they were when females were fertile. Intrusion pressure was also similar on territories with mated or unmated males.

Buitron (1983) found that 'monogamous' territorial female magpies were visited by extra-pair males more often when they were fertile. These visiting males, however, were nearly always experienced territory holders from up to 2.5 km away, rather than being non-territorial males. The 3 extra-pair copulations that I have observed also involved neighbour territory owners. I have never observed female song sparrows perform solicitation displays in the presence of floaters, nor have I observed floaters to approach territorial females. It is possible that floater males intrude secretively when seeking copulations, but do so conspicuously only to challenge territorial males. However, territorial males often follow their mates closely while they are laying and it seems unlikely that floaters would go undetected. These observations suggest that floater male song sparrows do not intrude primarily to copulate with territorial females.

Age, Tenure and Intrusion Pressure

I found strikingly consistent relationships between age, intrusion pressure and tenure during 2 years. Tenure and intrusion pressure could be non-linearly related to age for two reasons. First, young birds are inexperienced in skills related to resource defence, such as foraging and fighting. Second, old birds may be less vigorous because of physiological changes associated with age, or because of injuries and ailments that compound with age to cause a handicap.

I first consider young birds. Song sparrows on Mandarte forage extensively on leaf-rollers (Tortricidae, Lepidoptera) and slow-flying insects (Diptera and Hymenoptera) early in spring, but these prey are uncommon in summer by the time most young are foraging for themselves. Thus, yearling sparrows have had little previous experience with the main food items available in spring, the most intense period of territorial activity (Tompa 1964), and therefore probably have less energy available for territory defence than more experienced birds. Territorial birds, including song sparrows (Chap. 6), increase their time spent in territorial defence when provided with supplemental food (Searcy 1979; Ydenberg 1984; Tamm 1985). Foraging efficiency is similarly important to territory defence in unsupplemented populations (Davies & Houston 1983a,b), and foraging efficiency in birds first increases with age (Orians 1969; Dunn 1972; Verbeek 1977; Groves 1978; Quinney & Smith

1980), and then reaches a plateau (Pugesek 1983).

Fighting ability affects access to territory and mates in many species (LeBeouf & Peterson 1969; Geist 1971; Wiley 1973; Kikkawa 1981; Clutton-Brock et al. 1982; Howard 1983; Arcese & Smith 1985). Fighting success clearly increases as juvenile birds and mammals mature (Geist 1971; Ewald & Rohwer 1980; Kikkawa 1981; Clutton-Brock et al. 1982). A lack of fighting experience among 1-year-old song sparrows could also explain their lower ability to defend territories.

Long-term data on fighting success are sparse. The data presented here suggest that the fighting success of male song sparrows declines after the age of 2 or 3 years. I found that visible handicaps were more common in birds older than 2 years, and these handicaps were associated with territory loss. Such handicaps could reduce foraging efficiency as well as fighting ability. Similar observations have been made on ungulates and primates, where post-reproductive males showed poor muscle-tone, poor condition, and pot-bellies (Geist 1971; Jarman 1979; Clutton-Brock et al. 1982; Dunbar 1984). Further evidence for other birds is indirect, but survival (Coulson & Wooller 1976) and reproductive success (Burley 1980; Haymes & Blokpoel 1980; Collias et al. 1986; Robinson 1986) decline beyond middle-age in some species. While the mechanisms for such declines remain uncertain, this study demonstrates that the effect of age on the ability to defend resources is non-linear

even in a relatively short-lived monogamous species.

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CHAPTER 5. THE FORM AND FUNCTION OF SONG IN FEMALE SONG
SPARROWS

INTRODUCTION

Nice (1943) reviewed the occurrence of female bird song and speculated on its evolution. After a considerable gap, renewed interest in the song of female birds has concerned its role in courtship and maintenance of the pair bond, family unit and territory (Beletsky 1982, 1983a, b; Richison 1983, 1986). In this study, I focused on singing female song sparrows (Melospiza melodia) in a color-marked island population. I discuss the context of female song, present sonagrams from 3 females, and I compare my observations to those of Nice (1943). Finally, I speculate on the function of female song in song sparrows.

Except in a few species, singing by female passerines is rare (reviews in Nice 1943; Nottebohm 1975; Richison 1983). Nice (1943) suggested that female passerines fell into two groups depending on whether song was a common or exceptional aspect of their behaviour. She placed song sparrows in the latter group. Nice (1943) speculated further that the female song sparrows she observed singing were unusually aggressive individuals, and had abnormally high levels of androgens. Her suggestion is reasonable because, in some species in which females rarely or never sing, singing can be induced by implanting testosterone (references in Nice 1943; Nottebohm

1975). However, Wingfield (1984a,b) has shown that in wild song sparrows, circulating levels of testosterone in females at the time of territory establishment and just prior to nest building are almost as high as those recorded in males at the same time. This is the period during which Nice (1943) heard females singing.

If singing by female song sparrows results from unusually high levels of androgens in a few birds, such behaviour may be aberrant and therefore unimportant. Alternatively, singing females may be rarely but regularly observed under particular and interesting circumstances, thus suggesting a function for female song. For example, Richison (1983) concluded that singing by female black-headed grosbeaks (Pheucticus melanocephalus) functioned in family group maintenance: females sang most frequently during the fledgling period and young birds oriented themselves towards their parents song after becoming separated from them. Beletsky (1983a,b) showed that female red-winged blackbirds (Agelaius phoeniceus) sang different song types in the context of intrasexual aggression or pair-bond maintenance, and that these songs also differed from the familiar territorial song of males.

In this paper, I show that singing by female song sparrows occurred primarily in the context of territory defence against female intruders. I suggest that singing by female song sparrows indicates high levels of androgens, and that such high

levels are a normal consequence of aggressive interactions. Androgens may be secreted in response to repeated or prolonged conflicts between females for territory ownership, as demonstrated for male song sparrows by Wingfield (1984b).

RESULTS

The Form of Female Song

Female 60194 was first observed to sing on 20 February 1984. The song was composed of a series of clear, melodic whistles, lasting about 2 seconds, sung 1-6 times from a perch above the shrub canopy. The song was loud (audible from 3 territories distant, about 80 meters) and resembled that of a subadult purple finch (Carpodacus purpureus). The songs of 11 other females heard subsequently varied in volume, length and complexity, but most resembled the songs of 60194.

The female songs recorded were similar to male songs in frequency range, timing and overall structure (Fig. 5.1, compare F1-4 with M1-2). P. Marler and S. Peters (personal communication) have also recorded songs from live-tutored, captive females implanted with testosterone (Fig. 5.1, T1-2). Sonagrams of recordings from 2 of these females show a simple (T1) and more complex song (T2) that nearly span the range of song variability recorded in the wild (Fig. 5.1). Overall, males and females sang similar syllable types including pure

tones, buzzes, frequency modulated notes and rapid sweeps (Fig. 5.1). On average, however, females tended to sing shorter songs that included fewer different note types in each song than did males. Nevertheless, the longer songs could easily pass for male songs to a human listener and might have done so in unbanded populations.

Male song sparrows on Mandarte sing 4-12 song types and 30 or more variations on each type (Hiebert, Stoddard, & Arcese ms). These males sing 5-40 songs of one type, alternating among variations, before switching to another type. The females that were recorded sang variations the way males do, and 1 female was recorded long enough (60 songs) to discover that she had at least two discrete song types.

The Occurrence of Female Song

Singing females were rarely observed over the study period (Table 5.1). Only 12 of approximately 140 females were heard singing during 267 female-years of observation. Of these 12, 10 sang on only 1 day or 2 consecutive days. Two females were heard singing in more than 1 year. In contrast, territorial males on Mandarte Island sang more or less throughout the year, with peaks during late winter, spring and fall.

Table 5.1 shows that female song sparrows sang mainly between 20 February and the beginning of egg-laying, which

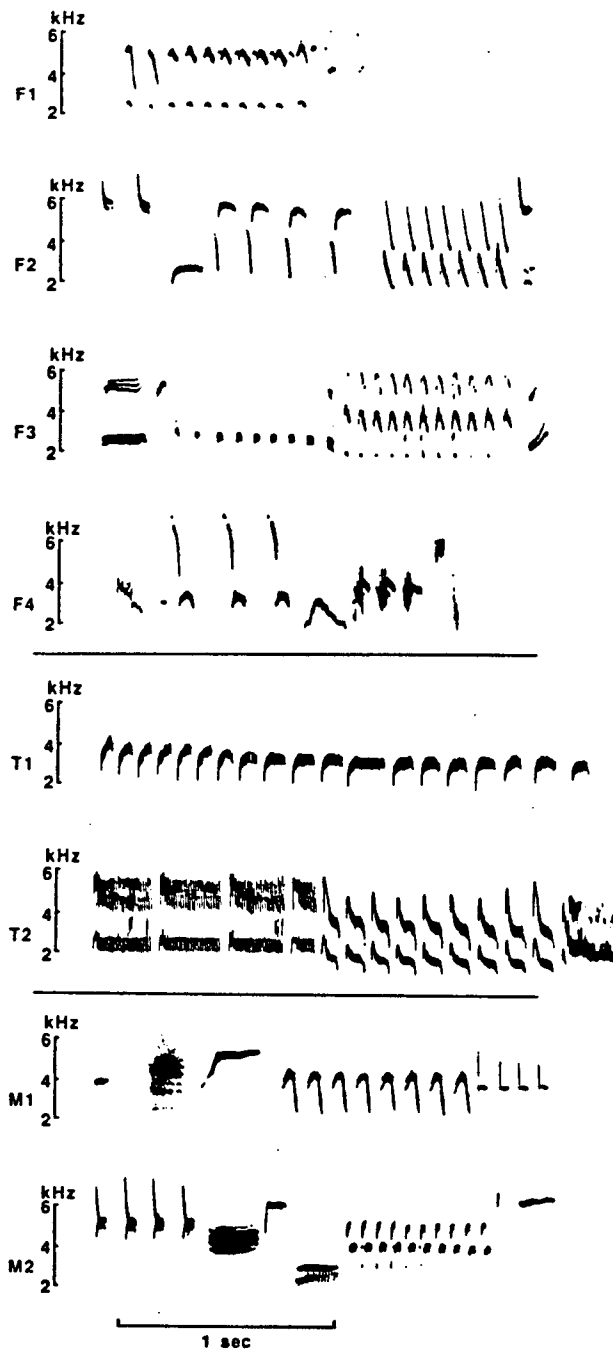


Figure 5.1. Sonagrams from 3 females recorded on Mandarte Island (F1-3), 1 from Discovery Park, Seattle (F4), and 2 recorded in New York by P Marler and S. Peters from captive, live-tutored females implanted with testosterone (T1-2). Two male songs (M1-2) from Mandarte Island are presented for comparison.

occurred between late March and mid-April. Only 1 female (60300) was heard singing after she had begun to lay eggs. This female sang regularly from 7 April to 18 June, 1985, usually when she came up from her nest and before she returned to incubate eggs or brood nestlings.

Singing by females, though always uncommon, has been heard more often in this population when population density was high. F.S. Tompa (personal communication) heard a female sing in this population only during the year of highest population density during his 4-year study. This was also the only year in which he observed territorial conflicts between females (Tompa 1964, personal communication). J.N.M. Smith (personal communication) also heard a female sing in this population in the year of highest density during the period from 1974-79. No female was heard singing in this study prior to 1984, despite intensive observation. Three females were observed singing in 1984, 9 in 1985 and 2 in 1986 (Table 5.1). Figure 5.2 shows that fewer than the overall average number of females were observed singing when population density was low, while more than expected were observed in high density years.

The Context of Female Song

Female song was nearly always associated with territory defence and it resulted most frequently when females disputed territory ownership. This can be seen by considering each

Table 5.1. The occurrence and context of female song in the song sparrow.
No females were observed singing in 1982 or 1983.

Female Number	Year		
	1984	1985	1986
60194	20 Feb: Evicting a female floater. 22 Feb: Evicting same and settling new boundary.	3 Apr: In response to male playback. 15 Apr: Evicting a female floater.	Not heard singing.
60279	20 Feb: Taking over new territory by evicting former female owner.	Not heard singing.	Not heard singing.
60300	10 Mar: Taking over new territory by evicting former female owner.	3 Apr: In response to male playback. 7 Apr: Evicting a female floater, then regularly to at least 18 June.	Not heard singing.
60204	Not heard singing.	8 Apr: Evicting a female floater.	(Deceased)

Table 5.1. Cont.

60108	Not heard singing.	25 Apr: On border as adjacent female is evicted by a floater female.	(Deceased)
60254	Not heard singing.	17 Apr: No apparent conflict.	Not heard singing.
60126	Not heard singing.	3 Apr: Response to male playback.	Not heard singing.
59239	(Year of hatch)	19 Apr: Attempting to settle between established territories.	Not heard singing.
59114	(Year of hatch)	18 Apr: Taking over adjacent territory by evicting owner.	Not heard singing.

Table 5.1. Cont.

58909	(Year of hatch)	29-30 Apr: Near female (Deceased) floater that settles on adjacent territory.	
59133	(Year of hatch)	Not heard singing.	16 Mar: No apparent conflict, but settled within the previous month.
59150	(Year of hatch)	Not heard singing. sing.	3-4 Apr: During intense fights with female floater.

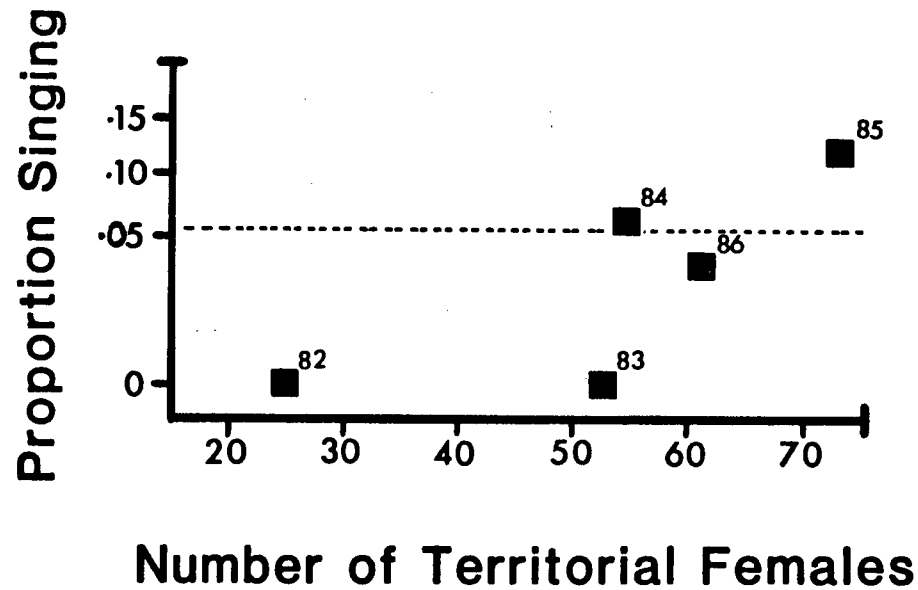


Figure 5.2. The proportion of females (transformed axis) heard singing in relation to the total number of females breeding. The dashed line indicates the average proportion of females heard singing over the study. The data are heterogeneous across years ($G_v = 12.8$, $df=4$, $P < 0.025$).

observation of a single day or series of 2 days of singing by a female as an event. Of 17 such events, 12 (70.5%) occurred during vigorous conflicts between females for territory ownership (Table 5.1). In these 12 cases, songs were heard from 8 territorial females and 4 intruders (3 neighbor territory holders, 1 non-territorial floater).

Figure 5.3 shows a typical territorial conflict between 3 females that took place over at least 3 days. Two of these females (60194 and 60279) sang repeatedly as the third (60182) was chased and ultimately evicted. The evicted female later settled 2 territories distant with an unmated yearling. Two additional females sang when no conflict was apparent. In both cases, however, home ranges of non-territorial females encompassed part of the singer's territory.

Three additional observations of female song were made after playing a tape recording of male song. One of these observations was made unintentionally while trying to stimulate a territorial male to sing. This is the only female (60126) that was not also observed singing under natural circumstances. Two other females that responded to playbacks with song were 60300 and 60194, the most active singers observed during the study (Table 5.1).

No other playbacks were conducted during spring or summer, but playbacks were frequently used as an aid during late winter

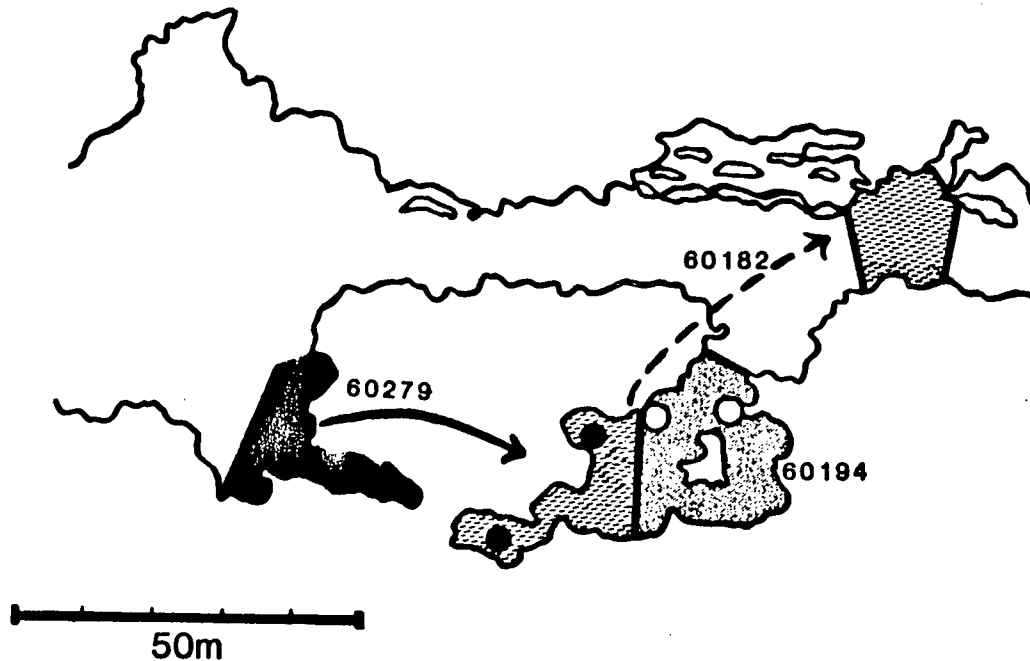


Figure 5.3. Depiction of a conflict between 3 females for the ownership of a breeding territory (band numbers refer to those in Table 5.1). Birds defend areas of shrub (outlined) surrounded by grassland or rocky intertidal. Female 60279 intruded from her previous territory (solid arrow), sang (black dots) and chased female 60182 from her former territory. Female 60194 chased female 60182 whenever she entered her territory and she sang repeatedly (open dots). Female 60182 settled several days later with an unmated male (broken arrow).

censuses. Females never responded to these with song, though "tiks", "tchunks" and "caterwauls" (Nice 1943:274) were common. Females were never observed responding to intruding or neighboring males with song, though they did sometimes respond to these birds aggressively (i.e. supplant, chase and puff-wave posture -as described for males as "puff-sing-wave" by Nice 1943:274).

DISCUSSION

Recent experimental studies indicate that female song in passerines plays a role in courtship, pair-bond and family group maintenance, and in territory defence (Beletsky 1982, 1983a,b; Richison 1983,1986). However, these studies have dealt only with species in which females commonly sing. No function has been suggested for female song in species where such behaviour is rare (e.g. Rufous-sided towhee (Pipilo erythrophthalmus), indigo bunting (Passerina cyanea), Nolan 1958 song sparrow, Nice 1943; this study). Nice (1943) believed female song served no function in the song sparrow, and that it resulted from unusually high levels of androgens in a few abnormal individuals. In the following discussion, I compare my results with those of Nice (1943) and speculate about the implications of female song in my study population.

Nice (1943:127) described the song of females that she observed as "short, simple and entirely unmusical", with the

exception of 1 bird (K135). On April 2, 1934, Nice (1943:127) noted that female K135 "has a special place on the locust where she sings; her song is shrill and loud; it reminds me a little of a white-throat ((Zonotrichia albicollis)). There are at least two versions; they are not as unmusical as most female Song sparrows." The singing behaviour of most females that I have heard most closely resembled that described for K135 by Nice. However, not all females that sang on Mandarte produced musical, male-like songs. Sonagram F1 in Figure 5.1 represents one such song that more closely resembled the songs that Nice reported.

There is also considerable variation in the similarity of song types of males and females across species. For example, in some species in which females commonly sing, such as the red-winged blackbird, female songs do not resemble those of males (Beletsky 1983a,b). In others, however, females sing songs that are either nearly as well-developed as males (i.e. black-headed grosbeak, Richison 1983) or equally well-developed (reviewed in Farabaugh 1982). In species in which females rarely sing, female songs are usually less well-developed than those of males, and are often described as resembling those of immature males (e.g. Nolan 1958; Nice 1943; this study). This suggests that there may be a reduced capacity for female song learning and/or performance in species in which males commonly sing but females rarely do so.

Nice (1943) defined five stages and Mulligan (1966) four in the song development of male song sparrows. These began with a soft warbling stage and culminated in full crystallized song. The females we recorded appeared to be nearing the final stage. More of their songs were fragments than would be expected of a mature male, but they did sing full, complex songs. Further, in all of the female songs recorded, internote intervals were similar to those of crystallized male song. This suggests either that: 1) practice singing by females does not have as important a role in song development as in males, 2) that some females practice singing as yearlings, or 3) that the song learning process is somewhat different for male and female song sparrows.

Nice (1943:127) observed young, unbanded but suspected females singing in fall; a female that she hand-raised also produced juvenile male-like warbles. However, I have never made such observations on known juvenile females. I therefore suggest that practice-singing is less important for female song sparrows than it is for males, perhaps because females sing fewer and simpler song types. Further, the song learning process for males and females might differ if female song learning functioned in species recognition, mate choice or inbreeding avoidance (review in Payne 1983) as well as in territory establishment and defence. In this case, song learning in females might be more highly developed for recognition than for performance.

I observed singing females almost exclusively during the period just prior to nest-building (late February to early April). This period matches closely the dates given by Nice (1943:127) of 12 February for the earliest song and 19 April for the latest. Nice (1943) also notes that Wetherbee (cited in Nice) reported a color-banded female song sparrow that sang frequently from April through at least 17 June, matching my record for female 60300 (Table 5.1).

Nice (1943) observed at least 2 females to sing when they participated with their mates in evicting intruding males (one unbanded). For example, "On Feb. 26, 1932, K56 was singing almost constantly, whenever she was resting from chasing 120M (a male), a new arrival that morning. At times she chased while her mate sang. She perched on top of elders and sang very loudly, often answering her mate's songs" (Nice 1943:127). Nice (1943) mentioned no territorial conflicts when she observed other females to sing.

My observations are consistent with Nice's, with the notable exception that 83% (10 of 12) of the females that I heard singing were involved in conflicts with other females over territory ownership. In contrast, I never observed females to sing when non-territorial male floaters attempted to evict territorial males or to settle between territorial neighbors, even though such attempts were common during the study (Chap.

3). This clearly shows that on Mandarte Island, singing by female song sparrows is related to competition with other females for breeding space. In this regard, my observation of an increase in the incidence of female song with breeding density is consistent with two effects of density on breeding performance: average reproductive success is strongly depressed (Arcese & Smith 1988), but variation in reproductive success is increased among females at high population density (Smith & Arcese 1986).

I suggest that, as population density and variation in reproductive success increase, competition among females for high quality territories or males becomes more intense. Such competition commonly leads to territorial conflicts between females at high population densities (personal observations). Androgen levels may increase in females involved in prolonged conflicts, as has been demonstrated in wild male song sparrows (Wingfield 1985b). P. Marler and S. Peters (personal communication) have repeatedly found that singing can be easily induced in female song sparrows with testosterone implants. It is therefore reasonable to conclude that conflict-induced elevations in androgen would have a similar effect in highly stimulated females. Androgen levels in wild females are known to normally approach the levels observed in males during the periods in which Nice (1943) and I observed females singing (Wingfield 1984a,b).

I therefore suggest that singing by female song sparrows is a rare but normal aspect of female behaviour that can be explained in two ways: (1) mechanistically, in terms of the relationship between circulating levels of androgens and the frequency and intensity of aggressive interactions, and (2) evolutionarily, in terms of the role of female vocalizations in aggressive contests over resources that affect reproductive success. These conclusions remain tentative, however, because the specific relation of androgen levels to territorial conflict in females has not been studied. Therefore, experimental studies are now needed to test if female songs or perhaps other vocalizations (e.g. caterwauls, chitters, threat notes; Nice 1943) in the song sparrow, serve a territorial function as in species such as the blue grouse (Dendragapus obscurus, Hannon 1980).

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CHAPTER 6. INTRASEXUAL COMPETITION AND MATING SYSTEM IN A
 PRIMARILY MONOGAMOUS SPARROW

INTRODUCTION

A classical question in the study of mating systems has been: how do individuals of each sex maximize their reproductive success? (e.g. Wittenberger 1979; Murray 1984). Orrians (1969) and Trivers (1972) have suggested that, because of the difference in size of male and female gametes, females should be more careful than males in their selection of mates. It follows that males should maximize their reproductive success by defending access to as many fertile females as possible; females should do so by mating with males that possess superior phenotypic or genetic qualities, or males that are able to defend exclusive access to resources crucial to reproduction (Orrians 1969; Trivers 1972; Bradbury & Vehrencamp 1977; Emlen & Oring 1977; Wittenberger 1979; Oring 1982; Murray 1984).

Although a role for direct competition for resources between females in the evolution and maintenance of mating systems is recognized (e.g. Trivers 1972:153; Altman et al. 1977; Wittenberger & Tilson 1980; Oring 1982:14), it has usually been downplayed in comparison to the role of female choice of mates (Darwin 1871; Orrians 1969, 1980; Emlen & Oring 1977; Searcy 1982; Mock 1983). As a result, models of mating systems that emphasize female aggression and resource defence remain

under-developed and largely untested. In this chapter, I consider the level and influence of intrasexual competition in the mating system of the primarily monogamous song sparrow population resident on Mandarte Island, B.C.

Although the majority of all birds mate in monogamous pairs (Lack 1968), many primarily monogamous species occasionally mate in polygynous groups (Verner & Willson 1969; Moller 1986). Mating in groups other than monogamous pairs can have substantial consequences for individual reproductive success even in primarily monogamous species (e.g. Davies & Houston 1986), and this makes such species interesting subjects for study (e.g. Smith et al. 1982; Hannon 1984; Dhondt 1987). However, primarily monogamous species have so far received much less attention than polygynous species (reviews in Trivers 1972; Wittenberger 1979; Emlen & Oring 1977; Oring 1982; Mock 1983).

Two outstanding questions concerning primarily monogamous species are: 1) how do polygynous groups arise? And, 2) what behavioural mechanisms determine which females and males within a population mate in polygynous groups? Here, I first briefly discuss how territory defence, time budgets and the availability of resources essential for the production of young could influence female competition and affect mating patterns and reproductive success. I then derive several predictions based on the hypothesis that intrasexual competition in each sex affects mating patterns in my study population, and consequently

affects the reproductive success of males and females. Next, I test these predictions using observational data collected over 5 years. Finally, I present results from a food addition experiment designed to alter the time budgets and territorial behaviour of males and females.

When Should Females Compete?

Because males should rarely suffer reduced reproductive success when additional females settle on their territories (Wittenberger & Tilson 1980), females can not rely on males to ensure exclusive access to territorial resources. Thus, females should attempt to prevent settlement by additional females on their mate's territory whenever doing so prevents the loss of exclusive access to resources such as parental care, food or nest sites. When the distribution of females is influenced by territorial behaviour, variation in the costs and benefits of resource defence by females will influence the frequency of polygyny by affecting the ability of males to defend more than one female (Orlans 1969; Trivers 1972; Bradbury & Vehrencamp 1977; Oring 1982; Davies & Lundberg 1984).

The total time devoted to reproduction by females necessarily equals the time spent in activities directly devoted to reproduction (i.e. nest building, egg production, incubation, etc.), plus that indirectly devoted to reproduction (i.e. defence of food, nest sites, and/or exclusive access to

male care). Thus, the time that females expend in defence should depend on the value of the benefits derived (e.g. exclusive access to food, nest sites, male care) and costs incurred by engaging in defence (e.g. energetic expenditure, delay in breeding, risk of injury).

Predictions

Given that both females and males defend limiting resources against others of the same sex, several predictions about the behavior and reproductive success of individuals follow. For example, because male aid in brood-rearing approximately doubles the number of young that female song sparrows on Mandarte can produce (Smith et al. 1982), I predicted that females should behave in ways that reduce polygyny (prediction 1), but that males should behave in ways that promote it (prediction 2).

Further, when monogamous females raise more young than those mated to polygynous males, and the probability of polygyny depends on competitive ability, then the females least able to engage in territory defence should most often breed in polygynous groups. In contrast, the most competitively able males should become polygynous most often whenever unaided females can raise at least some young. On Mandarte, the competitive ability of song sparrows varies with age (Nol & Smith 1987; Chap. 3 & 4). I therefore expected that polygyny would be most frequent among the youngest and oldest females

(prediction 3), and in contrast, most frequent among middle-aged males (prediction 4).

In early spring, when cool weather and short days limit feeding time and cause high expenditure of energy, birds are probably limited in the amount of time and energy available for direct investment in reproduction (Martin 1987; Arcese & Smith 1988). Thus, the amount of time spent in territory defence at this time by females and males should depend on the direct investment of each sex to reproduction. Because female song sparrows are responsible for the bulk of reproductive activities, while males only feed young, females probably have less time than males to devote to territory defence. To test if females adjust their territorial behaviour according to energetic constraints, I added food on 15 territories in 1985, prior to and during the laying period. I predicted that territorial females would be released from the constraints of foraging and would thus devote more time to territory defence (prediction 5). Further, if females defend territories primarily to prevent settlement by floater females, then fed females should be more effective at excluding floaters than controls (prediction 6). In contrast, if settlement by female song sparrows occurs primarily by choice of superior territories, female floaters should settle preferentially on territories with added food. Two predictions analogous to predictions 5 & 6 for females were also expected for males (predictions 7 & 8).

Next, because all females must substantially decrease time spent in defence once incubation begins, and because the long breeding period on Mandarte allows multiple breeding attempts (Smith & Roff 1980), I expected all females to eventually settle. More importantly, however, I further expected that if territory defence determines which females mate in polygynous groups, then any cases of polygyny that resulted from settlement by female floaters should occur on territories where previously settled females had begun incubation (prediction 9).

Finally, if the relative levels of intrasexual competition within populations influence the long-term, level of polygyny in the population, then polygyny should be less common as the ratio of males to females increases (Emlen & Oring 1977; Smith et al. 1982; prediction 10). This is because females should more often be able to defend their mate's entire territory when competition for space in males exceeds that in females.

In summary, if aggressive competition is the primary means by which breeding territories are occupied, superior competitors should acquire the best breeding opportunities. With regard to polygyny in the song sparrow on Mandarte Island, males should behave in ways that promote polygyny as long as doing so leads to the production of more young than could be raised in monogamy. The reverse is expected for females. Thus, females of low and males of high competitive ability should be most

likely to breed in polygynous groups.

RESULTS

Observational Study

Frequency of polygyny

Thirty-six of all 175 females (21%) that bred from 1982-6 did so in a polygynous group at least once. However, only 3 females bred exclusively in polygynous groups, each breeding for one season, and only 2 bred in polygynous groups in more than one season. Seventeen of 136 males (13%) bred polygynously during their lifetimes. Two males bred in trigamous groups. When analysed as the total number of matings, 9.5% of all matings (67 of 706) involved polygyny, because most females that bred in polygynous groups also bred monogamously in the same season.

Origins of polygyny

Polygynous matings arose in two ways (Table 6.1). Seven cases resulted when non-territorial females settled on the territory of a pair or trio (1 case). In 5 of these 7 cases, floating females settled on the territories of females that were incubating eggs and therefore could not prevent the incoming female from settling. Another 12 cases occurred when mated

territorial males usurped a neighbouring territory and female, either by evicting the neighbour or after the neighbour disappeared (one case led to a trigamous group).

Territory takeovers by neighbours most often resulted in polygyny when they took place during the main breeding period, from April through June (Table 6.1). Overall, 20% (11 of 56) of takeovers resulted in polygyny when they occurred from April through June, compared to only 3% (1 of 34) outside of the breeding period ($P=0.03$, Fisher's exact test).

Ages of birds in polygynous groups

Females 1- and 4-years-old were more likely to be part of a polygynous group than were 2- or 3-year-olds when compared to the numbers expected from the age-distribution of monogamous females (Fig. 6.1a; $G = 10.00$, $P < 0.01$, $df=3$, 1-tailed, prediction 3). The opposite pattern was observed for males (Fig. 6.1b). One-year-old males never became polygynous, 2-year-olds did so much more frequently than expected by the age-distribution of monogamous birds, and 3- and 4-year-olds did so as often as expected ($X^2 = 7.68$, $P < 0.05$, $df=3$, 1-tailed, prediction 4).

Table 6.1. Seasonal frequency of territory takeovers by neighbouring owners that did or did not lead to polygynous matings, and the frequency of polygynous matings that resulted from the settlement of floater females.

Takeovers	Month											
	J	F	M	A	M	J	J	A	S	O	N	D
Led to Polygyny	0	1	0	3	5	3	0	0	0	0	0	0
Did Not	4	3	13	16	19	6	1	2	4	2	1	3
Female Settlement	0	1	1	4	1	0	0	0	0	0	0	0

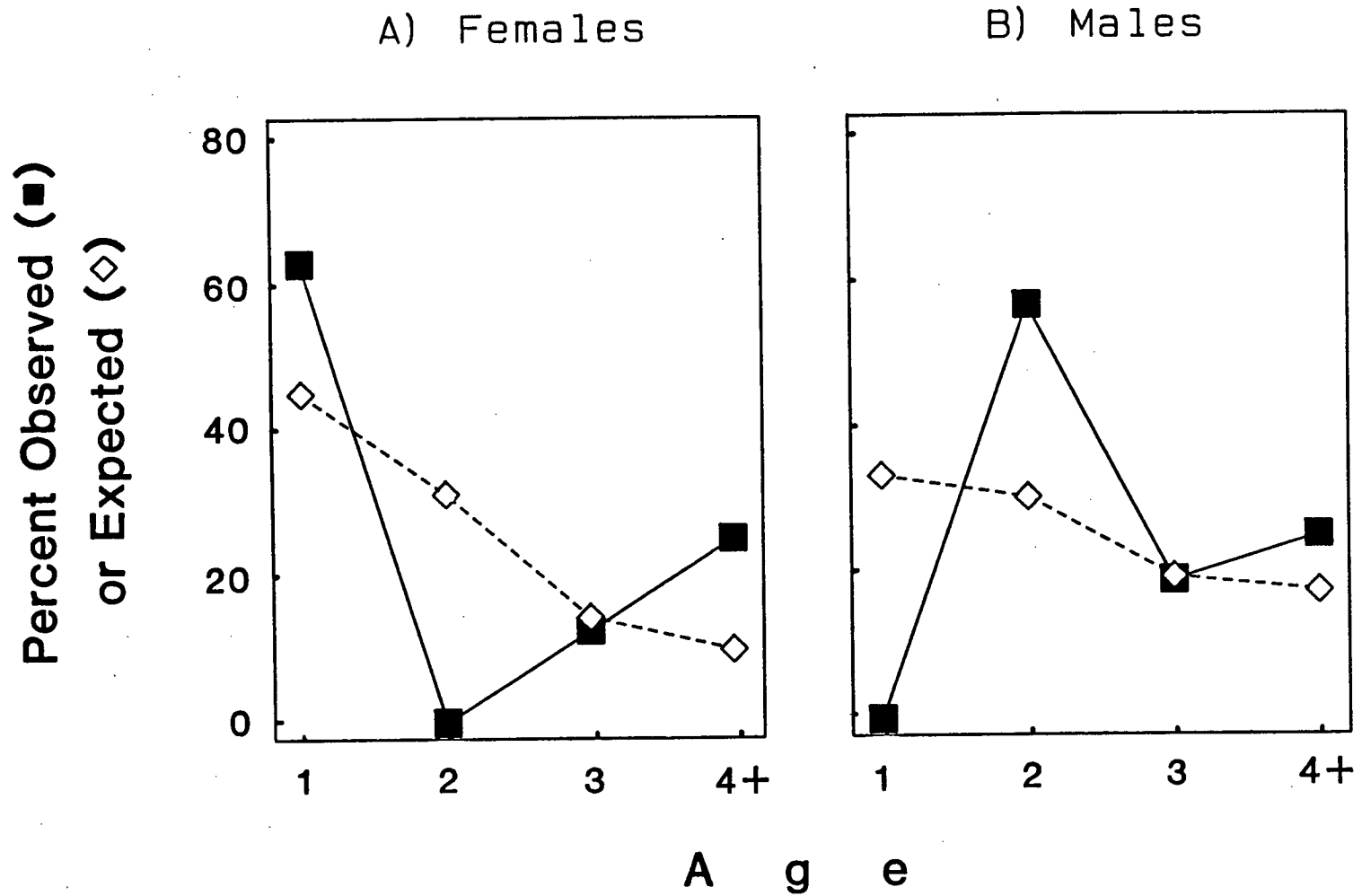


Figure 6.1. The percent of males and females observed to mate in polygynous groups in relation to age, compared to that expected by the number of monogamous breeders of each age over the study.

Male aid and female reproductive success

Monogamous males typically gave alarm calls when humans or predators entered their territories, especially when active nests or newly fledged young were present. These males also fed their young regularly from hatching to independence (between day 25-32). Polygynous males behaved similarly, but typically spent most of their time near only one female. The second female in a territory was frequently ignored by her mate, and in no case did polygynous males simultaneously feed more than one brood of young. Thus, females mated to polygynous males frequently lacked male vigilance during incubation and male assistance while feeding nestlings and fledglings.

Unaided females produced fewer independent offspring per breeding attempt than aided or monogamous females in all 5 years of this study (Table 6.2). Unaided females produced from 0-34% as many young per nesting attempt on average as did females with male aid. Overall, both monogamous and aided females produced significantly more young per attempt than unaided females ($P=0.004$ and $P=0.005$, respectively; Mann-Whitney U-tests on residuals standardized for yearly differences in reproductive success, see Table 6.2; Arcese & Smith 1988). However, monogamous and aided females in polygynous groups produced approximately equal numbers of young ($P=0.48$, U-test as above, Table 6.2).

Table 6.2. Mean and SE of the number of independent young raised per nesting attempt by monogamous, aided and unaided females. Females known or presumed to have had access to supplemental food in 1985 are excluded.

Year	Monogamous	Aided	Unaided
1982	2.02±0.19	-	0.50±0.50
Females, Attempts	26,60	0,0	2,2
1983	1.42±0.12	1.70±0.52	0.20±0.20
Females, Attempts	50,121	3,7	3,5
1984	0.96±0.09	2.00	0.33±0.21
Females, Attempts	53,135	1,1	5,6
1985	0.45±0.07	0.50±0.50	0.11±0.10
Females, Attempts	49,129	2,2	5,9
1986	0.42±0.06	0.45±0.21	0.00±0.00
Females, Attempts	54,144	8,16	9,15

The number of young raised per nesting attempt also changed as expected when females gained or lost the aid of males within breeding seasons. In 5 of 8 cases female reproductive success declined when females lost male aid. In all 7 cases where females formerly without help gained the aid of a male, reproductive success increased ($P=0.04$, Fisher's exact test; there was no change in reproductive success in 3 cases of each type).

Male reproductive success

Polygynous males sired 1.4-4 times more independent young on average than did monogamous males, except in 1984 when only one polygynous male bred (Table 6.3). Although the sample sizes for each year were small, the overall difference in the reproductive success of monogamous and polygynous males was statistically significant ($P<0.01$, $N=242$ male-years, $N=14$ male-years, U-test as for females). Further, 11 of the 14 polygynous males known not to have had access to supplemental food raised more young (relative to the population mean for the year) when polygynous than they had previously raised when monogamous. In comparison, 5 of these males bred monogamously later, and all raised fewer young ($P=0.01$, Fisher's exact test; 2 males died before the next season, 7 males bred polygynously in the last year of study).

Table 6.3. Mean and SE of number of independent young raised each year by monogamous and polygynous males. Males known or presumed to have had access to supplemental food in 1985 are excluded.

Year	Monogamous	Polygynous
1982	4.33±0.83	-
N	27	0
1983	2.46±0.27	5.00±1.00
N	55	3
1984	2.35±0.25	2.00
N	58	1
1985	0.80±0.14	3.00±0.58
N	45	3
1986	1.16±0.14	1.67±0.31
N	58	6

Use of space by females

Although no quantitative analysis of overlap was conducted, the areas utilized by males and females in monogamous pairs were indistinguishable even after intensive observation, except during the early periods of nest-building. During this period, females frequently expanded territory boundaries around newly located nest-sites, which were sometimes beyond their mate's previous boundaries (Table 6.4). Such movements often preceded vigorous conflicts between neighbouring males, especially when the male being encroached upon was not occupied with feeding young. Males responded to females locating new nests near or outside a previous territory boundary by expanding their territories to include the new nest-site. In contrast, male boundary shifts rarely occurred when females built new nests well-within the limits of an established territory ($G = 21.44$, $P < 0.001$, $df = 2$, Table 6.4).

Most females in polygynous groups overlapped little in the areas they used, and they often engaged in aggressive displays (i.e. puff-wave, chatter, caterwaul, song; Nice 1943:274; Chap. 5) along borders that could be mapped easily. These displays were most obvious when females nested in close proximity, and when neither was incubating or caring for young. Males were not observed to participate in female conflicts.

In striking contrast to the behaviour of most females, 3

Table 6.4. Shifts in male territory boundaries subsequent to females placing their newly-built nests beyond (i.e. outside the territory), near (within 6m of a current boundary) or well-within (>6m from) their mate's previous territory boundaries. Data from 1982 only.

		Boundary Shift	
		<6m	≥6m
Distance of new	Beyond	0	5
nest from old	<6m	4	8
boundary	≥6m	16	1

females behaved aggressively only when territorial females entered the area immediately surrounding their nests. These birds were often chased by territorial female neighbours, but they regularly fed secretively throughout territories adjacent to their nests. Each of these females behaved most prominently (by vocalization and posture) when their neighbour incubated or tended young, and at these times they often interacted with the male whose territory included their nest-site. One such female was prevented from incubating a newly-laid clutch by an aggressive female neighbour incubating 3m distant. None of these females successfully hatched young in polygynous groups, but all raised young later in monogamous attempts (1 the same year, 2 the following year).

Aggression among females was common when female floaters attempted to settle within the boundaries of territorial females. On these occasions, fights involving physical contact were common and females sometimes sang (Chap.5; see also Nice 1937; Tompa 1963). However, territorial females seldom engaged in defence after incubation began. At this time, over 45 min/hr were usually spent on the nest and time off the nest was primarily spent foraging (see below).

Sex ratio

The yearly proportion of polygynous males varied from 0-10.5% during this study, and from 0-9.8% during an earlier study

by Smith et al. (1982). Combining these data showed that the frequency of polygyny in males increased as the ratio of territorial females to males increased during 10 years ($r=0.68$, $N=10$, $P<0.02$, 1-tailed; prediction 10). One year, when sex ratio was altered experimentally, was excluded (1979, Smith et al. 1982).

Food Addition Study

Body mass

Females with supplemental food outweighed control females by over 3g on average only 2 weeks after feeding commenced (means (SE) for 6 fed and 7 control females: 26.62 (0.41) and 23.41 (0.23), $t=6.76$, $P<0.001$, $df=8.1$). The difference was only slightly less among males (8 fed and 10 controls; 27.46 (0.37) and 25.01 (0.31), $t=5.07$, $P<0.001$, $df=14.6$). Thus, males and females not only used the feeders immediately, but also gained considerable mass as a result.

Male response to taped song

To test the immediate effect of supplemental food on the response of males to simulated intrusions, I played 1 min of taped song from a recorder placed at the edge of 14 fed and 27 control territories, 3 days after feeding began. I subsequently observed the territories for 4 min to determine if

males responded by perching above the shrub canopy, approaching the speaker or vocalizing. Males that were not observed or heard were recorded as not responding. Ten of 14 fed males responded to playbacks, compared to 7 of 27 controls ($G = 7.65$, $P < 0.01$, $df = 1$). Responses by females to taped songs are described in chapter 5.

Time budgets

Supplemental food dramatically reduced the proportion of time females spent feeding, but increased their time spent preening slightly and in alert behaviour greatly (all $P < 0.001$, U-tests, $N = 13$, $N = 14$; Fig. 6.2). Fed females engaged in slightly more defence and display, and less time out of sight, but these differences were not statistically significant (all $P > 0.10$, U-tests as above; Fig. 6.2). Fed females spent slightly more time nest-building than controls ($P = 0.05$, U-test as above). Two of 14 controls flew to areas out of sight of their territories during their time budgets (presumably to feed), but no fed females did so.

Males responded to food addition in the same way as females (Fig. 6.3). Males fed much less, preened more and spent much more time in alert behavior when given food (all $P < 0.001$, U-tests, $N = 14$, $N = 14$, pooled as above). The proportion of time spent in defence or display did not differ with treatment ($P > 0.10$, U-tests). However, control males spent much more time

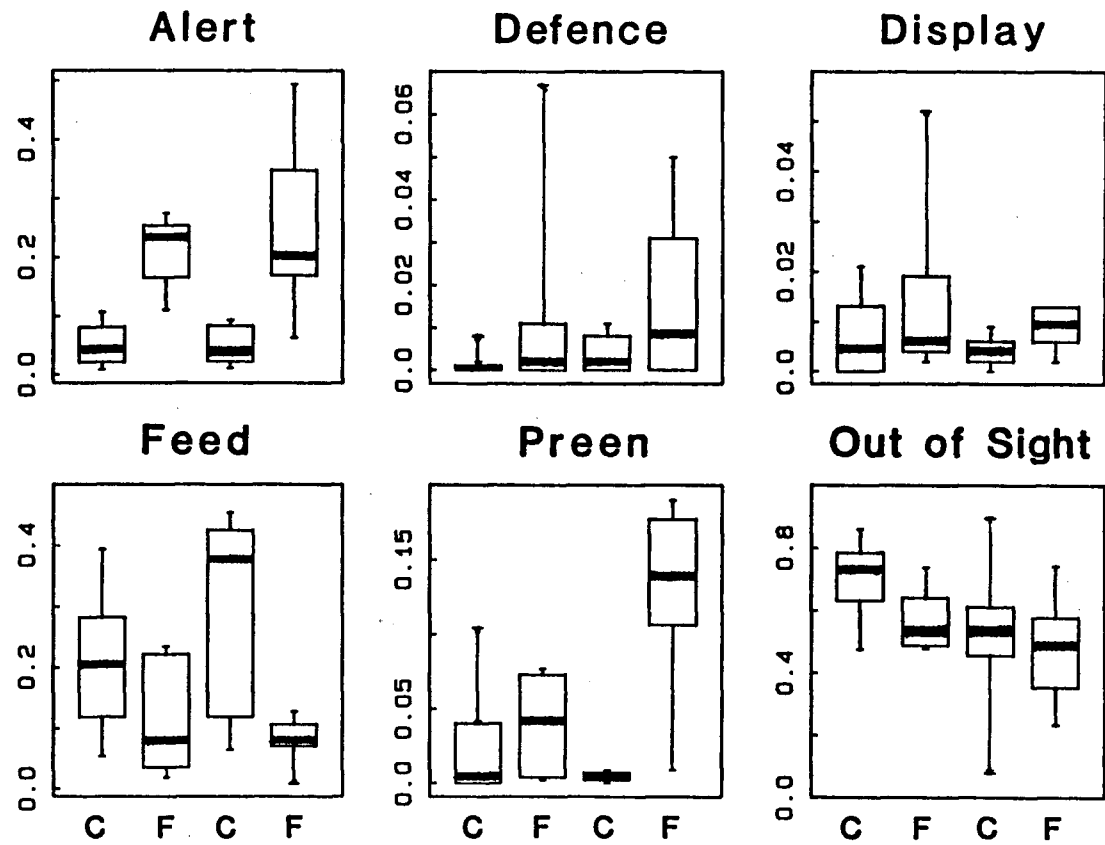


Figure 6.2. Median, inter-quartile range, and the range of the data for the percent of time spent in each of 6 behaviours by fed and control females (see Methods). C and F denote replicates from each fed (N=6,7) and control plot (N=7,7).

out of sight than fed males ($P < 0.001$, U-test). Further, 5 of 14 control males flew out of sight of their territories during time budgets, whereas none of 14 fed males did so ($P = 0.04$, Fisher's exact test).

Fed birds of each sex spent a large amount of time alert. Further, more chases of non-territorial intruders followed periods of alert behavior than expected if chases had followed all behaviors equally ($G = 87.25$, $P < 0.001$, $df = 3$; adjacent classes were pooled to avoid expected values < 5.0 ; Sokal & Rohlf 1981).

Settlement of non-territorial females

Four adult and 32 yearling females had not occupied territories when the feeding experiment commenced. At this time, 49 females occupied territories in monogamous pairs (34 controls and 15 fed pairs). Four unmated males also defended territories, of which 2 were on marginal sites never settled by females in the 5 years of this study. Egg-laying commenced in late-April, and by mid-May the last non-territorial female had either settled or disappeared from the island. Table 6.5 shows that 29 of these females eventually settled on Mandarte. One female settled on Halibut Island (1.3 km distant) and 6 females disappeared. Both males on marginal sites abandoned their territories and became floaters, 1 unmated male disappeared and the fourth gained a female.

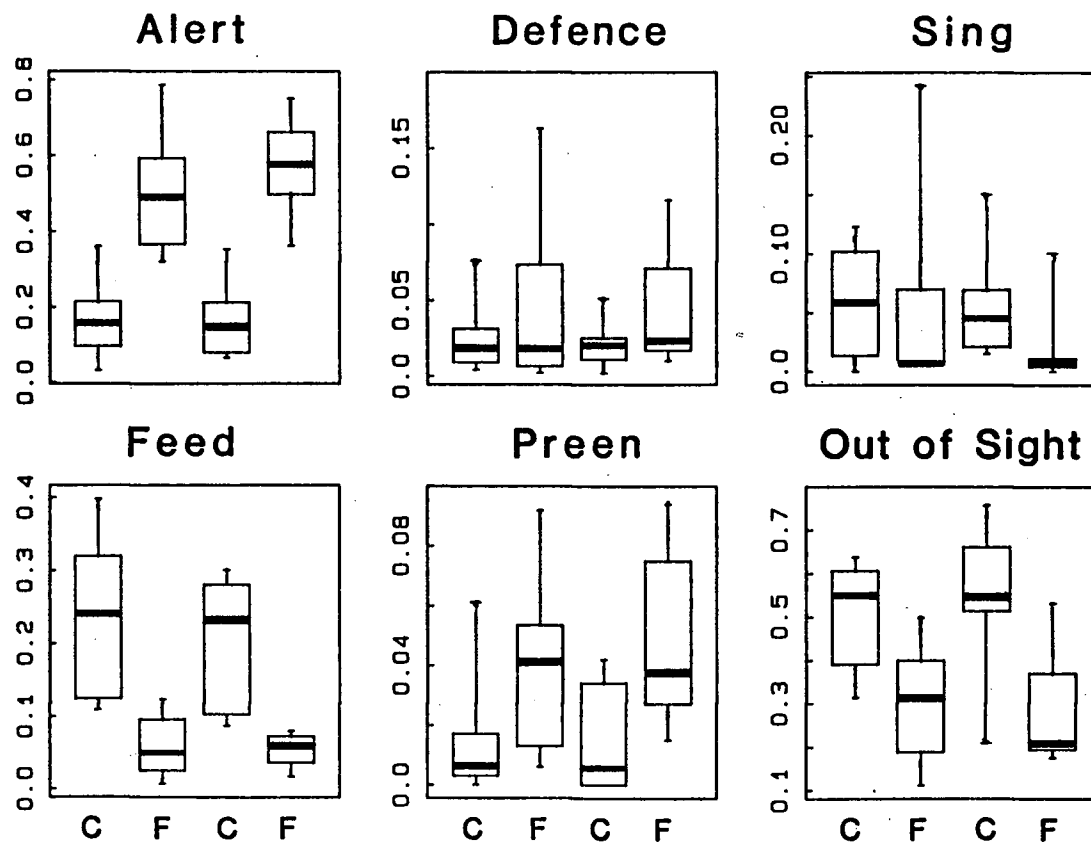


Figure 6.3. Percent of time spent in each of 6 behaviours for 6 and 8 fed, and 7 and 7 control males. Conventions as for Figure 6.3.

Of the 29 non-territorial females that settled on Mandarte, significantly fewer did so on fed territories than expected if the probability of settling on each territory defended at the outset of feeding had been equal ($G = 8.16$, $P < 0.002$, $df = 1$, 1-tailed, Table 6.5; prediction 6). Further, all 4 cases of polygyny that resulted from settlement by non-territorial females occurred on control territories.

Settlement of non-territorial males

Three adult and 32 yearling males also behaved as floaters when the feeding experiment commenced. However, only 17 (49%) of these males eventually settled, as compared to 29 of 36 (81%) female floaters ($G = 7.97$, $P < 0.005$, $df = 1$; Table 6.5). Nine males disappeared from the island and 9 remained non-territorial throughout the breeding period. Two males settled on fed territories (1 gained access to a feeder) and 15 settled on controls. Floater males settled less often than expected on fed territories, but this difference is not quite statistically significant ($G = 2.54$, $P < 0.07$, $df = 1$, 1-tailed, Table 6.5; prediction 8). This difference was highly significant when both sexes were pooled ($G = 10.06$, $P < 0.001$, $df = 1$).

Table 6.5. Observed settlement of male and female floaters as compared to that expected if the probability of settlement on each territory occupied at the outset of feeding had been equal.

	Control	Experimental	Total
Territories defended (28 February)	38	15	53
Observed female settlers	27	2	29
Expected female settlers	20.8	8.2	29
Observed male settlers	15	2	17
Expected male settlers	12.2	4.8	17

DISCUSSION

All 10 predictions that follow from the hypothesis that intrasexual competition in each sex affects the mating system of song sparrows were at least partly supported in this study. The outcome of such competition influences which individuals mate in polygynous groups, and thus affects reproductive success in both males and females. In the following sections, I discuss the resources that limit reproductive success in each sex, the specific predictions made regarding song sparrows on Mandarte Island and the influence of female competition in the maintenance of monogamy.

Competition for Limiting Resources

For females on Mandarte, the resources that limit reproduction are access to a high quality breeding site, food and male care (Smith 1988; Arcese & Smith 1988; Hochachka et al. ms; Table 6.2). Most females in this study eventually gained breeding sites (Table 6.5), but the fates of females that disappeared from the island remain unknown. In contrast, several males that remained in the population did not breed either because they could not gain a territory or could not hold one (Smith & Arcese ms; Chap. 3 & 4). However, many males simultaneously gained access to 2-3 females. This suggests that competition is more intense among males than females, as expected when females can raise young without male aid (Trivers

1972). However, the potential for intrasexual competition in females is substantial because females that defend high quality territories, in addition to exclusive access to a male, produce more offspring than those that do not (Arcese & Smith 1988; Hochachka et al. ms; Table 6.2).

Female competition and territory defence has been documented in many species including monogamous open-nesters (Smith 1978; Hannon & Zwickel 1979; Hannon 1984; Harper 1985) and hole-nesters (Gowaty 1981; Stutchbury & Robertson 1985), and in polygynous (Yasukawa & Searcy 1981, 1982; Hurley & Robertson 1984, 1985; Dickinson & Lien 1987; but see Searcy 1986) and polyandrous species (Oring 1982; Petrie 1983). A particularly striking example of the roles of male and female intrasexual competition in mating system organization is seen in the dunnock, (Prunella modularis). Davies & Lundberg (1984) showed that by adding supplemental food in a garden population of dunnocks, female territory size was reduced and males became better able to defend their mates against extra-pair copulations with subordinate, satellite males. Davies (1985) and Davies & Houston (1986) later concluded that female competition for space and exclusive access to males was intense in this population. Females that gained the aid of additional males subsequently raised more young. At the same time, several females mated in polygynous trios, shared their mate's aid and produced fewer young. This suggests that competition increased after the addition of food and caused a reduction in female territory size

(Hixon 1980; Norton et al. 1982). Stobo & McLaren (1975) described a similar scenario for a primarily monogamous, natural population of savannah sparrows, Passerculus sandwichensis.

Male Aid and Reproductive Success

In song sparrows and several other species (Weatherhead 1979; Greenlaw & Post 1985; Hannon 1984; Davies & Houston 1986), females that do not receive aid from their mate raise fewer young (Smith et al. 1982; Table 6.2). However, whether females in polygynous groups receive aid often depends on nesting synchrony (Verner 1964; Smith et al. 1982; this study). In other species, males partition their aid between concurrent nests (Martin 1979; Davies & Houston 1986).

Verner (1964) suggested that settled females should repel additional settlers when this prevented the loss of male aid, or that they should stagger nest initiation so that males might aid females in turn. Wittenberger (1979) and Orians (1980) used this idea to explain why in regularly polygynous species, females are most aggressive prior to nest initiation. Implicit in this reasoning is the assumption that the risk of losing male aid diminishes once a female initiates a nest.

However, three factors suggest that the risk of losing male aid does not diminish substantially for females that have begun incubation in species like the song sparrow. First, because

nest failure is frequent (Nice 1943; Arcese & Smith 1988), it is probably difficult for females to predict the risk of losing male aid when in polygynous groups. Second, when species are multi-brooded, receiving aid in a first attempt does not ensure it in later attempts. Third, in this study 5 of 7 cases where female floaters settled onto the territory of a monogamous pair occurred after the resident female had begun to incubate. For song sparrows, a reduction in defence time is inevitable once incubation begins. Thus, when male care is a key resource at risk, females might do better to delay nest initiation until most female floaters have settled each spring, than to initiate nesting early and try to ensure that their nests hatch before those of subsequent settlers.

The influence of female spacing behaviour should be smaller when reproductive success does not depend on male care (Orians 1969; Trivers 1972; Oring 1982; see Introduction). Yasukawa & Searcy (1982) tested this prediction by comparing female aggression and nesting synchrony in an eastern population of red-winged blackbirds where males provisioned nestlings, to that in a western population where they did not. Nest initiation was asynchronous where males fed young, but not where females raised young alone, suggesting that aggression by females spaced nesting attempts in time in populations where males provide non-shareable care that improves female reproduction.

Polygyny and Male Reproductive Success

In contrast to the case for females, polygyny increases male reproductive success in species with a variety of mating systems (Orians 1980; Davies & Houston 1986; Clutton-Brock et al. 1982; Freed 1987; Table 6.3). This is expected, given that females can raise some young without male aid, and it highlights an important difference between males and females that probably affects behaviour (Trivers 1972). In primarily monogamous species, the potential for additional matings probably explains the aggressive behaviour of males that increase territory size by evicting neighbours and preventing settlement by floaters (e.g. McLaren 1972; Ueda 1986; Freed 1987; Chap. 4; Table 6.1).

Frequency of Polygyny

Polygyny is an uncommon but recurrent feature of both the song sparrow population on Mandarte and passerine populations in general (Verner & Wilson 1969; Moller 1986). The low annual level of polygyny observed in this study confirms a general prediction made in the Introduction, given the substantial contribution of male aid and territory quality to female reproductive success (Smith et al. 1982; Arcese & Smith 1988; Hochachka et al. ms; Table 6.2). Nevertheless, over 5 years 21% of females and 13% of males bred in polygynous groups at least once. Although song sparrows display a low annual rate

of polygyny (0-10.5% of males; Nice 1943; Smith et al. 1982; Table 6.2 & 6.3), I suggest that the reproductive consequences of polygyny influences the behaviour of both males and females considerably.

Proximate Origins of Polygyny

Polygyny occurred most often when males annexed neighbouring territories, but also after floater females settled onto occupied territories (Table 6.1). In 5 of 7 cases, floater females settled onto the territories of incubating females. These results support the idea that the ability to engage in territory defence is an important determinant of which birds become polygynous in this population (McLaren 1972). This is also true for males in regularly polygynous territorial species, where competitive ability determines access to habitat and mates (e.g. Robinson 1986; review in Searcy & Yasukawa 1983).

Options of Females in Polygynous Groups

Following takeovers by neighbouring males or settlement by additional females, females could respond in four ways: (1) evict a female neighbour, (2) disperse, (3) attract an unmated male, or (4) remain in a polygynous group. The cost or benefit of each option will vary depending on a females current commitment of time and energy to reproduction, and with the

availability of alternative territories and males. Evicting territory owners is energetically costly and physically risky (Chap.3 & 4). Dispersal during the breeding period occurs (Smith et al. 1982), but is uncommon, probably because unmated territorial males are usually rare and frequently defend patches of habitat rarely used for breeding. Further, females that abandon territories to search for unmated males risk losing their old territory should they fail to locate a suitable site (see Krebs 1983; Chap. 3 & 4 for analogous examples in males). Mate attraction will only be successful if the present male cannot repel potential settlers, which is unlikely if polygyny initially resulted from a takeover. Females are therefore limited in their opportunities to avoid polygyny once breeding commences. In contrast, females should be most able to defend exclusive territories in fall, when feeding conditions are relatively good and there are no time or energy commitments to reproduction.

Early spring and fall are the times when female territorial behaviour is most often observed in song sparrows (Nice 1937; Tompa 1964; Smith et al. 1982; Chap. 5). Territory defence by females at these times could minimize future competition if it caused unsettled yearling females to disperse. In this study, the proportion of yearling females that recruited to the population declined as the density of territorial females in fall increased (range=66-32%; $R = -0.94$, $N=6$, $P<0.05$, 1981-86 cohorts). Further, late summer, fall and early spring are the

periods during which most yearlings disappear from the population (Tomba 1964; Chap. 7). This suggests that fall territoriality reduces population size and consequently reduces competition for breeding territories the following spring (Tomba 1964; Brown 1969; Watson & Moss 1970; Patterson 1980). Female territoriality has been shown to prevent recruitment in the song sparrow in late winter (Knapton & Krebs 1974), and in several other species during the breeding period (Village 1983; Hannon 1983, 1984; Hurley & Robertson 1985; Stutchbury & Robertson 1985).

Age and Polygyny

The probability of breeding in a polygynous group depended on age (Fig. 6.1). This confirms two important predictions concerning the relationship between polygyny and competitive ability in song sparrows (predictions 3 & 4), and suggests that polygyny arose most often among the females least able to engage in territory defence and the males most able to do so.

Habitat Saturation, Sex Ratio and Polygyny

All breeding habitat on Mandarte was defended even when density was low (e.g. 25 pairs). As density increased, so did the proportion of males that floated for part or all of the breeding season (Smith & Arcese ms). Female floaters occasionally existed in the early breeding season when density

was high (i.e. 60-70 pairs; Chap. 7), but these birds either settled or disappeared soon after breeding commenced. This could mean that in general there are more breeding positions available to floating females than to males.

This might arise in four ways. First, because yearling survival is slightly lower in females than males (Smith et al. 1980; Arcese & Smith 1985), the number of candidate males often exceeds that for females. Second, females that might otherwise float sometimes settle into polygynous groups. Third, the mortality rate among adult females slightly exceeds that for males (Nol & Smith 1987), which results in more empty territories available for females than males. Finally, females from Mandarte sometimes breed elsewhere and an immigrant female settles on Mandarte nearly every year (Chap. 7). However, just 2 immigrant and no emigrant males are known to have bred. Because the sex ratio of unbanded dispersers to Mandarte is roughly equal, this suggests that non-territorial females are more likely to settle outside the natal population than males.

These factors contribute slight to moderate biases in the ratio of territorial females to territorial males that has favored males in 14 of 15 years (range=0.64-1.07, mean=0.92, estimated each spring; Tompa 1963; Smith 1988; this study). Polygyny in males increased with the ratio of territorial females to males, as expected if the relative levels of intraspecific competition influence the population level of

polygyny (Emlen & Oring 1977; Smith et al. 1982; prediction 10). However, the ratio of territorial females to males frequently exceeded the total adult sex ratio because several males often behaved as floaters (adult sex ratio: range=0.49-1.07, mean=0.78, 1975-8 and 1981-6; Smith 1988; this study). Nevertheless, these measures of sex ratio were perfectly correlated ($R = 0.99$, $N=10$).

Emlen & Oring (1977) predicted that monogamy should predominate when the ratio of sexually active males to females (the 'operational sex ratio', OSR) equals 1, but that polygamy should occur when the OSR deviates from 1. In partial support of this hypothesis, Smith et al. (1982) increased the level of polygyny after raising the OSR by removing territorial males and their replacements during breeding. Further, in the dunnock, a species with several life history characteristics, habitat preferences and behaviours in common with song sparrows, polyandry occurred in 3 years when the OSR ranged from 0.67-0.89 (Davies & Lundberg 1984). In contrast, although sex ratios on Mandarte were often even more biased towards an excess of males than in the dunnock, simultaneous polyandry has never been observed. I suggest that the absence of polyandry is due the extreme intolerance towards intruders displayed by territorial male song sparrows (compare Davies 1985 and Chap. 3 & 4).

Use of Space by Females

Detailed observations over 5 breeding seasons strongly suggested that male and female territory boundaries were contiguous, except when males defended the territories of more than one female, or temporarily when females built their nests near or beyond their mate's territory boundaries. In the latter case, males nearly always aggressively expanded their territory to surround the new nest-site (Table 6.4). Such observations are common in early accounts of territory establishment in primarily monogamous birds (Lanyon 1956:486; Marler 1956:498; Snow 1956:441; Young 1956:449; Ficken 1962:626). More recently, Dickinson & Lein (1987) showed quantitatively that territory boundaries and the rate of aggressive interaction between male red-winged blackbirds depended on female nest placement. These results suggest that male and female territory boundaries are often contiguous because males defend the areas utilized by their mates, rather than because females restrict their movements within the areas that males defend (Stobo & McLaren 1975; Smith et al. 1982).

Effect of Food on Time Budgets

Adding high quality food on 15 territories dramatically decreased the amount of time that birds of each sex devoted to foraging, the main activity of control song sparrows during the same period (Fig. 6.2 & 6.3). Even so, fed birds outweighed

controls of their respective sex by 10-13% on average. Fed birds allocated slightly more time to self-maintenance (e.g. preening) and reproduction (e.g. nest building), but the most striking increase in each sex occurred for alert behavior. Alert birds perched prominently with feathers sleeked and wings erect and surveyed their surroundings. Chases of non-territorial intruders followed periods of alert behaviour significantly more often than periods of all other behaviours. Fed females spent even more time alert than control males ($P < 0.05$, U-test, Fig. 6.2 & 6.3). I conclude that, as predicted, birds responded to supplemental food by devoting a greater effort to preventing the settlement of additional local breeders.

Food Distribution, Territoriality and Mating System

Classical mating system theories posit female mate or territory choice as the principle mechanism determining mating patterns, while competition between females plays a minor role (Verner & Wilson 1966; Orians 1969; Bradbury & Vehrencamp 1977; Emlen & Oring 1977; Weatherhead & Robertson 1979; Wittenberger 1979; Murray 1984). Accordingly, floating females in this study should have settled preferentially on fed territories, assuming that they were able to sample territory quality, because reproductive success there was four times greater than on control territories (Arcese & Smith 1988). If one assumed no sampling by floaters, random settlement should have occurred.

However, female floaters showed a strong tendency to settle in areas where they subsequently reproduced poorly (Table 6.5). This strongly supports the hypothesis that intraspecific territoriality affects the maintenance of monogamy in song sparrows, and suggests that models that do not include the influence of female competition and spacing behaviour on mating systems can be rejected.

However, when female competition and individual variation in competitive ability are incorporated into current models of the organization of mating systems (Orlans 1969; Emlen & Oring 1977; Wittenberger 1979; Oring 1982, Murray 1984), several new predictions are generated (see Introduction). All of these are supported by this study. McLaren (1972) and Stobo & McLaren (1975) were the first to emphasize the importance of female spacing behaviour and the ability of males to defend territories in the maintenance of monogamy in birds. More recently, Davies (1985) and Davies & Houston (1986) have stressed that the nature and intensity of intrasexual competition in each sex determines mating patterns. They suggested in particular that a lack of consideration for female competition has hampered our understanding of mating systems. Although the evolution of monogamy as the predominant mating system of birds remains poorly understood, this study demonstrates how female resource defence plays a role in the maintenance of monogamy.

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CHAPTER 7. INTRASEXUAL COMPETITION, MATING SYSTEM AND NATAL DISPERSAL IN SONG SPARROWS

INTRODUCTION

Patterns of natal dispersal (i.e. distance from place of birth to first settlement; Howard 1960; Greenwood 1980) are linked to a wide range of other life history and demographic traits (Comins et al. 1980, Greenwood 1980; Murray 1984). Dispersal also influences population dynamics (Lidicker 1975; Krebs et al. 1976; Tamarin 1980), the genetic structure of populations (Wright 1977; Shields 1982) and the evolution of social behaviour (Hamilton 1964; Woolfenden & Fitzpatrick 1984; Brown 1987). For these reasons, dispersal is of intense interest to behaviourists and population and evolutionary ecologists (e.g. Gaines & McClenaghan 1980; Greenwood & Harvey 1982; Shields 1982; Dobson 1982; Waser & Jones 1983; Boonstra et al. 1987; Buechner 1987). In this chapter, I consider several correlates, causes and consequences of variation in dispersal behaviour in a resident and territorial population of song sparrows.

One area of particularly spirited debate is the cause of individual variation in dispersal behaviour (e.g. Moore & Ali 1984; Dobson & Jones 1985; Packer 1985; Waser 1985; Buechner 1987). Packer (1985) and Dobson & Jones (1985) have suggested that mate selection, relatedness and competition for resources

have too often been treated as mutually exclusive causes of dispersal. However, few bird or mammal species have been studied in sufficient detail to investigate the potential interplay of these factors. Moreover, competitive ability, sex, inheritance, the mating system, demography and resource availability are all implicated as either correlates, causes or consequences of dispersal (Krebs et al. 1976; Greenwood 1980; Dobson 1982). Few species are well-suited to a comprehensive study of these issues (e.g. Howard 1949; Myers & Krebs 1971; Greenwood et al. 1979a,b).

The song sparrows on Mandarte Island, B.C., offer a rare chance to study dispersal in particular detail. Nearly all birds that breed there hatch locally and are banded as nestlings. Individuals of known relatedness can thus be followed throughout their lives, and variation in dispersal can be related to individual characteristics, population demography, inbreeding and lifetime production of young. This allowed me to examine several assumptions and hypotheses about dispersal.

Here I describe: (1) patterns of natal dispersal in five cohorts of young, (2) relationships between dispersal distance and individual characteristics (i.e. sex, social dominance and age), probability of inbreeding, age of the acquired mate, and population density, (3) the effect of settling with a close relative on subsequent reproductive success and (4) the resemblance between siblings in dispersal distance. I also

present results from two experiments. First, I temporarily removed nearly all song sparrows from the closest island adjacent to Mandarte (Halibut Island, 1.3 km distant) in late summer to test if increasing the availability of unsaturated habitat near Mandarte caused an increase in the number of successful emigrants from Mandarte. Second, I conducted a feeding experiment throughout the breeding period in 1985 to test if dispersal is affected by the quality of the natal territory. Lastly, I compare my results with 5 previous studies of dispersal in song sparrows.

Hypotheses About Dispersal

The hypotheses, assumptions and predictions addressed in this study are summarized in Table 7.1 and discussed briefly below.

It is generally accepted that the mating systems of territorial species influence patterns of dispersal by males and females, and that these differences are linked to the amount of effort each sex spends competing for territories or mates versus, the effort spent in care of offspring and mate choice (Bradbury & Vehrencamp 1977; Greenwood 1980; Dobson 1982; Waser & Jones 1983). Greenwood (1980) and Greenwood & Harvey (1982) argued that female passerines often dispersed further than males because the cost of inbreeding outweighs the cost of dispersal in females, but not in males. They assumed that the cost of

Table 7.1. Hypotheses, predictions and assumptions about interactions between dispersal and inbreeding, competition for breeding resources and demography. Numbers in parentheses indicate the references listed below.

Class of Hypotheses	Specific Mechanism	Predictions/Assumptions
Mating System	Competition for mates (1-3)	1) Sex-bias depends on the effort expended by each sex in mate defence. 2) Distance related to mate quality (4). 3) Distance unaffected by food supplementation.
	Competition for environmental resources (1-3,5,6)	1) Sex-bias depends on the effort expended by each sex in resource defense. 2) Distance reduced when territory quality is enhanced by food supplementation.
	Intrasexual competition between parents	1) No sex bias in dispersal when the mating system is monogamy.

and offspring
(7)

2) Strong competition between parents and offspring over mates.

3) Dispersal depends on survival of parent of the same sex.

4) Food supplementation has no effect on dispersal.

Random
movement
models

Population
demography
(8-10)

1) Frequency of inbreeding decreases with distance dispersed.

2) Presence and direction of sex-bias depend on mortality rate of males and females.

3) Distance and time of settlement should be positively correlated.

4) Food supplementation affects dispersal only if it affects adult mortality.

5) Increasing open habitat increases dispersal.

Social
dominance

1) Subordinates disperse further than dominants.

	(11-12)	<p>2) Subordinates settle later than dominants.</p> <p>3) Sex-bias depends on sex-related differences in dominance.</p>
Inbreeding	Avoidance (13-18)	<p>1) Dispersal depends on survival of parent of the same sex.</p> <p>2) Reproduction strongly depressed by close inbreeding.</p> <p>3) Sex-bias depends on costs of dispersal in each sex, relative to the costs of inbreeding.</p> <p>4) Food supplementation does not affect dispersal.</p>
	Optimal outbreeding (19-20)	<p>1) Primarily short-distance dispersal.</p> <p>2) Reproduction strongly depressed by close inbreeding, enhanced by weak inbreeding.</p> <p>3) Food supplementation does not affect dispersal.</p>
Inheritance	Genetic tendency	<p>1) High familial similarity in distance dispersed.</p>

- (21-25)
- 2) Frequency of inbreeding decreases with distance dispersed.
 - 3) Bimodal distribution of dispersal distances.
 - 4) Food supplementation does not affect dispersal.

References: (1) Dobson 1982; (2) Greenwood & Harvey 1982; (3) Waser & Jones 1983; (4) Greenwood et al. 1979b; (5) Dobson 1980; (6) Krebs & DeLong 1965; (7) Lieberg & von Shantz 1985; (8) Murray 1967; (9) Waser 1985; (10) Buechner 1987; (11) Dhondt & Huble 1968; (12) Gauthreaux 1978; (13) Greenwood et al. 1978; (14) Packer 1979; (15) Koenig & Pitelka 1979; (16) Pusey 1980; (17) Hoogland 1982; (18) Woolfenden & Fitzpatrick 1984; (19) Shields 1982; (20) Bateson 1983; (21) Howard 1960; (22) Johnston 1961; (23) Myers & Krebs 1971; (24) Greenwood et al. 1979a; (25) Comins et al. 1980.

gaining a territory in males exceeds that for females, and that males that remain in their familiar, natal area are most likely to gain territories.

Among song sparrows on Mandarte, intra-sexual competition in both males and females strongly influences the pattern of matings (Smith et al. 1982; Chap. 3-6). Because territory establishment is highly competitive in females and males, and each sex defends its territory against members of the same sex, monogamy is the most frequent mating arrangement. For song sparrows on Mandarte Island, Greenwood's (1980) hypothesis therefore predicts that sex-biases in dispersal distance should be small or absent. Further, if dispersal is primarily the result of competition for good breeding sites, I predicted that supplementing areas with food would reduce dispersal distance approximately equally in each sex compared to controls.

Two related hypotheses based on the organization of the mating system make similar predictions to those of Greenwood (1980). Dobson (1982) emphasized competition for mates as opposed to territories. In song sparrows, however, this would be hard to test because these alternatives are difficult to distinguish (Smith et al. 1982; Chap. 6). Lieberg & von Schantz (1985) proposed a variation of Dobson and Greenwood's hypotheses that emphasize intrasexual competition between parents and offspring, and predicts that offspring dispersal should depend on survival and philopatry in the parent of the

same sex.

Several simulation models of dispersal based on competition for breeding sites, demography, and movement rules for dispersers predict that sex-biases in dispersal arise through differences in the mortality rates of territorial males and females (Murray 1967; Waser & Jones 1983; Waser 1985; Buechner 1987). I therefore expected dispersal to be related to differences in adult survival in song sparrows. For mathematical convenience, dispersers are typically modelled as moving in straight lines to the first empty territory encountered (Murray 1967), or searching in concentric rings around the natal site in their path outwards from it (Waser 1985). Such models predict positive correlations between distance dispersed and time of settlement.

Several models posit social dominance as the mechanism causing dispersal and settling conflicts over breeding resources (Dhondt & Huble 1968; Gauthreaux 1978; Waser 1985; De Laet 1985; Beuchner 1987). Three predictions of these models are tested here: (1) dispersal distance should increase as dominance decreases, (2) settlement should be delayed in subordinates, and (3) females should disperse further than males because they are usually subordinate to them during the non-breeding period (Smith 1982; Arcese & Smith 1985).

Inbreeding avoidance is a primary cause of dispersal in

some group-living species (Koenig & Pitelka 1979; Packer 1979; Pusey 1980; Hoogland 1982; Woolfenden & Fitzpatrick 1984; Pusey & Packer 1987). However, inbreeding can be either a rare or a regular event (Shields 1982), and it occurs even in species with sex-biased dispersal (Bulmer 1973; van Noordwijk & Scharloo 1981; Moore & Ali 1984; Rowley et al. 1986). Further, both theoretical and field studies show that inbreeding is not always deleterious (Richdale 1949; Bengtsson 1978; Smith 1979; van Noordwijk & Scharloo 1981; Shields 1982; Rowley et al. 1986, Temple 1986). On the contrary, Shields (1982) and Bateson (1983) have suggested that outbreeding could be deleterious if individuals possess heritable traits that are highly adapted to the local habitat. I test three predictions of these hypotheses: (1) close inbreeding (sib and parent-offspring matings; Shields 1982) depresses reproductive success, (2) close inbreeding is avoided either passively by sex-biases in dispersal, or actively by behaviours that inhibit the settlement or reproduction of young in their natal area when a parent is the likely mate (Koenig & Pitelka 1979; Holmes 1984; Cockburn et al. 1985; Pusey & Packer 1987), and (3) the relatedness of potential mates declines as the number of territories dispersed increases.

A final group of models characterizes dispersal as a genetically heritable trait that is maintained in populations in different degrees depending on opportunities to: 1) colonize vacant habitats; 2) increase the vigour of offspring by

outcrossing; or 3) avoid competition for crucial resources with close kin (Howard 1960; Johnston 1961; Greenwood et al. 1979a; Smith 1979; Comins et al. 1980; Gaines & McClenaghan 1980). These hypotheses predict that dispersal distances will be more similar within families than between them, and that these differences are not due to common environment (van Noordwijk 1984).

RESULTS

Dispersal Within Mandarte Island

Yearly variation in dispersal

There were some differences in the median distances moved by males and females between years (Fig. 7.1), but these were not statistically significant ($P > 0.10$ and $P > 0.50$, Kruskal-Wallis tests; males and females, respectively). When comparing distances in units of territories, however, there were significant differences among years in each sex ($P < 0.025$ and $P < 0.005$, K-W tests; males and females, respectively; Fig. 7.2).

These differences were positively related to population density in the year of hatch when dispersal was measured in territories traversed ($r = 0.76$ and $r = 0.85$, $N = 5$ years; males and females, respectively), but not when measured in meters ($r = -0.13$

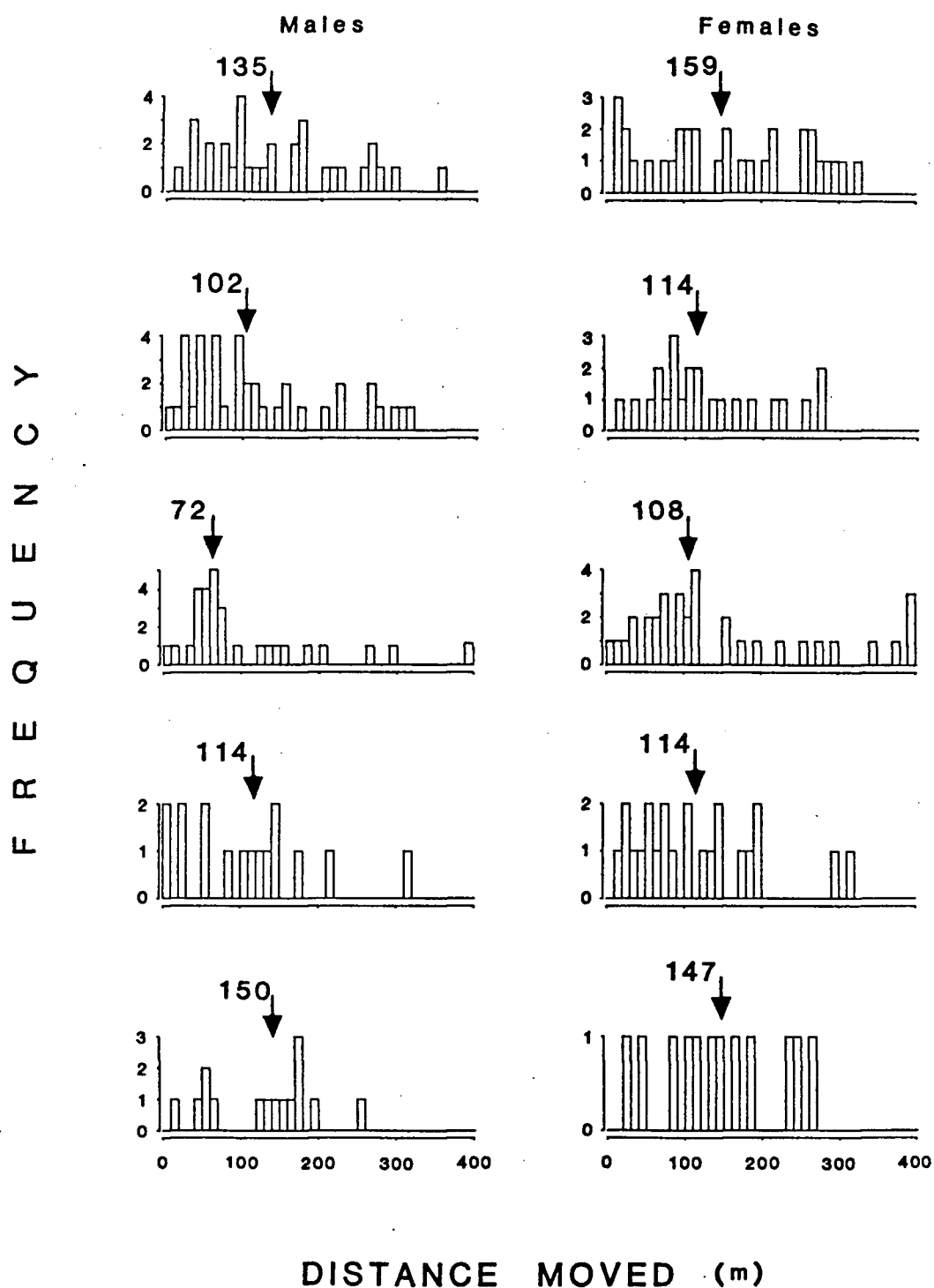


Figure 7.1. Natal distance dispersed in 5 cohorts hatched from 1982-6 (top to bottom). Arrows and numbers indicate median distances dispersed by each sex.

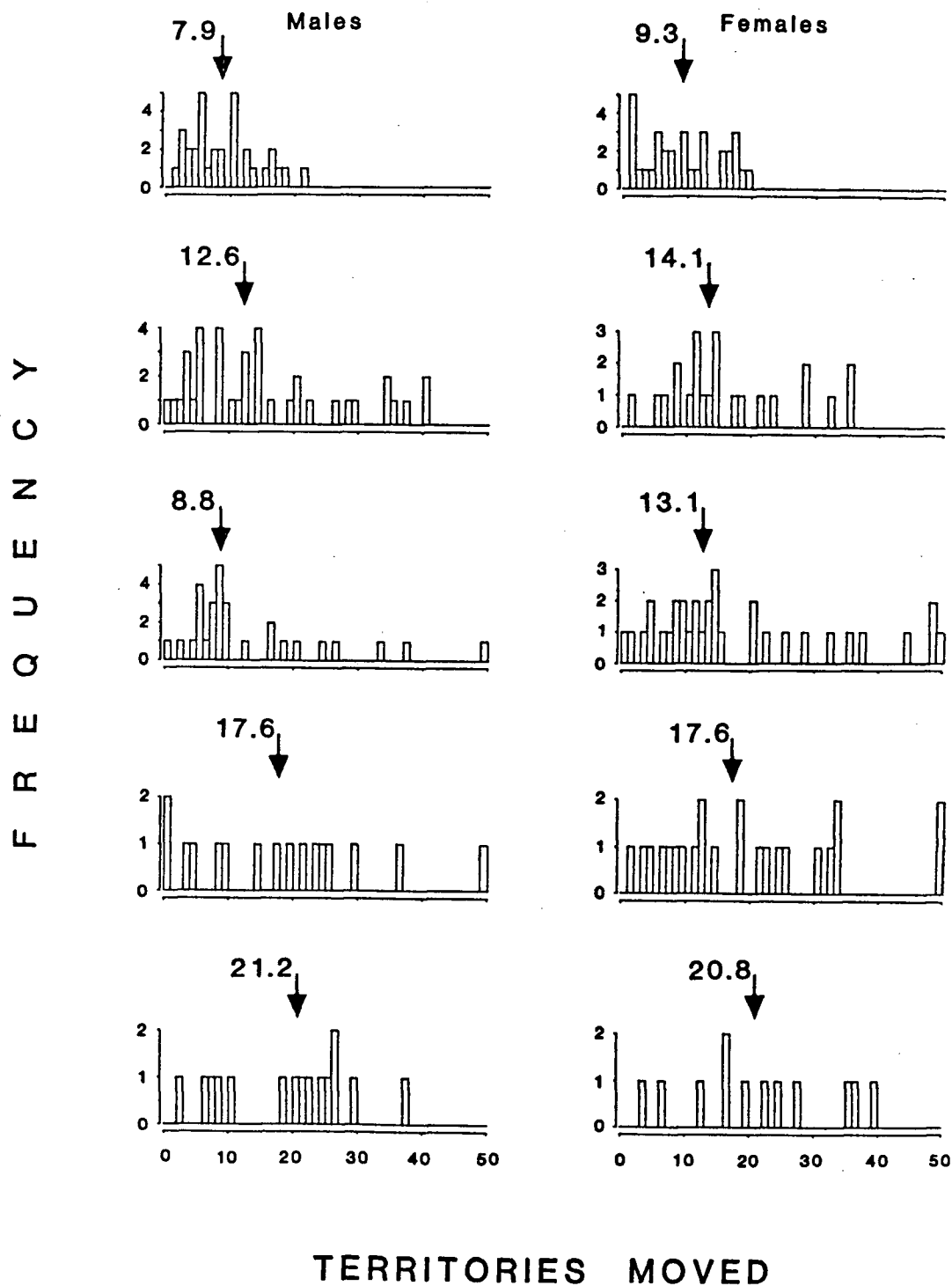


Figure 7.2. Natal distance dispersed in units of territories moved.

Conventions as for Figure 7.1.

and $r = -0.60$, as above). This was because birds of each sex dispersed approximately equal numbers of meters between years (Fig. 7.1), but territory size varied by roughly 3 times during the course of the study. Distances moved each year by males and females were positively correlated ($r = 0.84$ and $r = 0.97$, meters and territories, respectively).

Point of origin and distance dispersed

There were significant differences in the number of territories dispersed by young originating from different portions of the island in 2 years (Fig. 7.3; 1982 and 1984 cohorts, $P < 0.001$, K-W tests). The pattern was similar in 1985 and 1986 but not significant by the revised level of acceptance (i.e. $P < 0.01$). However, when the data for all years were pooled, point of origin and the number of territories dispersed were strongly linked ($P < 0.001$, K-W test). This was because birds hatched near the ends of the island had a larger set of distances over which to disperse than those hatched near the center.

Sex differences in dispersal

In 3 years the median dispersal distance by females slightly exceeded that for males, but in 2 years there was no difference (Fig. 7.1 & 7.2). There were no statistically significant differences in any year, or when the data for all 5

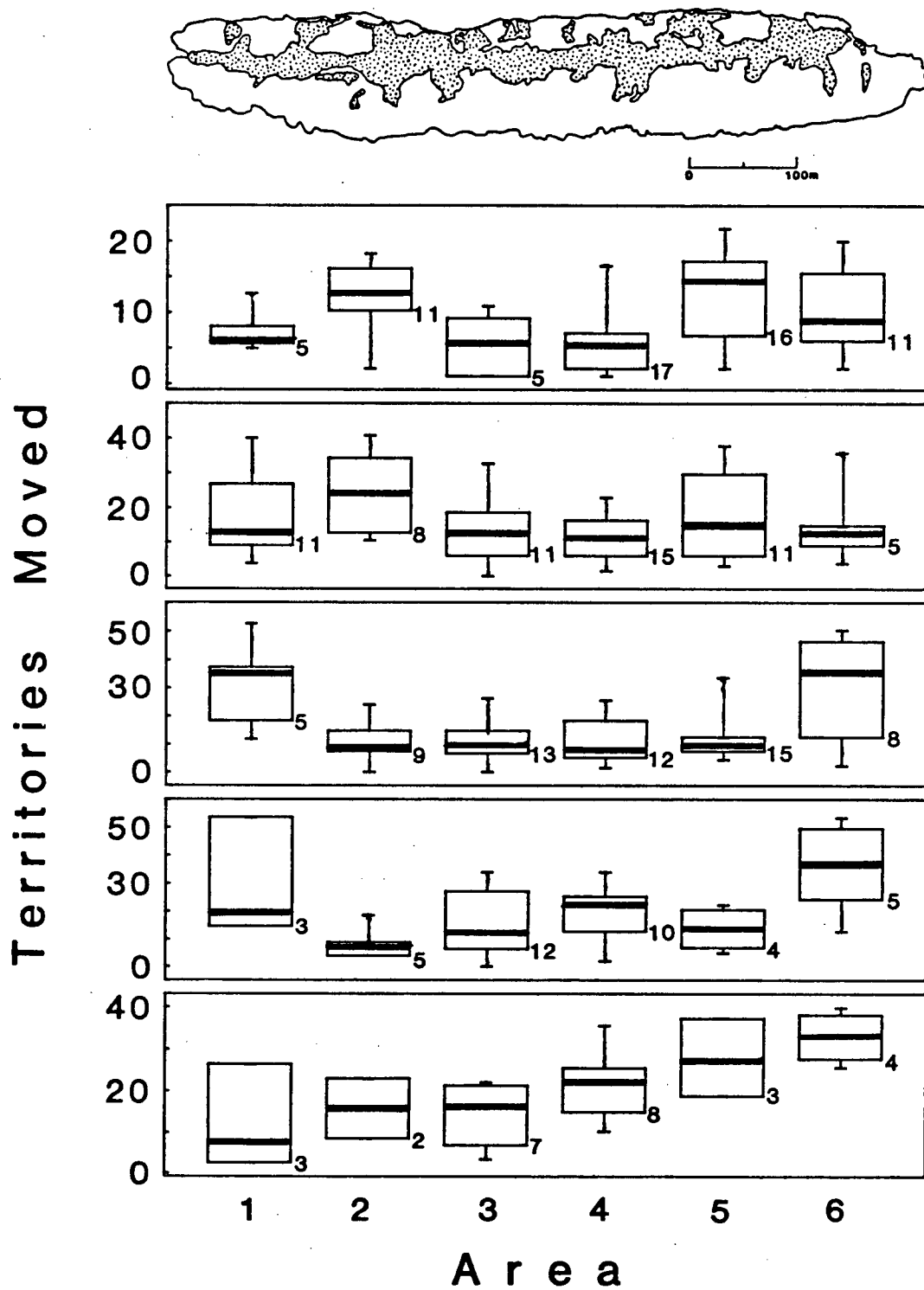


Figure 7.3. Median, inter-quartile range, and the range of the data for the distribution of dispersal distances in 5 cohorts of young hatched in different portions of the island, from 1982-6 (top to bottom).

years were pooled (all $P > 0.20$, Mann-Whitney U-tests).

Dominance, hatch date and distance moved

Dominance was not significantly related to dispersal distance in either sex in the 3 years that it was estimated (range $r = -0.26$ to $+0.40$, 4 positive and 2 negative coefficients, $N = 12-38$, all $P > 0.05$). Similar results were obtained in weighted analyses. Hatch date is highly correlated with dominance (Arcese & Smith 1985), but was unrelated to distance dispersed in all 5 cohorts (range $r = -0.32$ to $+0.28$, 6 positive and 4 negative coefficients, $N = 26-65$, all $P > 0.05$).

To control for the influence of point of origin, I repeated the above analysis on date of hatch using only birds hatched in portions of the island that allowed similar opportunities for dispersal (i.e. Fig. 7.3, areas 1 & 6, 2 & 5, 3 & 4; sexes pooled). However, none of 15 correlations were statistically significant (range $r = -0.75$ to $+0.55$, 10 positive and 5 negative coefficients, $N = 7-27$, all $P > 0.05$).

Dominance, hatch date and settlement time on Mandarte

Dominance was related to the probability of settlement on Mandarte in males and females during the first two years of this study (Arcese & Smith 1985). Table 7.2 shows that dominant males and females in the 1984 cohort were also more likely to

settle by the end of April the following year than were subordinates of the same sex ($G = 5.04$ and $G = 6.80$, males and females, respectively; $df=1$, $P < 0.025$ in each case).

In males, hatch date was also related to territorial status in the following spring (Fig. 7.4a). No females from the 1982 and 1983 cohorts behaved as floaters, but a few females did so in the springs of 1985 and 1986 when densities were particularly high (Chap. 1, Fig. 1.1). Figure 7.4b shows that hatch date was related to the territorial status of females in late April when the 1982-5 cohorts were pooled.

In males, where I was able to estimate the date of settlement in 4 cohorts (1982-85), birds hatched earlier in the year often settled earlier (Fig. 7.5). However, the effect of hatch date on settlement date was strong only among the 18 males that settled before 1 January of the year following hatching. Seventeen of these males were also hatched before the mean hatch date of their cohort, compared to the 10.3 and 7.7 males expected to have settled before and after the new year by the distribution of hatch dates ($G = 12.23$, $df=1$, $P < 0.001$). I found no relationship between distance moved and time spent as a disperser ($r = -0.12$, $N = 103$, $P > 0.05$). Of males that eventually settled on Mandarte from the 1982-4 cohorts, those of higher status often settled earlier than more subordinate males. However, this result was statistically significant only in a weighted analysis of the pooled data ($P < 0.01$, $r = -0.42$, $N = 94$).

Table 7.2. Territorial status at the end of April, 1985 in relation to the dominance of yearlings hatched the previous year.

Sex	Dominance status	Territorial Status		
		Owner	Floater	Absent
Male	Dominant	9	4	5
	Subordinate	6	12	14
Female	Dominant	15	0	2
	Subordinate	19	2	15

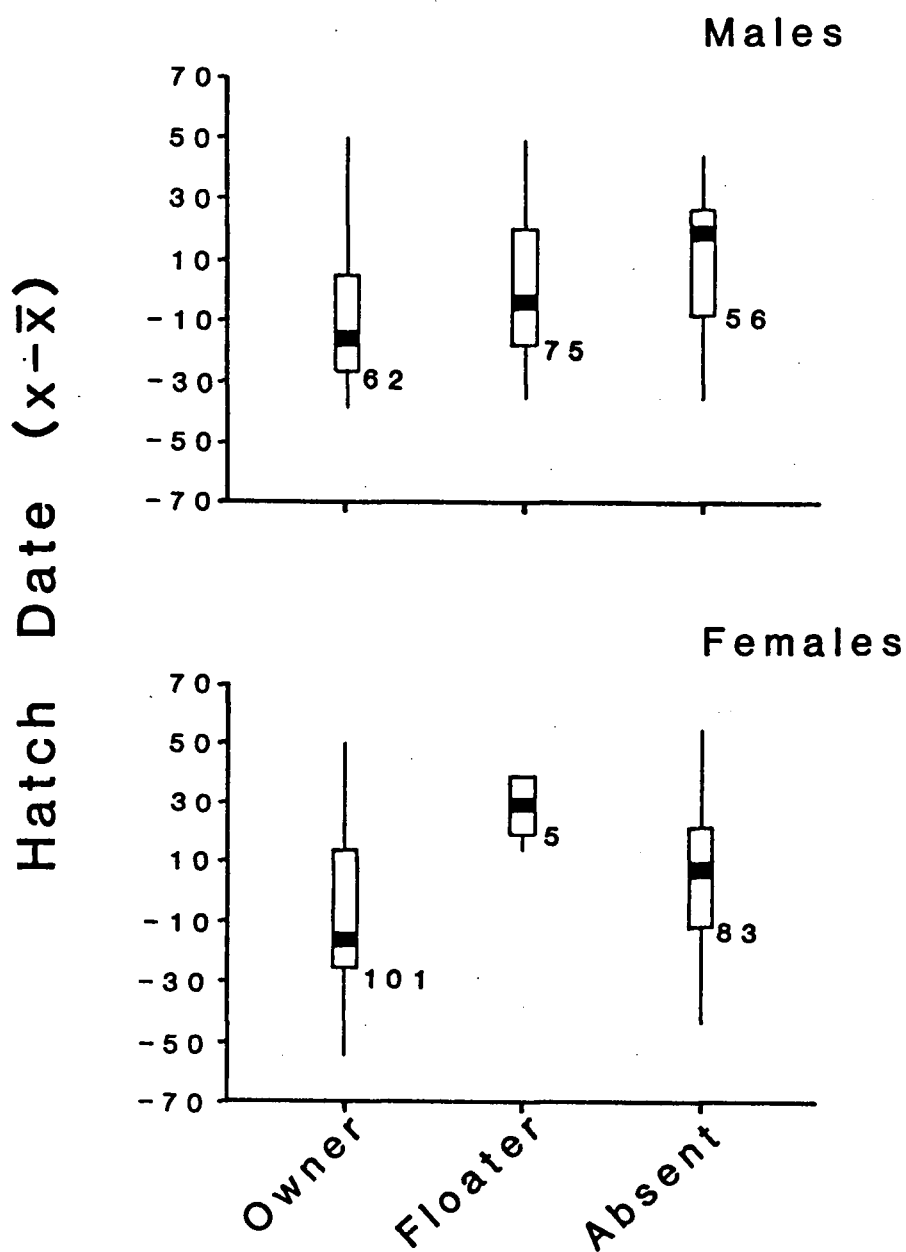


Figure 7.4: Territorial status of males and females at the end of April in the year following hatch versus date hatched the previous year (median, inter-quartile range, and the range of the data). Data are from the 1982-5 cohorts. Numbers indicate sample size.

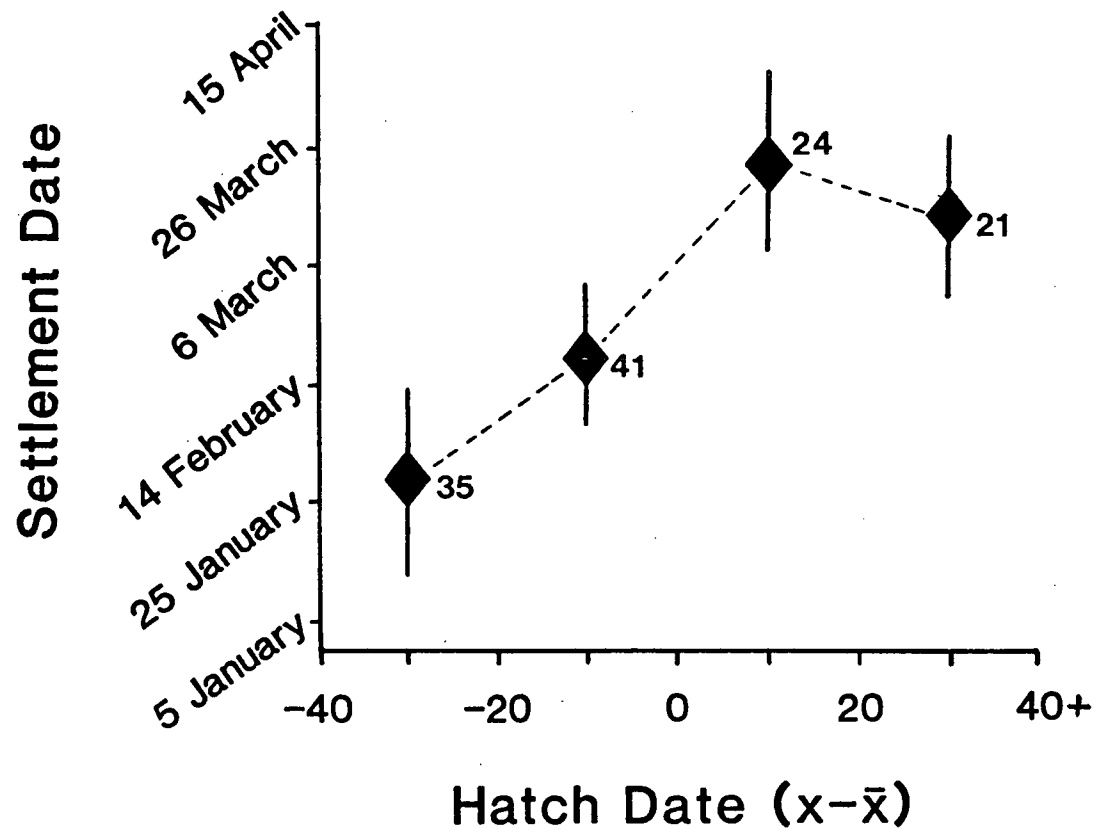


Figure 7.5. Settlement date of male recruits (mean \pm SE) in relation to four categories of date of hatch ($F_{3,117}=2.83$, $P<0.05$). Numbers indicate the number of male settlers.

Sibling resemblance in dispersal

I found no evidence of sibling resemblance in dispersal distance when the young that were compared had been hatched in portions of the island that allowed similar opportunities for dispersal (Table 7.3). When families from the entire island were compared, significant differences between families occurred because the points of origin were not controlled for ($P < 0.01$, 1982 and 1984, $P < 0.05$, 1985 and 1986; K-W tests).

Age of the acquired mate

For both male and female disperser's, the age of the dispersers first mate was unrelated to the distance moved ($G = 2.11$ and $G = 1.03$, males and females, respectively, $df = 6$, $P > 0.50$). This result was obtained by pooling yearly data into three distance categories and comparing distance moved with the age of the acquired mate (after Greenwood et al. 1979).

Inheritance of natal territories

Only 4 males and 1 female settled on their natal territory (Fig. 7.2), even though adult mortality rates overwinter (27-43%) would have allowed substantially higher rates of philopatry without inbreeding as a consequence. In males, 3 natal settlements took place after floater sons evicted their fathers.

Table 7.3. Results of Kruskal-Wallis ANOVA's on differences between families in dispersal from end, intermediate and middle portions of the island. Low recruitment from the 1985 and 1986 cohorts prevented useful comparisons. No result was statistically significant (all $P > 0.10$).

Cohort	Area	Families	Young	H	DF
1982	End	5	15	4.45	4
	Intermediate	7	21	7.41	6
	Middle	5	19	1.65	4
1983	End	4	10	1.23	3
	Intermediate	6	17	2.52	5
	Middle	9	20	3.30	8
1984	End	4	11	2.49	3
	Intermediate	7	17	9.92	6
	Middle	6	20	4.68	5

I do not know by what method the lone female settled on her natal territory. However, 3 of these 5 settlers (1 female, 2 males) subsequently mated with a parent, and two of the males evicted their fathers to do so.

Mortality, recruitment and sex-biases in dispersal

Yearly differences in dispersal bore no clear relation to the proportion of adults surviving from the previous year (Table 7.4, Fig. 7.1 & 7.2). Differences between adult male and female survival, as well as differences in sex-specific recruitment rates, were also unrelated to the direction or presence of a sex-bias (Table 7.4, Fig.s 7.1 & 7.2).

Distance and reproductive success

The total production of independent young per bird (i.e. a truncated estimate of lifetime reproductive success) was unrelated to dispersal distance in all 5 cohorts ($r = -0.20$ to $+0.12$, 3 negative and 2 positive correlations, $N = 27-57$, all $P > 0.05$).

Inbreeding, Dispersal, Density and Reproduction

Of a total 178 birds of known pedigree settling with their first mate, 8 (4.5%) settled with a closely related mate, 19 (11%) with a moderately related mate and 151 (84.5%) with

Table 7.4. Number of territorial adults at the end of April each year, their survival over winter, and the rate of recruitment the next year of independent young to the breeding population.

Year	Numbers		Survival		Recruitment of Young	
	Males	Females	Males	Females	Males	Females
1982	35	26	0.86	0.81	0.50	0.57
1983	59	54	0.68	0.56	0.23	0.23
1984	64	53	0.77	0.89	0.43	0.39
1985	78	72	0.72	0.58	0.15	0.35
1986	67	63	0.73	0.73	0.40	0.32

unrelated mates. However, the number of territories moved was unrelated to the probability of settling with a relative ($G = 0.51$, $df=2$, $P>0.90$; Table 7.5).

The proportion of young that settled with relatives declined as population density increased (Fig. 7.6). However, the number of independent young raised by individuals during the study was independent of the relatedness of their first mate (Table 7.6), possibly because most birds changed mates regularly as birds died or were evicted from their territories (Chap. 3-5).

Effect of supplemental food

The distance moved by late August 1985 by young provisioned with supplemental food was much less than that moved by control young (median number of territories moved: 1.7 versus 10.7 for 34 fed and 18 control young; $P<0.001$, U-test). This early difference was maintained the following year in those young that gained territories (Fig. 7.7). Fed males and females each settled closer to their natal territory than did controls (median number of territories moved: 4.4 versus 22.3 for 6 fed and 10 control males and 11.2 versus 24.3 for 12 fed and 11 control females; both $P<0.03$, U-tests). However, there were no significant differences in the distances dispersed by males and females within treatments ($P>0.20$, U-tests).

Table 7.5. Relationship between the number of territories moved and the probability of settling with a close relative.

Cohort	Greater/less than median number	Relatedness of Mate		
		Close	Moderate	Outbred
1982	≥	0	3	11
	<	2	4	7
1983	≥	2	2	18
	<	2	2	20
1984	≥	1	1	22
	<	1	1	22
1985	≥	0	1	14
	<	0	1	17
1986	≥	0	3	9
	<	0	1	11
Total	≥	3	10	74
	<	5	9	77

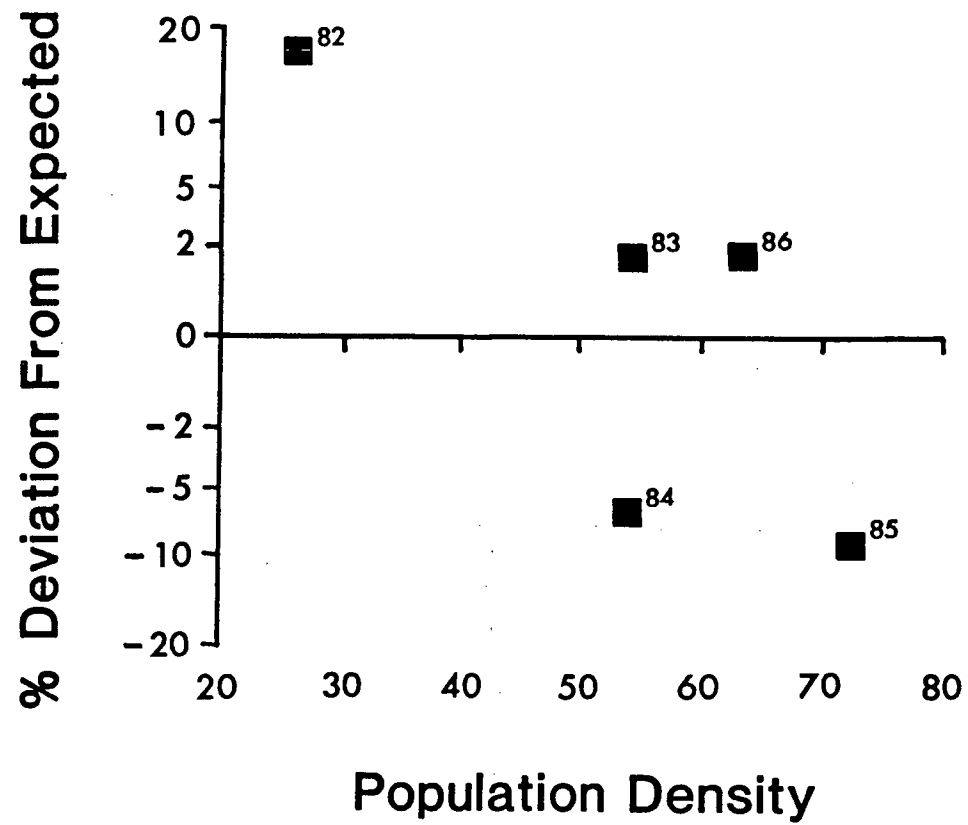


Figure 7.6. Percent deviation from the expected rate of inbreeding based on the pooled results of the probability of settling with a close relative.

Table 7.6. Total production of independent young versus the relatedness of the first mate in 5 cohorts of dispersers with known lineages (mean \pm SE).

Cohort	Relatedness		
	Close	Moderate	Outbred
1982	5.50 \pm 3.50	4.83 \pm 1.97	3.00 \pm 0.87
N	2	6	18
1983	2.75 \pm 0.25	6.75 \pm 2.72	3.94 \pm 0.58
N	4	4	31
1984	0.50 \pm 0.50	1.50 \pm 0.50	2.78 \pm 0.37
N	2	2	36
1985	-	3.00 \pm 1.00	1.77 \pm 0.32
N	-	2	31
1986	-	0.75 \pm 0.25	1.50 \pm 0.25
N	-	4	20
Pooled	-0.18 \pm 0.24	0.23 \pm 0.27	0.13 \pm 0.09
N	8	18	136

The difference between fed and control young could have resulted partly because most control territories were located nearer the ends of the island than were fed territories. However, the stipled area of Figure 7.7 shows that differences in dispersal distance due to food addition were maintained when only young hatched in the same portions of the island were compared (medians for sexes pooled: 13 versus 26 territories for 13 fed and 9 control young; $P < 0.03$, U-test). A further, unexpected result of food addition was a reduction in the survival of adults on fed territories (Arcese & Smith 1988). During the winter following the food experiment, significantly more fed than control adults were also observed as floaters, presumably because they had been evicted by yearlings that concentrated in territories previously supplied with food (Arcese & Smith 1988). Additional effects of food supplementation are described in Arcese & Smith (1988).

Dispersal Between Populations

Emigration

Four male and 3 female yearlings were sighted or captured on islands other than Mandarte during the first 3 years of this study, when occasional visits were made to most neighbouring islands, and regular visits were made to Halibut Island (1-3 visits each spring and fall). Six of these birds were observed on Halibut Is. and 1 male visited a feeder on Vancouver Is.

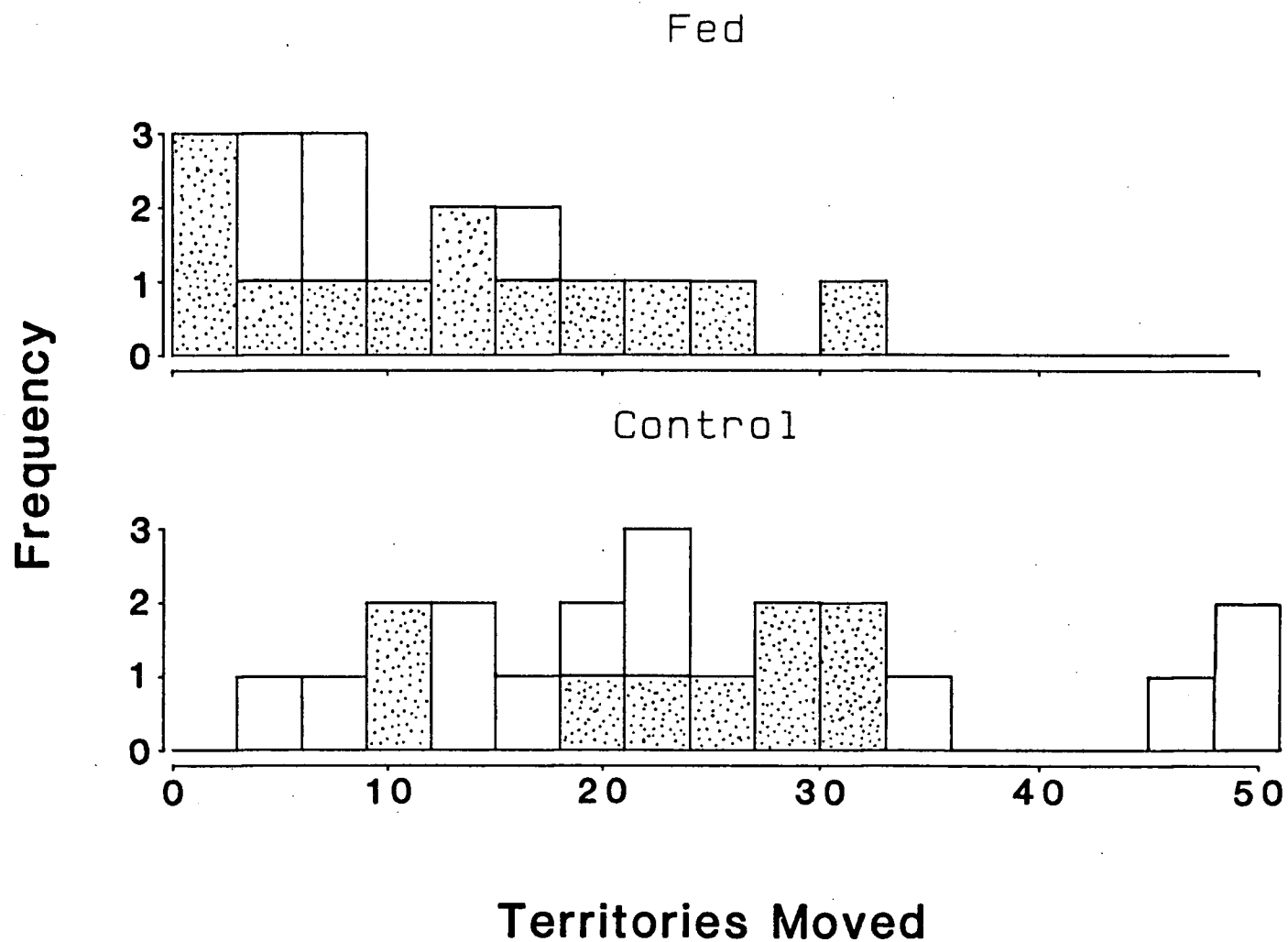


Figure 7.7. Dispersal distance of fed and control young from the entire island (all bars), and only those young hatched in the central portion of the island (areas 3,4; Fig. 7.3; stippled bars).

(Oak Bay), about 25 km distant. All 7 birds were subordinates within their sex (of a possible 186). In comparison, none of 121 dominants were observed off Mandarte ($P=0.028$, 1-tailed Fisher's exact test). No dispersing males were known to have settled elsewhere, but one returned from Halibut to Mandarte and became territorial. Two female dispersers settled and bred on Halibut Is., and at least one of these raised independent young. The third female returned to Mandarte and bred successfully for 4 years.

Immigration

Young dispersers arriving on Mandarte in late summer were common each year, but only one such male successfully settled and bred (in 1986). In contrast, an immigrant female settled and subsequently bred on Mandarte in 1982 and 1984, and 2 females did so in 1985. Four of these immigrants (3 females, 1 male) produced recruits that themselves bred on Mandarte. Population density was unrelated to the proportion of recruits that were immigrants ($r=0.23$, $N=5$ yrs).

Halibut Island removal experiment

From 28 August to 7 September, 1984, 20 song sparrows were netted and removed from Halibut island. Tompa (1963) estimated the total number of pairs on Halibut at 9-11 from 1961-1963. This accords well with my observations, and suggests that the

removals dramatically reduced the number of residents and opened a large amount of undefended habitat to potential settlers. Captured birds were released on the mainland (ca. 45 km distant), but by 15 October 3 banded residents returned to Halibut. No subsequent returns were observed.

In 5 days of netting and observing the song sparrows on Halibut, and in monthly subsequent visits through March, only 3 male song sparrows from Mandarte were sighted on Halibut. One of these returned to Mandarte and gained a territory in late February. A second male floated on Halibut and occasionally visited Mandarte until disappearing in December. One female that was resident on Mandarte as a floater until mid-February later settled successfully on Halibut. Thus, 4 dispersers in total were observed on Halibut subsequent to the removal of residents. This compares with four birds observed in slightly fewer total visits to Halibut from May 1981 to August 1984. This suggests that successful settlement by dispersers from Mandarte is unaffected by the amount of habitat available on Halibut Is.

Seasonal patterns of disappearance

For each of 5 cohorts there were usually two main periods of disappearance of juveniles from the population (Fig. 7.8). The largest and most similar number of disappearances across years occurred from late June, after the majority of young had

reached independence, through late September, during the peak period of fall territorial behaviour. A smaller, more variable period of disappearance usually coincided with the resurgence of intense territorial activity from mid-January through April each year (Tompa 1963; Chapters 3 & 4). However, in 1985-6 most birds disappeared in November and December. With the exception of 1985-6, major periods of disappearance did not coincide with snow, when seeds, the main winter food, might have been difficult to reach. Late winter and spring disappearances were, however, often coincident with known occurrences of predation by the hawks, owls and falcons that were regularly sighted on the island throughout the winter each year.

DISCUSSION

The song sparrow is an archetypal monogamous and territorial passerine (Nice 1943, Johnston 1956a,b; Tompa 1963; Smith 1988). One might therefore have expected to observe primarily males defending territories, females choosing among mates or breeding sites, and consequently female-biased natal dispersal (Greenwood 1980, 1983; Greenwood & Harvey 1982). I found, however, that natal dispersal in song sparrows differed from this expectation in several important ways (Table 7.1). First, I found no sex-bias in dispersal. Second, young of each sex dispersed less far when raised on territories supplemented with food. Third, dominance was associated with the time and probability of settlement on Mandarte, and with the probability

Frequency

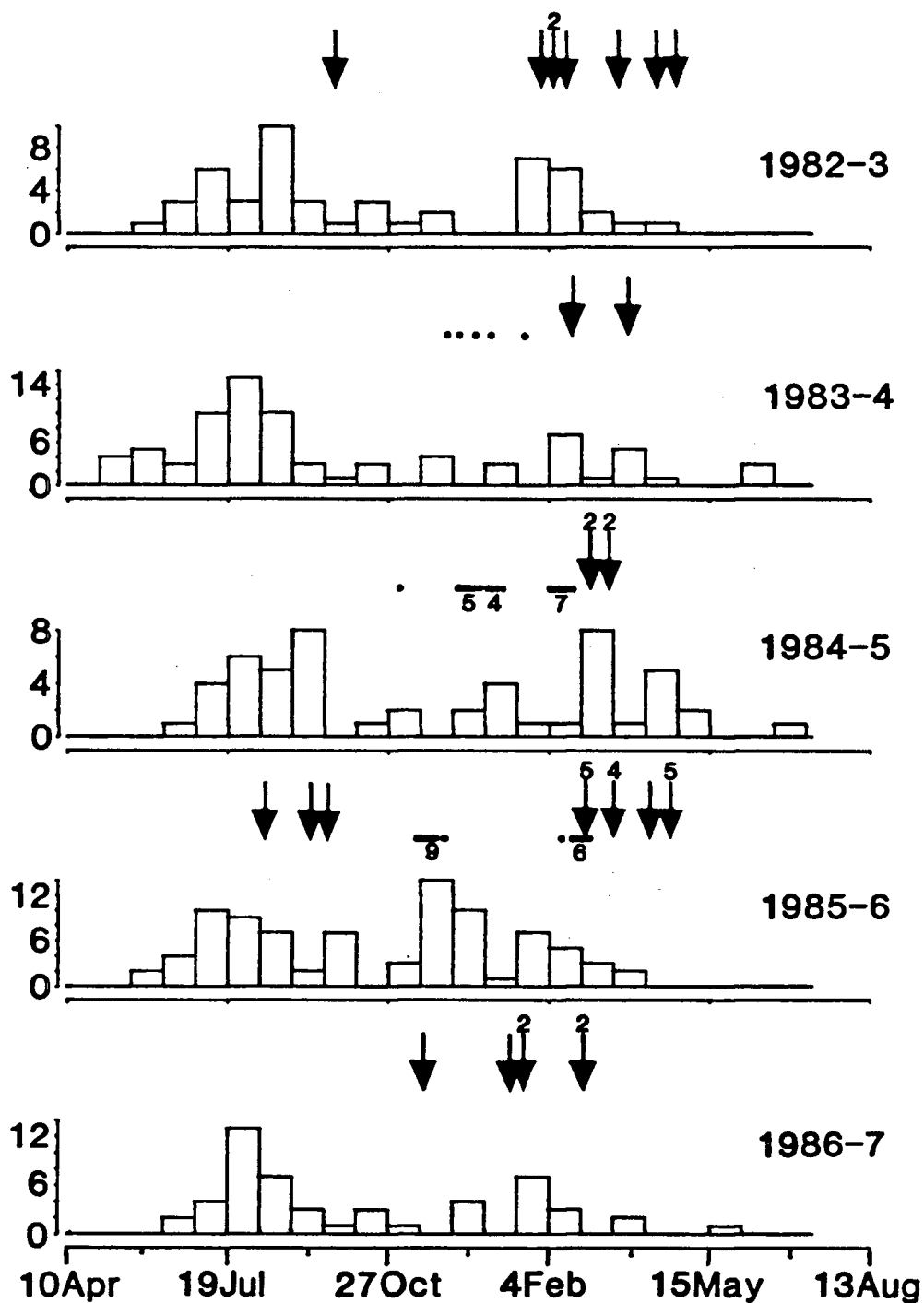


Figure 7.8. Number of yearlings last seen during a given period versus season for 5 cohorts. Arrows indicate incidences of predation, dots indicate days when snow fell, and numbers indicate consecutive incidences of predation or days of snow.

of emigration. Fourth, dispersal distance was strongly affected by point of origin on the island, but not by common parentage. Finally, the probability of settling with a relative was independent of the number of territories moved, and settling with a relative had no effect on reproductive success.

These results suggest that competition for high quality breeding territories plays a major role in natal dispersal in this population, but that genetical factors (e.g. inbreeding, inheritance) do not. In the discussion that follows, I discuss the measurement of dispersal, interpret and summarize my results with respect to the hypotheses listed in Table 7.1, and draw comparisons from previous studies of dispersal in the song sparrow (Table 7.7).

Measures of Dispersal

Greenwood & Harvey (1982), Shields (1982) and others have suggested that it is more biologically meaningful to describe dispersal in terms of the number of territories traversed than in meters for two reasons. First, they assume that the relatedness of potential mates declines as distance from the natal site increases. Thus, the number of territories (or home ranges) traversed implies a closer estimate of the degree of inbreeding avoidance than does the number of meters. Second, estimating dispersal in units of territories facilitates comparisons between species with different patterns of

Table 7.7 Studies of natal dispersal in the song sparrow.

Study	Location	Habitat Type	Density (prs/ha)	Territory Size (m ²)	Median Distance Moved (m)			Territories ¹		Site ² Fidelity
					Males	Females	Pooled	Traversed	N	
Nice 1937	Interpoint, OH	Urban, riverine scrub	2-3	3300-5600	280	270	275	5	34	High
Johnston 1956	San Francisco Bay, CA	Tidal marsh and bordering scrub	20-26	380-500	-	-	185	11	34	High
Tompa 1963	Mandarte Is., BC	Protected sea island scrub	31-49	200-290	200-240	150-200	ca.200 ³	16	120	High
Halliburton & Mewaldt 1976	Point Reyes, CA	Northern coastal scrub	ca. 1	ca. 10000 ⁴	-	-	225	3	36	High
Weatherhead & Boak 1986	Queen's Univ. Biol. St., ON	Northern lakeshore, old-field, gardens	ca. 5	ca. 2000 ⁵	?	?	?	5 ⁶	1	Low
This study	Mandarte Is., BC	Protected sea island scrub	18-51	200-450	75-150	108-159	114	8	253	High

1) Approximate number of territories traversed, estimated from the diameters of circular territories of average size.

2) Fidelity to the natal site as estimated qualitatively by the authors. 3) Estimated from Tompa (1963:61).

4) Estimated as 'home range size' from Baker & Mewaldt (1979). 5) Estimated average, but density varied greatly with habitat structure (Weatherhead, personal communication). 6) Only one male out of 176 banded young returned to the study site.

dispersion (e.g. dense colonial versus dispersed territorial).

However, measuring distance as territory units also raises some practical problems. First, relatedness was independent of the number of territories traversed in this study (Table 7.5). This has yet to be tested in other populations, but it could apply generally because dispersal distances in song sparrows are typical of several bird and mammal species (Shields 1982). This suggests that the degree of inbreeding avoidance may be a step-function, rather than a linear function of distance dispersed. If so, substantial inbreeding avoidance may only occur when individuals disperse beyond the bounds of local populations, or when kin recognition facilitates mate selection (e.g. Koenig & Pitelka 1979; Holmes 1984).

Second, modelling territories as units of area that are traversed completely or not at all, implies that dispersers only settle in vacant sites (e.g. Murray 1967; Waser 1985). In song sparrows and a variety of other species, dispersers create their own sites of settlement by deposing owners, splitting empty territories and inserting themselves within defended areas (Knapton & Krebs 1974; Ueda 1986; Freed 1987; Picman 1987; Chap. 3 & 4). In growing populations, this will result in shorter dispersal distances than expected if territories always remained intact.

Finally, field measurements of the number of territories

dispersed may be impractical when dispersers traverse fragmented habitats that vary in density (e.g. Newton & Marquiss 1983). Thus, although viewing dispersal in units of territories facilitates inter-specific comparisons, it probably oversimplifies the relationship between dispersal and territory establishment, and between dispersal and inbreeding, and may be difficult to achieve in the field.

Population Density and Dispersal

Greenwood et al. (1979a) compared density in the year of first breeding to dispersal, but neglected that, other effects being equal, density in subsequent years is a function of distance dispersed and rate of recruitment by young hatched the previous year. When measured in this way, density and dispersal are not independent. Further, using territories or meters as measures of distance gave different results in their study and in mine. This points to problems of interpretation when the mechanisms of dispersal, and the ways in which dispersers perceive distance, are not well-understood.

For example, I found that young moved similar numbers of meters each year, but that this amounted to an increasing number of territories as density increased and territories were compressed (Fig. 7.1 & 7.2). Between populations, song sparrows tended to move longer distances in less dense populations, but fewer territory diameters (Table 7.7).

Measured in meters, my results suggest that dispersal was unaffected by density, but the comparative results suggest a negative relationship between distance in meters and density (Table 7.7). However, under the assumption that distance is best measured in territory units, opposite conclusions are suggested. Newton & Marquiss (1983) also found no relationship between density and meters dispersed, but did not convert to territory equivalents for some of the reasons summarized here.

The problem of choosing the appropriate units in which to measure dispersal arises because explanations of dispersal distance are possible at different levels, and because distance in territory units depends on population density, the same variable to which it is being compared. On average, dispersers must travel further in meters in highly dispersed populations, but this might amount to a similar number of territories (e.g. Shields 1982). In contrast, for a given population dispersion, dispersal distance might be expected to increase with density if competition causes dispersal (e.g. Greenwood et al. 1979a). Within populations, territory units might therefore be considered an appropriate measure of dispersal if competitor density were well-represented by the density of territory holders. However, because the diameter of a territory unit depends on density (Greenwood et al. 1979a; Shields 1982), dispersal is no longer independent of the variable to which it is being compared. Van Noordwijk (1984) discusses how this interdependence of dispersal and population density could affect

estimates of heritability in dispersal distance when parents and offspring share common environments with respect to density. While it is intuitively reasonable that dispersers would travel further at high density (Greenwood et al. 1979a), I suggest that converting distance to territories for within species comparisons presupposes that the mechanisms underlying dispersal, and the ways in which dispersers perceive distance, are well-understood. This is not yet true for birds.

Inheritance and Point of Origin

Within a given area, distance dispersed depends on the range of distances between all possible natal and breeding sites (van Noordwijk 1984). Thus, young hatched nearer the ends of Mandarte Island had a larger set of potential dispersal distances than those nearer the center, and this resulted in point of origin having a strong effect on dispersal distance (Fig. 7.3). Van Noordwijk (1984) showed how this effect caused Greenwood et al. (1979a) to erroneously conclude that dispersal in the great tit was highly heritable.

I avoided this problem by comparing only among broods hatched in portions of the island that allowed similar opportunities for dispersal. Analysed in this way, siblings were not more similar in distances dispersed than were non-sibs (Table 7.3), suggesting that dispersal was not strongly affected by inheritance. Keppie (1980) found a high similarity in

distance dispersed among sibling spruce grouse (Canachites canadensis), but did not rule out point of origin as the cause of this resemblance. Newton & Marquiss (1983) reported a high mother-offspring resemblance in dispersing sparrowhawks, but this is expected since distance also depended on natal habitat (i.e. 'upland' versus 'lowland': Newton & Marquiss (1983); see van Noordwijk (1984) for a summary of problems in parent-offspring comparisons of dispersal). There is considerable genetic evidence from small mammals to indicate differences between dispersers and residents (Myers & Krebs 1971; Krebs et al. 1976; Gaines & McClenaghan 1980). However, evidence from birds remains indirect and consistent with the hypothesis that common environment rather than inheritance accounts for similarities in dispersal among siblings and parents and offspring.

Sex, Dominance, Distance and Settlement Time

Nice (1937) and Tompa (1963) each reported median dispersal distances for males that only slightly exceeded those for females (Table 7.7). These findings are supported by this study (Fig. 7.1 & 7.2). The lack of a large sex-bias in dispersal is contrary to the much more prevalent pattern of female-biased natal dispersal in birds (Greenwood 1980; note, however, that Greenwood cites Nice (1937) incorrectly).

Distance dispersed on Mandarte was also unrelated to

dominance within or between sexes. However, subordinate birds of each sex settled later than dominants and emigrated from Mandarte more often. This illustrates an unresolved problem concerning my study area. Subordinates that disappeared from the population may have died or emigrated. However, because known emigrants from Mandarte were subordinates, it seems likely that had the distances of all emigrants (seen and unseen) been included, dominance and dispersal distance would have been negatively related. Only a portion of all independent young recruited to the population (ca. 23-54%, Table 7.4), most of which were dominant birds (Arcese & Smith 1985; Table 7.2). Thus, dominance probably had a larger influence on dispersal distance than I was able to measure among recruits.

It is interesting that even among recruits, settlement time was retarded in subordinates and young hatched late in the season, but was unrelated to distance dispersed. I suggest that this occurred because year-round territoriality by each sex results in queues for ownership that are ordered by social status. Non-territorial floaters in these queues occupy home ranges that encompass 1-10 or more territories (Chap. 4). Floaters become owners when an owner dies or when they successfully challenge for ownership by inserting into established territories or deposing vulnerable owners (Chap. 3 & 4). Evidence of queues for territory ownership comes from a variety of other birds (e.g. Orians 1961; Smith 1978, 1987; Jamieson 1983; Jamieson & Zwickel 1983; Beletsky & Orians

1987a,b; Eden 1987a,b), and these territorial systems are generally viewed as a step towards the evolution of the retention of young, helping behaviour and cooperative breeding (Emlen & Vehrencamp 1983; Woolfenden & Fitzpatrick 1984; Brown 1987). An interesting question remains, however, in how dispersal distance relates to the establishment of home ranges in the non-territorial phase of life.

Effect of Supplemental Food

Adding food to territories throughout the breeding period resulted in reduced dispersal of fed juveniles as compared to controls in late August, even though food was not supplied after the end of July. This suggests that young had either established home ranges by late July, or were using previous experience as a cue for choosing areas in which to localize. Because large differences between fed and control young were maintained the following spring among recruits, food availability on the natal territory appears to be an extremely important factor affecting dispersal distance.

Dispersal, Mate Quality and Reproductive Success

Greenwood et al. (1979b) suggested that male great tits dispersed further when doing so allowed them to mate with adult rather than yearling females. In song sparrows, reproductive success peaks in middle-age (2-3 yrs, Nol & Smith 1987), but I

found that male and female dispersers mated with different-aged birds independently of distance moved. Dispersal distance was also unrelated to subsequent reproductive success, suggesting that remaining close to the natal site was of little consequence as long as a breeding position was secured. However, remaining close to the natal site might confer an advantage primarily by affecting the chances of settling rather than by affecting reproductive success subsequent to settlement. To test this, future studies should measure the probability of recruitment as distance from the natal site increases.

Factors Associated with Inbreeding

Song Sparrows regularly settled with relatives regardless of distance dispersed (Table 7.5). This might be expected given the small and semi-isolated nature of the population. However, dispersal is also highly restricted in some other song sparrow populations (Table 7.7; Shields 1982), and this may have contributed to considerable geographic divergence in morphology, coloration and blood group frequencies (Miller 1947; Marshall 1948a,b; Ferrell 1966; Aldrich 1984).

The frequency of inbred matings declined as population size increased (Fig. 7.6). This is expected by chance, and the peculiar demography of this population. First, the probability of settling with close relatives declines as population size increases when mating is random (Bulmer 1973; Falconer 1981).

Second, because the mean number of young raised declined from over 4 to less than 1 as density increased from 26-72 females (Arcese & Smith 1988), the probability of sib-matings declined faster than expected by population size alone. This suggests a unique prediction of the hypothesis that sex-biased dispersal evolved as a mechanism to avoid inbreeding: sex-biases should be most pronounced in species where the number of young raised each year, and thus the probability of sib-matings in the absence of a sex-bias, is high.

Van Noordwijk & Scharloo (1981), Bulmer (1973) and Greenwood et al. (1978) all found reduced fledging success among inbred pairs of great tits. However, van Noordwijk & Scharloo (1981) also found that inbred young recruited to the population at a slightly higher rate than others, and suggested that the effect of inbreeding on lifetime reproductive success might be minimal. Rowley et al. (1986) reported no deleterious effect of inbreeding on reproduction in the splendid wren (Malurus splendens), where a very high proportion of all matings were between close relatives (19.4%). In a preliminary analysis, I found no effect of the relatedness of the first mate on subsequent reproductive success (Table 7.6). However, it remains to be determined if any effect of inbreeding was masked by subsequent mate replacement. I suggest that in the study population, where competition for territories promotes rapid mate replacement (Chap. 2 & 3) and is perhaps the main determinant of reproductive success (Smith 1988; Hochachka et

al. ms; Chap. 8), passing over territories occupied by relatives is probably more deleterious than inbreeding (see also Bengtsson 1978; Smith 1979). Rowley et al. (1986) reached a similar conclusion.

Dispersal Between Populations

The results of this study suggest that dispersal between populations in the vicinity of Mandarte takes place at low frequencies, but that successful immigration is not often achieved and is unaffected by local fluctuations in population density. However, female emigrants may acquire breeding territories more often than males.

In comparison, Tompa (1963) identified 40 juvenile emigrants (21 males, 19 females) on Halibut Island from 1961-3, during fewer visits than I made from 1982-5. Further, 27 of these young subsequently returned to Mandarte. Immigrants accounted for about 1% of the breeding population each year, matching Smith's (1988) estimate of immigration during the period 1974-9. Finally, after Tompa (personal communication) removed half the residents from Halibut in the fall of 1963, several young hatched on Mandarte subsequently settled there. The contrast between Tompa's and my own observations suggests that the degree of inter-island dispersal was much lower from 1982-6 than from 1961-4. The reason for this remains unclear.

Seasonal Patterns of Disappearance

Tompa (1964) suggested that territorial behaviour regulated population density on Mandarte partly by influencing emigration. This hypothesis is indirectly supported by the pattern of disappearances among yearlings each year (Fig. 7.8). Disappearances occurred most frequently in late summer and fall, when aggressive interactions among maturing juveniles, and later between territorial adults and yearlings, were frequent (Tompa 1964; Arcese & Smith 1985; personal observations). With the exception of 1 year, relatively few birds disappeared during mid-winter, when snow sometimes covered the ground for several days. But several birds typically disappeared in late winter after pronounced territorial activity resumed (Tompa 1964; Chaps. 3,5).

Hypotheses and Proximate Causes of Dispersal in Song Sparrows

Male and female song sparrows disperse approximately equally (Fig. 7.1 & 7.2, Table 7.7), in accordance with all three hypotheses involving mating system organisation (Table 7.1). Greenwood (1980) and Dobson's (1982) hypothesis of competition for environmental resources was strongly supported by two main results. First, dispersal was dramatically reduced when territory quality was enhanced. Further, contrary to the common pattern of dispersal in birds (Greenwood 1980; Greenwood & Harvey 1982), the lack of a sex-bias in dispersal was

correctly predicted after detailed studies of the territorial and mating systems of song sparrows (Smith et al. 1982, Chaps. 4-6).

Young usually dispersed from the natal site regardless of parental survival. However, the results of the food addition study suggest that high natal-site fidelity may have reduced adult survival by increasing competition (Arcese & Smith 1988). Inheritance of the natal site was usually achieved by evicting a parent of the same sex, and 3 of 5 young that did settle on the natal site subsequently mated with a parent. Thus, Lieberg & von Schantz's (1985) hypothesis is partly supported by this study. Dispersal was not sex-biased and offspring may represent a potential threat to continued reproduction by parents, but natal philopatry did not depend on the likelihood of inbreeding (see Table 7.1). Further, the probability of mating with a relative was unrelated to distance dispersed, suggesting that dispersing further is not an effective means of avoiding inbreeding, or of choosing optimally outbred matings, within populations. Finally, the relatedness of the first mate had no effect on subsequent reproductive success, showing that settling with a relative had little selective consequence. It is possible that small effective population size (Miller 1947), periodic bottlenecks (Schluter & Smith 1986; Smith 1988) and low rates of effective immigration (Marshall 1948a,b; Johnston 1956a,b, Tompa 1963; Ferrell 1966; this study) sometimes reduce the negative effects of inbreeding in song sparrow populations

(Wright 1977; Bengtsson 1978; Smith 1979; Shields 1982; Falconer 1981).

The assumptions and predictions of dispersal models based strictly on demography were also generally unsupported: dispersal distance on Mandarte was unrelated to inbreeding, time to settlement, population trajectory and adult or juvenile survival (Table 7.1). Increasing the availability of habitat on Halibut Island also had no detectable effect on dispersal from Mandarte, but this could have been because few prospective settlers from Mandarte visited Halibut Island.

Social dominance, a factor included in many demographic models of dispersal (Waser 1985; Buechner 1987), correctly predicted which individuals emigrated from Mandarte, and settlement time on the island, but failed to predict equal dispersal among females and males (Table 7.1), because males are dominant to females (Smith et al. 1980; Arcese & Smith 1985). Finally, contrary to the main assumption of genetic models of dispersal, I found no evidence that dispersal distance was a strongly heritable trait.

I suggest that the process of dispersal in song sparrows results from movements undertaken to sequester resources crucial for reproduction (see also Weatherhead & Boak 1986). Because all breeding habitat on Mandarte is defended even at low breeding densities (Arcese & Smith 1988), resource acquisition

is a highly competitive process that has major consequences for lifetime reproductive success (Smith 1988; Smith & Arcese ms; Hochachka et al. ms). Young may disperse from natal sites in late summer, before most adult mortality occurs, but be constrained in their ability to return to natal sites in the event of parental death because of investment in home range establishment elsewhere (e.g. Krebs 1982). Success in competition for breeding sites on Mandarte, and emigration from the island, are determined in part by dominance status. Sex-biases in dispersal behaviour probably depend on strong differences in the intrasexual competitive environment, which were absent in this population. However, higher success among female emigrants from, and immigrants to Mandarte may reflect a reduced cost of dispersal in females relative to males. This hypothesis can not be tested, however, until dispersal and mortality are separated.

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CHAPTER 8. GENERAL DISCUSSION

Territorial Behaviour and Social Organization

I conclude by discussing how dispersal, territoriality, the mating system and their effects on reproductive success are related to one another in song sparrows, I first consider some effects of territoriality on individuals and populations. On Mandarte Island, both male and female song sparrows are territorial year-round. However, more young were raised in most years than were needed to replace all breeders that die before the subsequent year (Tomba 1964; Arcese & Smith 1988). Population density increased during this study (Fig. 1.1), but the rate of recruitment fell by half (Table 7.4). These conditions suggest that access to territories is restricted by the behaviour of territory owners (Brown 1969; Watson & Moss 1970; Patterson 1980).

Population limitation by territorial behaviour in preferred breeding habitats is a feature of many bird and mammal populations (e.g. Hannon 1983; Woolfenden & Fitzpatrick 1984; Watson 1985; Dobson 1979; Galindo & Krebs 1987). A recurring feature that emerges from studies of such species is the existence of non-territorial 'underworlds' (Smith 1978), which can be considered as queues for territory ownership. Individuals within these queues are usually ordered by dominance and are thought to advance to ownership status when territory

owners die (Smith 1978; Birkhead & Clarkson 1985; Eden 1987). In song sparrows, however, I have shown that relatively few floaters gain breeding territories by passively replacing dead owners (Chap. 3, 4, 5 & 6). Instead, floaters create their own opportunities by actively evicting owners from all or part of their territories. In males, floaters actively seek out and challenge those owners least able to defend themselves against intruders (Chap. 4), and I suspect that the same process occurs in females (e.g. Chap. 5, 6). This propensity for aggressive acquisition of breeding sites affects adult survival (Kluyver 1970; Caro & Collins 1987; Arcese & Smith 1988), natal dispersal distance (Chap. 7) and population density (Tompa 1964; Knapton & Krebs 1974). I therefore suggest that it may also be an important factor affecting population dynamics and social organization that has not previously been widely considered.

Competitive Ability and Reproductive Success

Because a territory is required for successful reproduction in song sparrows (Smith 1988), I now consider how competition for breeding territories affects reproductive success in males and females.

Males

One symptom of increased population density among males is a parallel increase in the proportion of non-territorial males in the population (Chap. 4; Smith & Arcese ms). In chapters 3 & 4, I showed how this surplus of males maintained a high level of competition between floaters and territory owners throughout most of the year, but particularly prior to and during the breeding period. I suggested that males remained in their natal population even when settlement was unlikely because successful immigration by male song sparrows from local populations near Mandarte is rare (Tompa 1964; Chap. 3 & 7). Nevertheless, males hatched into dense populations produced relatively few young because they recruited later in life on average, and recruited less often overall (Smith 1988; Hochachka et al. ms; Smith & Arcese ms; Chap. 7).

By spring each year, males could be categorized as territory owners, floaters, or as being absent from the population (Chap. 3, 6 & 7). However, the status of males in the two former classes changed frequently as floaters settled and former territory owners disappeared or became floaters themselves (Chap. 3 & 4). Some deposed territory owners regained territories later in life, suggesting that male competitive ability varies in time and that this leads to changes in territorial status.

Age was correlated with changes in territorial status and

competitive ability (Chap. 3,4,6 & 7). Relative age within a cohort had a profound effect on which males became territorial, remained as floaters, or disappeared from the population (Arcese & Smith 1985; Chap. 3,4,6, & 7). Between cohorts, competitive ability increased from 1- to 2-years of age, but either leveled off or declined after 3-years of age. However, although age was the primary correlate of ability that I identified, two results suggest that consistent differences among males persisted throughout life. First, in consecutive years particular males experienced similar levels of intrusion pressure with respect to the means of their age-class, even though intrusion pressure changed as expected by comparisons across age-classes when males aged (Chap. 4). Second, males that began their first breeding season as a floater also became floaters later in life after gaining a territory more often than males that gained territories earlier in life (Chap. 3).

I suggest that competition among males was important not only in recruitment, but also in territory maintenance and longevity as a breeder. Smith (1988) and Hochachka et al. (ms) have concluded that, aside from chance effects that result from population size and trajectory at the time of hatch, recruitment and longevity as a breeder are the major factors affecting lifetime reproductive success in male song sparrows. I therefore conclude that competitive ability is a key factor affecting male reproductive success.

Females

Although the data presented for females are more limited than for males, my results strongly suggest that competition for territories among females also plays a major role in female reproductive success (Chap. 5, 6, & 7). As for males, recruitment declined as female density increased (Chap. 6 & 7), and the number of observations of aggressive contests over territory ownership among females increased dramatically (Chap. 5). Within cohorts of females, dominance status was related to recruitment (Arcese & Smith 1985; Chap. 7), and date of hatch was related to both recruitment and territorial status in the following year (Chap. 7).

However, one potentially important difference in the relative levels of male and female competition concerned the opportunity for dispersal between populations. Females dispersed more successfully between populations than males. This is particularly interesting because the sex-ratio of yearling dispersers to Mandarte in late summer was approximately equal (unpublished results), suggesting that females have a greater opportunity to reproduce outside their natal population than do males. This could occur because females suffer slightly higher annual mortality than males (Arcese & Smith 1985; Nol & Smith 1987), which will affect the instantaneous rate of territory vacancy and the probability of gaining a territory without aggressively evicting owners (Murray 1984;

Waser 1985; Chap. 3 & 7).

Dispersal Strategies and Competition for Resources

When habitats are saturated with breeders, as they are on Mandarte Island year-round, potential recruits must wait until an owner dies or becomes vulnerable to a takeover attempt, or disperse from the natal area in search of empty habitat elsewhere. This problem is general to all resident species, and can be characterized as the decision to remain and compete for resources locally or disperse to avoid competition (Comins et al. 1980; Horn 1983). In general, high dispersal tendencies are characteristic of marine species, and of terrestrial species that colonize temporary habitats or exploit periodically abundant resources (Horn 1983).

In birds and mammals, however, dispersal is typically more restricted. Most species studied so far usually breed within one to several home range (or territory) diameters of their natal site (Shields 1982), but little is known about dispersal in highly vagile, eruptive species (reviews in Greenwood 1980; Dobson 1982; Waser & Jones 1983). The problem here is that it is inherently difficult to study dispersers, as pointed out in this study (Chap. 3 & 7). My data do not allow me to come to a conclusion about how trade-offs between local competition and searching for empty sites elsewhere affect dispersal in song sparrows. A comparison of several studies (Chap. 7, Table

7.8), however, suggests that in all but sparsely populated areas (e.g. Weatherhead & Boak 1986) dispersing song sparrows are likely to encounter moderate to strong competition in all suitable breeding habitats.

If one considers dispersal strictly on the local scale, however, two recent studies offer particularly striking parallels to the stay versus disperse dilemma. In both magpies (Pica pica; Eden 1987) and black-capped chickadees (Parus atricapillus; Smith 1987), most non-territorial birds live in flocks ordered by dominance, from which they advance to territorial status as the breeding season commences and/or territory openings occur. However, a minority of birds either travel solitarily and attempt to occupy territories opportunistically (magpies) or switch between flocks and assume the position of more dominant birds after they disappear (chickadees). In both cases, evidence suggests that the success of flock-switchers and loners is equal to that of regular flock members.

Several theoretical models and empirical studies posit competition for breeding resources as the primary cause of dispersal in birds and mammals (reviewed in Chap. 7; Table 7.1), and the results of this study are consistent with this hypothesis with regard to both inter- and intra-population movements. However, until individuals that leave natal populations can be followed as closely as those that remain, one

cannot assess the affect of each option on reproductive success.

Conflicts of Interest Between Males and Females

An emerging theme in a few recent studies that relate dispersal, territoriality and mating systems to reproductive success has been that males and females often employ different tactics to maximize the number of young that they produce, and that this difference sometimes leads to a conflict of interest between males and females (Clutton-Brock et al. 1982; Woolfenden & Fitzpatrick 1984; Davies 1985; Pusey & Packer 1987). For song sparrows, I have shown that conflicts between males and females are probably restricted primarily to the mating system, although males and females may also compete directly for access to food resources in the non-breeding period (Smith et al. 1980; Arcese & Smith 1985).

Although a variety of both male and female behaviours could affect mating system organization, research has historically centered on the aggressive nature of males, and on the choosiness of females. (Selander 1972; Halliday 1978; Parker 1978; Mock 1983; Payne 1984). However, several recent studies show that aggressive behaviour in females affects spacing patterns (e.g. Hannon 1983; Hurley & Robertson 1985), reproductive success (Davies & Houston 1986; Clutton-Brock et al. 1987), dispersal (Dobson 1979; Galindo & Krebs 1987) and mating systems (Hannon 1984; Davies & Houston 1986). These

possibilities have been recognized in theory (e.g. Trivers 1972; Oring 1982; Murray 1984), but have only recently been regularly investigated in the field (e.g. for small mammals see: Dobson 1979; Taitt & Krebs 1982; Boonstra & Rood 1983; Galindo & Krebs 1987). With the exception of studies of polygynous species (e.g. Petrie 1983), female aggressive behaviour has also only recently become a prime topic of study in birds (Smith 1982; Hannon 1983; 1984; Hurley & Robertson 1985; Stutchbury & Robertson 1985; Searcy 1986).

In this study, however, I have shown that aggressive behaviour in both males and females plays a fundamental role in determining which individuals recruit to the breeding population, and in the degree to which males and females are able to monopolize access to mates of opposite sex. In turn, these factors contribute to the overall variation in reproductive success among individuals hatched into the Mandarte Island song sparrow population (Chap. 4, 6, & 7).

In a particularly striking example of differences in male and female reproductive interests, Davies (1985) showed how dunnocks of each sex aggressively spaced themselves out to maximize the likelihood of obtaining extra mates. Males that defended the territories of more than one female increased the number of young that they sired. However, females that failed to defend the entire territory of their mate lost male care and raised few young. Females with larger territories often

received aid from more than one male and raised more young than otherwise possible (Davies & Houston 1986). Davies & Houston's results are remarkably similar to my own, with the noteworthy exception that females on Mandarte Island never became simultaneously polyandrous. Possible explanations for this difference between dunnocks and song sparrows were discussed in Chapters 3 & 4.

Male Aggression and Female Choice

The historical emphasis on male aggressive behaviour and general dismissal of the importance of aggressive behaviour in females probably results from two main factors. First, males in many species are larger, brighter and more elaborately endowed with weaponry and other features used in aggressive and sexual displays than are females (Darwin 1871; Selander 1972; Payne 1984). As a result, males are often more visible, spectacular and tractable subjects for study than females (Wasser 1983). Second, male, as opposed to female competition is regarded as more intense and thus more important in terms of natural selection (Trivers 1972; Wilson 1975; Wittenberger 1979). Nevertheless, I suggest that researchers sometimes fail to recognize that although large differences in the scale of intrasexual competition between males and females may exist, it does not necessarily follow that the influence of competition in females is either weak or absent. Because females and males differ in life history, competition may manifest itself

behaviourally in different ways or at different times in each sex. If so, a thorough knowledge of sex-specific behaviours and their consequences is needed before one can determine the relative contributions of different behaviours to the evolution of present-day behavioural repertoires.

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