MEPereyra

CHAPTER 3: Social System and Behavior

As noted in the previous chapter, migrants, recently arrived at montane areas, are faced with finding the appropriate breeding habitat and surviving until conditions are favorable for beginning reproduction, a difficult task in some years because of lingering winter conditions and the occurrence of storms. But even in years when environmental conditions are mild there is a pause before nesting actually begins. During this pre-nesting period important elements of the social system are activated and expressed. These include establishment of territories and behaviors associated with mating, including pair formation, mate guarding, and copulation. Eventually, over many reproductive seasons a more comprehensive understanding of the social structure can be obtained as it becomes possible to measure mate fidelity, age of mates, frequency of polygamous pairings, and aggressive behaviors, as well as the functions of vocalizations.

TERRITORY ESTABLISHMENT

Almost immediately upon arrival most *oriantha* males began exhibiting preferences for specific locations. Forays, sometimes hundreds of meters in length, did occur but usually they sang from a few favorite spots and entered traps repeatedly at about the same place on the study area. In heavy snow years they showed preferences for certain clumps of large pines at meadow borders until patches of willows and small pines melted out. They then moved onto the breeding habitat proper. For returning males this was usually on or near their territory of the previous year. Gradually, over a period of two to three weeks as the vegetation developed, and after considerable singing and some chasing and fighting, firmly delineated territories were established.

PAIRING

Newly arrived females were sometimes observed occupying small willow patches by themselves, but within a few days they were usually being accompanied by a male. As in Northern Wheatears, pairing began even before all members of the population had arrived (Conder 1989). This pattern was typical only during moderate or light snow years, however. In heavy snow years pair formation could be much delayed. In 1995, for example, pairs were not present until 13 June. This was more than two weeks after the first females had arrived (see Fig. 2.1, upper). Radio transmitter data showed that during May and June of 1995 individuals, especially females, were regularly visiting lower elevations for several days at a time, and were ranging widely in search of food even on the breeding areas themselves. Not until enough vegetation had emerged from beneath the snow to give focal points for territories did they pair and remain at one location. Returning females, like males, tended to take up residence in the same general area as the year before (see below).

The greatest share of dispersal in passerines occurs prior to the first nesting effort, but successive nests are not usually placed in precisely the same location and the dispersal process continues as nesting is repeated throughout the bird's lifetime. If a breeder survives from one year to the next, the distance between its nests in successive years can be determined. This is the between-year breeding dispersal distance.

TABLE 3.1. Between-year Breeding Dispersal Distances (m) in *Oriantha* in Relation to Nesting Success (Fledging at Least One Offspring) and to Change of Mates

	Males				Females			
Status	Mean	SD	N	P[a]	Mean	SD	N	P[a]
Successful								
Yes	115.2	121.1	72		137.2	120.8	74	
				0.684				0.638
No	104.6	73.7	17		112.9	88.1	24	
Mate change								
Yes	142.2	227.6	69		232.9	69.9	64	
				0.249				<0.001
No	82.9	63.8	31		77.8	60.0	30	

[a] P-value from test of medians (Mann-Whitney U).

BETWEEN-YEAR BREEDING DISPERSAL

In *oriantha,* as in most organisms that have been studied, dispersal distances were highly skewed; the greater the distance from the point of origin, the lower the density of individuals present. Yet there was often a year-to-year consistency in the pattern observed and the between-year breeding dispersal distance was no exception. No significant interannual variation in this distance occurred during 15 consecutive years of data collection (Morton 1997). The majority of birds of both sexes had their first nest of the season within 200 m of their first nest of the previous year. The between-year distance was greater in females, however, than in males (female median = 119.5 m, male median = 72.5 m; Kolmogorov-Smirnov 2-sample test: N_1 = 124, N_2 = 103, D = 0.339, P < 0.001). Strong site fidelity of this type might well be an alternative strategy to habitat quality reassessment at the time of spring arrival (Bédard and LaPointe 1984).

In a few cases, nests were located far from those of the year before. Along creeks, where territories were long and narrow, or where a lake arm bisected breeding habitat this distance could exceed 300 m. One female moved 750 m from her previous year's nesting spot because it was buried for too long under a deep snowpack (Morton 1997).

Between-year breeding dispersal in passerines is thought to occur because natural selection is operating on experience-based choices. For example, reproductive success promotes fidelity to a breeding site whereas failure promotes movement to a new site the next year (Darley et al. 1977, Nolan 1978, Freer 1979, Herlugson 1981, Gavin and Bollinger 1988, Bollinger and Gavin 1989, Pärt and Gustafson 1989). In *oriantha,* however, a failure to fledge young in one year did not affect their choice of breeding site the next year because dispersal distance did not change with reproductive success (Table 3.1). It did increase, however, particularly in females, when mates were changed between years (Table 3.1). This last effect could have occurred because of a tendency for passerine males to be more site-tenacious than females, to intra-sexual competition being more intense in females than in males, and/or because females were more discriminating than males when choosing a mate (Knapton 1979, Searcy 1979, Payne and Payne 1993). Any of these could lead to the result, consistently obtained in avian studies, that females tend to move greater distances than males (Darley et al. 1977, Nolan 1978, Gratto et al. 1985).
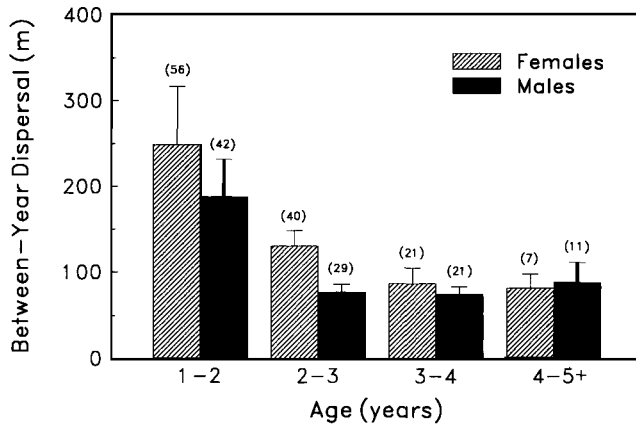
FIGURE 3.1.   Between-year breeding dispersal distances in *oriantha* according to age. Bars show means (+ 1 SE); number of individuals in parentheses.

Another common pattern in passerines is that between-year breeding dispersal distances decrease with age (Greenwood and Harvey 1982, Payne and Payne 1993). At Tioga Pass, in agreement with this generalization, breeding dispersal distance was greatest in both sexes between their first and second seasons. It then decreased and remained stable thereafter (Fig. 3.1). The effect of age here was significant in females (Kruskal Wallis test, $P = 0.014$), but not in males ($P = 0.380$). There were some unusually long movements by females between their first and second years. In two cases females moved to completely different meadows, nearly 3 km away, something never observed in males. Greenwood and Harvey (1982) suggested that large movements between the first and second breeding seasons occur because one-year-olds often occupy territories of poorer quality than those of older birds. As two-year-olds they are able to move to better sites and thereafter dispersal is slight. The *oriantha* data fit this movement pattern, at least for females, but can it be shown that their behavior was related to territory quality?

Identifying variations in this parameter is a difficult problem. It is addressed here by letting the birds define territory quality through their nesting behavior. It was assumed that the more often an area was used for nesting over the years, the higher was its quality. In this case "area" was defined as being specific, individual hectares on TPM. These hectares could be identified from a detailed map overlain with horizontal and vertical 100-m grid lines. There were 44 one-hectare quadrats on which, over a period of 21 years, there was at least one *oriantha* nest. A total of 652 nests were involved and the number found per quadrat ranged from one to 67. For purposes of analysis, "low density" quadrats were arbitrarily designated as being ones that had held 30 or fewer nests. There were 38 of these and they accounted for a total of 385 nests. "High density" quadrats each held 31 nests or more. There were six of these and they accounted for a total of 267 nests.

The age distribution of breeding birds for the two quadrat types indicates that there was a tendency for one-year-olds to occupy low density areas whereas there were proportionately more older birds in the high density areas (Fig. 3.2). The age distributions in low density areas vs. high density areas was significantly
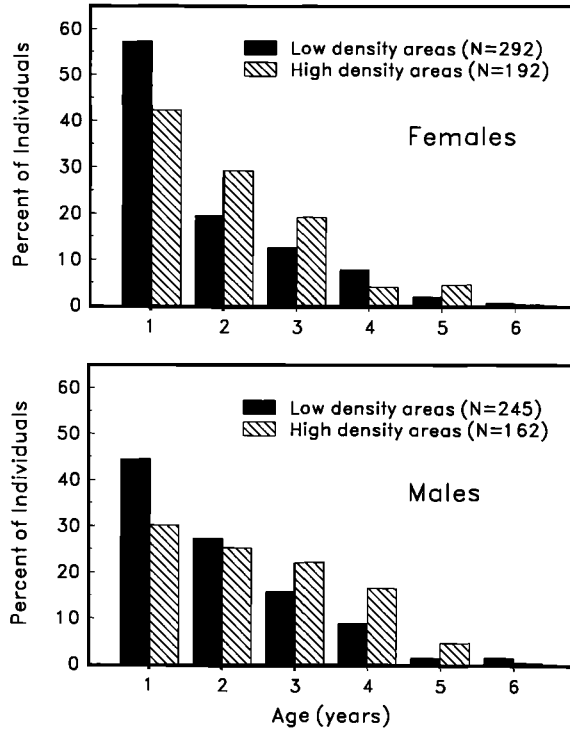
FIGURE 3.2. Age distribution of breeding *oriantha* in relation to density of nests on 1-ha quadrats (see text). Sample sizes are for total number of nests.

different in both sexes (females: Kolmogorov-Smirnov $Z = 6.155$, $P < 0.001$; males: $Z = 7.094$, $P < 0.001$). The mean age of females nesting in low density areas was 1.80 yr (SD = 1.13 yr) and 2.02 yr (SD = 1.14 yr) in high density areas. For males, the comparable data were 2.01 yr (SD = 1.17 yr) and 2.43 yr (SD = 1.25 yr).

One possible prediction from these data is that when between-year breeding dispersal occurred, nests would sometimes be located in different quadrats. Furthermore, when such a shift did occur, it should be to a higher-quality territory. In other words, the birds should relocate to a quadrat that was habitually nested in more often than their original one. Data relevant to this hypothesis were obtained for 109 females and 98 males and they show that 30 females remained in the same quadrat and 79 moved to another one (Table 3.2). Of those that shifted, 29 moved to a lower density area and 50 to a higher density area, a significant difference (one-way Chi-square = 5.58, df = 1, P = 0.018). Females, therefore,

TABLE 3.2. BETWEEN-YEAR BREEDING DISPERSAL IN *Oriantha* WITH RESPECT TO QUADRAT OCCUPANCY

Dispersal outcome	Females	Males
1. Remained in same quadrat	30	42
2. Moved to new quadrat	79	56
a. Lower density	29	24
b. Higher density	50	32

tended to move between years to higher quality territories. Males had similar tendencies but they were not statistically significant. Of those that moved, a larger number went to areas of higher density than lower density (32 vs. 24; one-way Chi-square = 1.143, df = 1, P = 0.285). These data also repeat the familiar theme of sex-specific mobility; a greater proportion of females than males moved to new quadrats between years (72.5% vs. 57.1%; Chi-square = 5.349, df = 1, P = 0.021).

Additional analyses were performed to see if territory quality, as assayed by low density vs. high density occupancy rates, affected reproductive parameters. The parameters chosen were settling date (as measured by first egg dates), clutch size, nest predation rate, nesting success (at least one fledgling produced), and mean number of fledglings produced per successful nest. There were no significant differences in any of these comparisons; the only difference found was the one on distribution of ages shown in Fig. 3.2. An apparent conundrum here is that the birds preferred to nest in certain areas even though this preference did not seem to enhance their reproductive success. If such an effect exists, perhaps it takes place over a longer time frame than we have evaluated, lifetimes rather than between years. On the other hand, the observed settling pattern might be nothing more than the one expected if the birds were following an ideal free distribution, as envisioned by Fretwell (1972).

Territory-quality may have affected female attentiveness because the incubation period was shorter in older females (age 3+ yr) than in younger ones (age 1 or 2 yr, Chapter 7). Perhaps living on a high quality territory spares more time for tending eggs because less time is required for foraging.

COPULATIONS

At the beginning of the season copulations began during the pre-nesting period, sometimes a week or more before the onset of nest building, and continued through the laying period. If nests were subsequently lost the courtship sequence, including copulations, was repeated, although over a more compressed time frame. Most copulations were observed in the morning hours, but there was not enough systematically gathered information to plot their diurnal frequency with confidence. Although copulation frequency in some avian species is often highest and mate guarding most intense in the hour or so after laying (Hankinson 1999), this close relationship between mating behavior and reproductive function is by no means uniform. Furthermore, timing of copulation may not be a reliable indicator of egg fertility (Adkins-Regan 1995).

Recently, M. E. Pereyra (pers. comm.) has observed that *oriantha* sometimes engage in flurries of copulations during the last few minutes of daylight, just before going to roost, a pattern also noted in Smith's Longspurs (*Calcarius pictus*; Briskie 1992). The ovum of birds must be fertilized during a small window of time that occurs immediately after ovulation because access by sperm is soon blocked by deposition of the perivitelline layer and albumen around the yolk (Howarth 1974). Ovulation of the next egg occurs about the same time as laying of the current one and *oriantha* lay in the early morning hours, soon after daylight (Chapter 6), so these late-evening copulations seem ill-timed as an insemination strategy unless fertilization is occurring, at least some of the time, from stored

sperm. This is a distinct possibility given the efficacy of this mechanism (Birkhead 1992, Birkhead and Møller 1992).

MATE GUARDING

Females became paired soon after settlement and their mates began to exhibit guarding behavior. Males often watched from elevated perches and shadowed the female by moving along through the tree tops, terrain permitting. Most commonly, they guarded at close range, hopping alongside or slightly behind as the female moved about in her activities, driving off other males that came too near. Mate guarding appeared to lessen in intensity once incubation began, but it could be observed on the study area at almost any time in the summer because of the reproductive cycle being renewed in renesting pairs.

Guarding behavior appears to be stimulated by testosterone (Moore 1984) and its function, of course, is that it helps a male to assure his paternity by preventing other males from fertilizing his mate (Davies 1985, Montgomerie 1988). It may also help prevent the female from seeking fertilizations from extra-pair males (Gowaty and Plissner 1987, Gowaty and Bridges 1991, Møller and Birkhead 1991, Lifjeld et al. 1994).

Sometimes unmated (floater) males (usually one, although as many as six were observed) followed an *oriantha* pair and attempted to obtain copulations. When such processions occurred, the mated male positioned himself between the female and the other male(s). If the female quickly changed position by flying, skirmishing sometimes broke out as her mate tried to deal with the female's new exposure by chasing away the intruders. Floaters sometimes followed a pair for several hours at a time, especially when the female was soliciting copulations. The mated male could usually keep a lone follower away simply by maintaining an intermediate position on the ground or in vegetation, but the situation could destabilize quickly. For example, nearby territory-holding males sometimes flew straight toward the female. Her mate then usually launched aggressive, prolonged aerial chases of these intruders, leaving the female unguarded in the interim and potentially free to engage in extra-pair sexual activity. Although no extra-pair copulations were observed, electrophoretic analyses of four polymorphic loci showed that at least 34 to 38% of chicks hatched on the study area were not the offspring of one of the putative parents (Sherman and Morton 1988). Because females did not engage in brood parasitism, the mismatched young must have been the result of extra-pair fertilizations. In a much larger follow-up study on this same population, using microsatellites to determine paternity, MacDougall-Shackleton (2001) found that 41.2% of 342 nestlings were fathered by a male other than the social mate.

Oriantha have a monogamous mating system, as defined by Lack (1968), in that they form pairs and raise broods together. They behave similarly to most other so-called monogamous avian species, however, in that they do not maintain an exclusive mating relationship (McKinney et al. 1984, Birkhead 1987, Westneat et al. 1990). In actuality, as shown above, they are socially, not genetically, monogamous.

MATE SWITCHING

To detect continuity of pairings from year to year, there must be data on multiple-year nestings by females whose mates were known. Information of this type

TABLE 3.3. FREQUENCY DISTRIBUTION OF NUMBER OF MATES PER LIFETIME IN FEMALE AND MALE *Oriantha*

Number of mates	Frequency	
	Females	Males
1	194	121
2	43	40
3	7	19
4	1	5
5	0	0
6	1	0

on *oriantha* shows that half of the time (82 of 164 cases) the male from the previous year was still alive. In 54 of these 82 cases (65.9%) the two birds were paired again and in 28 they were not. The frequency of mate switching (also called the divorce rate by some investigators; see Ens 1992), therefore, was 34.1%. There were also three histories wherein a mated pair was together the first year, mated to new partners the second year, then re-mated to one another the third year.

MATES PER LIFETIME

Because small passerines, such as *oriantha*, usually live for only a short time, it was no surprise that the modal number of mates per adult lifetime for both sexes was one (Table 3.3). The average number of mates was 1.26 for females (SD = 0.60, N = 246) and 1.50 for males (SD = 0.47, N = 185). This imbalance between the sexes was significant (Chi-square = 17.96, df = 4, P < 0.001) and, when their distributions were modeled, was found to be due to proportionately greater numbers of females having had only one mate. Still the record, six different mates in a lifetime, was held by a female that nested for seven consecutive years on TPM (Table 3.3).

Natural mortality, along with mate-switching behavior, caused long-term pairings to be rare. There were only two cases wherein an uninterrupted sequence of pairings by the same two birds occurred for as long as four years; all other same-pair sequences were for two or three years. It is instructive that these long-term pairs were often found at locations where the breeding habitat was demarcated by well-defined boundaries. One such location, the southwest corner of TPM, contained a cluster of small pines that was suitable in size for only one territory and it was contiguous with only one other territory in most years. When both members of a pair survived that had used this corner of the meadow they could often be found there together again. The same pattern occurred in pairs that occupied the "vernal pool" territory, an isolated patch of habitat located on the West Slope. There, upon an expanse of dry hillside, encircling a spring, was a patch of willows that was used nearly every year as a nesting site. Thus, site fidelity contributes to re-pairing in *oriantha*, perhaps more so than mate fidelity.

AGE OF MATES

Although there was considerable turnover in mates, recall that if both members of a pair survived to the next breeding season about two-thirds of the time they were paired again. Thus, as individuals grew older the mean age of their mates

FIGURE 3.3.   Mean age of mates, according to age, in *oriantha*. Line shows 1 SE; sample sizes in parentheses.

increased (Fig. 3.3), a change that was highly significant in both sexes (females: ANOVA $F_{7,689} = 17.26$, $P < 0.001$; males: ANOVA $F_{7,689} = 13.48$, $P < 0.001$). The mates of one-year-olds (yearlings) were, on average, 1.5 yr old. At age two the interactions of mate retention and mate change resulted in both members of the pair being about the same age. Thereafter, the mates of older birds tended to be younger than they were (Fig. 3.3). Much the same pattern, and for the same reasons, occurs in Great Tits (*Parus major*; Greenwood et al. 1979). These age relationships are unexpected when mate choice is absent. In that situation, mean age of mates should not change with the age of an individual (Reid 1988). The tendency of mates of females to be comparatively older than those of males at the same age (Fig. 3.3) is probably the result of many yearling males (but not females) being unmated (see discussion on floaters below).

Mate choice in birds is often regarded as being within the purview of females and dependent upon two criteria: the genetic quality of the male and the quality of his territory. Since these should be positively correlated, the actual criteria applied by females when selecting males is operationally difficult to detect (Wittenberger 1976). Nonetheless, the *oriantha* data suggest that females, as well as males, have a strong affinity for their previously occupied breeding area. This preference for a specific location should, on average, lead to a reduction in mate quality, but this potential cost seems to be countered by engagement in extra-pair sexual activity.

FLOATERS

In both monogamous (Lack 1968) and polygynous passerines (Orians 1969) there is usually a readily observable population of floating, unmated males, whereas evidence for the existence of unmated females beyond the early part of the nesting season is slim. This general picture fits the *oriantha* data in that all females trapped during the nesting season were known to be associated with specific nests, or at least had a brood patch indicating that they had a nest somewhere. Although extra males were observed and females were not, there were indications that unmated females were present well after the breeding season was under way (also noted in Song Sparrows; Searcy 1984).

For example, on 30 June 1994 the female on the vernal pool territory disappeared and her four nestlings (Days 2 and 3) died that night. The male did not desert the area, however. He remained and began to sing for prolonged periods—as though advertising for a mate. On 10 July a new, unbanded female, presumably a yearling, started a two-egg clutch in the vernal pool willows and this newly-formed pair eventually fledged two chicks. The female had a just-developing brood patch, rather than a fully formed one, when she began to lay indicating that this was her first nest of the season. Also, on several occasions females were observed to insert late-season nests between or within pre-existing territories containing females that were already caring for nestlings. These inserting females were always yearlings and they did not bring a male with them; instead they paired with one of the territorial males already present and he fed the nestlings of both females. These data suggest that floating females do exist, at least during the first half of the season, and they also prompt discussion of two additional phenomena, polygyny and female aggression.

POLYGYNY

The scenario described above shows how polygyny sometimes developed but it also occurred in situations wherein the territories in question were established and maintained from the beginning of the season and the females involved were older than one year. Interestingly, in these latter cases the territories were often separated by a topographic feature such as a rocky knoll or grove of trees that may have been outside of both territories. In other words, the territories were adjacent, but not contiguous, and the females were probably not in close contact. Thus, female-female competition ordinarily may serve to decrease the frequency of polygynous matings.

Polygyny occurred in nine of the 17 years that mating patterns were carefully studied. Of the 429 males observed during that time, 15 (3.5%) were polygynous, and none for more than one season. Of these males, 13 were bigamous and two were trigamous. Note that polygyny was defined not on the basis of copulations, or known paternity, but by paternal care. A male that fed nestlings at two (or three) different nests, each one belonging to a different female, was declared to be polygynous. No more than one male was ever observed to feed nestlings at a given nest.

The mean age of males during the time that they were polygynous was 2.80 yr (SD = 1.52 yr, min = 1 yr, max = 5 yr), and their survival rate was high. Eleven of the 15 reappeared the year following the polygynous one, a return rate of 73.3%. Analysis of reproductive success in these males shows that they fledged more young during years when they were polygynous (mean = 5.47, SD = 2.53, N = 15) than in years when they were monogamous (mean = 3.07, SD = 1.25, N = 28), a significant difference (t = 3.45, P = 0.003).

There were 28 females involved in these polygynous matings, only one of them for multiple years, one year as the partner of a bigamous male and the other year a trigamous male. The mean age of females participating in polygynous relationships was 2.29 yr (SD = 1.44 yr, min = 1 yr, max = 5 yr). Of the 28 females, 15 were present again after the season of polygyny, a return rate of 53.6%. The mating pattern did not affect the number of fledglings produced by these females: with monogamous males their mean number of fledglings was 3.22 (SD = 1.75,

N = 32), with polygynous males it was 3.26 (SD = 1.84, N = 23; t = 0.086, P = 0.932). A few cases of polygyny have also been observed in *nuttalli,* and reproductive success of polygynous pairs was not different from that of normal pairs (Petrinovich and Patterson 1978). As in Savannah Sparrows (Wheelwright et al. 1992), female fitness in White-crowned Sparrows seems to be unaffected by mate sharing.

Polygyny was not age-restricted in *oriantha,* it did not appear to decrease survival (see Chapter 4), and reproductive success was unaffected in females and enhanced in males. Why, then, is this system not more prevalent? There are many factors to consider. Among these is that polygyny is advantageous to males so its occurrence may depend upon its effects on female success (Leonard 1990). This, in turn, hinges upon territory quality because polygyny is promoted by a high variance in quality among male territories (Pleszczynska 1978) and mating with a polygynous male on a high-quality territory may be more productive than mating with a bachelor on a low-quality territory (Verner 1964, Orians 1969). In addition, environmental conditions that promote polygynous matings could vary from year to year and there may be undetected consequences for lifetime reproduction as well. Cuckoldry rates could be higher in polygynous males, for example, and, lack of evidence from the present study notwithstanding, polygyny could be detrimental to male survival, especially if it is chronic. This is mentioned because although prolonged, high levels of testosterone in the blood are associated with polygyny (testosterone implants can induce it; Wingfield 1984a), Dufty (1989) found that this condition or manipulation significantly reduced survival.

Finally, the dynamics of intrasexual competition should be considered. For example, female-female competition appeared to prevent polygyny but this was sometimes circumvented as when yearling females did not settle until territory-holding females already had young. The aggressive tendencies of the latter were then starting to decrease and they sometimes let an unmated female become established and even share the resident male. House Wrens (*Troglodytes aedon*) exhibit a similar pattern (Quinn and Holroyd 1992). Note that the nests of females sharing a male in such instances will usually be out of synchrony making it unlikely that the male would need to feed two groups of dependent young simultaneously. On the other hand, the surplus of males may generate intense male-male competition for territories and mates, circumstances that tend to drive the system toward monogyny and that have probably caused the rate of polygyny to be stabilized at the rate observed.

Given the relative rarity and sporadic nature of polygyny in *oriantha* (and its conspecific, *nuttalli*), it seems reasonable to conclude that this permutation of their mating system is relatively unimportant and should be thought of as a facultative response. At the same time, the temporally separated clutch starts of male-sharing females tends to support the thesis of Slagsvold and Lifjeld (1994) that, due to competition for male help with dependent young, mated females may benefit from trying to prevent or delay settlement of other females, especially in poor years (Catchpole et al. 1985, Bart and Tornes 1989). Clearly, female aggression may have had a major role in the evolution of avian mating systems.

AGGRESSION

Most studies of aggression in passerines have focused on male-male interactions. These have been observed under uncontrolled field conditions and/or ex-

perimentally through the use of tools such as song playback and live or mounted conspecifics (decoys) placed upon the territory. Aggressive behaviors are not usually so overtly expressed in females as in males, and only recently has it become clear that females of many species compete not only for high-quality males, but also for limited resources such as food and nest sites (Hill 1986, Searcy 1988, Dunn and Hannon 1991, Slagsvold et al. 1992, Berglund et al. 1993, Slagsvold 1993, Cristol and Johnsen 1994, Liker and Szekely 1997).

In the Tioga Pass study the role of female aggressiveness in such important functions as mate selection and territory acquisition and defense were not specifically investigated, but some intriguing, relevant behaviors were noted. For example, returning females tended to settle on or near their previous territory regardless of the male that was present. As mentioned above, the strength of this site fidelity suggests that they discriminate much the way males are thought to do when it comes to territory choice and retention. Also, yearling females were sometimes unable to settle until the season was well along. Perhaps they could not find an unmated male with a suitable territory, but it could be that they were being excluded by other females. Females also expressed overt, classical types of aggression in that they sometimes sang vigorously during the pre-nesting period, much in the manner of males, and they were known to return from foraging trips and physically displace a conspecific adult near their nest.

These observations, and others, stimulated us to think about how aggression could be compared in males and females. Playback experiments using alarm or contact calls that are shared by the sexes could be used and so could the propensity to attack decoys. The method of using decoys was selected, then employed in a test that was objective and easy to conduct. It relied upon the observation that a bird in a trap often stimulated the territory holder to attack it through the trap wall. This response was exploited in an experimental paradigm that could be used to test aggressiveness simultaneously in both sexes.

In the period before nest building (pre-nesting), two four-cell traps were placed 5 m apart on an area occupied by a pair. One trap contained an adult female decoy (leaving three cells free for making captures) and the other trap contained an adult male decoy. Materials (snow, ice, rocks, dirt clods, vegetation) were placed, alone or in combination, against the sides and top of the cell containing the decoy so an attacking bird would likely be diverted into an open cell and thus be captured. No supplementary food, such as seed, was added and numerous direct observations verified that the territory holders were indeed attempting to attack the decoys. Each trapping session lasted for 20 min. Experiments like this were conducted during all stages of the nesting sequence except that, once the nest was built, the two traps were placed 5 m from it and from one another such that an equilateral triangle with 5 m sides was formed. A total of 144 experiments were performed in 1993 and 1994, 134 on birds engaged in their first nesting effort of the season and 10 on renesters. Seven different periods or stages were sampled: pre-nesting (before nest construction), pre-laying (nest constructed but not yet laid in), laying, incubation, nestlings present, fledglings present (first five d after fledging), and fledglings present (six to 10 d after fledging).

In the 134 experiments conducted on pairs engaged in their first nesting effort of the season, females were captured 63 times and males 54 times (Table 3.4, part A), a capture ratio that was not different (Chi-square = 1.23, df = 1, P =

TABLE 3.4. FREQUENCY THAT FEMALE AND MALE *Oriantha* WERE CAPTURED IN DECOY TRAPS ON THEIR TERRITORIES, IN RELATION TO STAGE OF THE NESTING CYCLE

| | | Captures | | | |
| | Number of experiments | Females | | Males | |
Stage		N	%	N	%
A. First nests					
Pre-nesting	25	7	28.0	17	68.0
Pre-laying	23	11	47.8	13	56.5
Laying	34	17	50.0	10	29.4
Incubation	19	14	73.7	7	36.8
Nestlings	17	10	58.8	5	29.4
Fledglings (days 1–5)	10	4	40.0	2	20.0
Fledglings (days 6–10)	6	0	0.0	0	0.0
B. Replacement nests					
Incubation	10	2	20.0	0	0.0

0.268). There was no evidence that the parent birds were affected by decoy sex. Females were captured 31 times with the female decoy and 32 times with the male decoy (Chi-square = 0.02, df = 1, P = 0.900). For males these same trapping frequencies were 21 and 33 (Chi-square = 2.67, df = 1, P = 0.102). On a few occasions an adult from a neighboring territory was captured, but those data were not included in Table 3.4.

Males were most sensitive to the presence of the decoys early in the season, before the nest was built (Table 3.4). Once the nest was in place, their capture frequency tended to decrease through the various nesting stages. In contrast, females strongly defended the immediate area of the nest and were captured with greater frequency as nesting progressed, with the peak rate occurring during incubation. By the time fledglings were more than five days out of the nest both parents had stopped reacting to the decoys. Even when decoy traps were placed near their fledglings neither parent was captured. Ten experiments were also conducted during the incubation period on pairs engaged in renesting efforts, and trapping success during incubation decreased substantially, although not significantly, from what it had been with first nests (Chi-square = 2.55, df = 1, P = 0.111; Table 3.4, part B).

These data show that territory or nest defense occurs in both males and females and that more information is needed on the relative roles played by the sexes in determining parameters such as territory configuration, settlement pattern, mate acquisition, and territory defense.

VOCALIZATIONS

The vocalizations of birds are an essential component of their social interactions, including sexual displays, and the study of song and other types of utterances has been an enormously productive line of inquiry into avian social systems. As a group, White-crowned Sparrows have had an important impact in this field because they are widely available and have vocal repertoires that are relatively easy to record and analyze. Their songs are composed of separable, distinctive, sequentially-arranged elements that can be quantified and compared (Fig. 3.4). In addition, they have dialects and the various components of songs often vary dis-
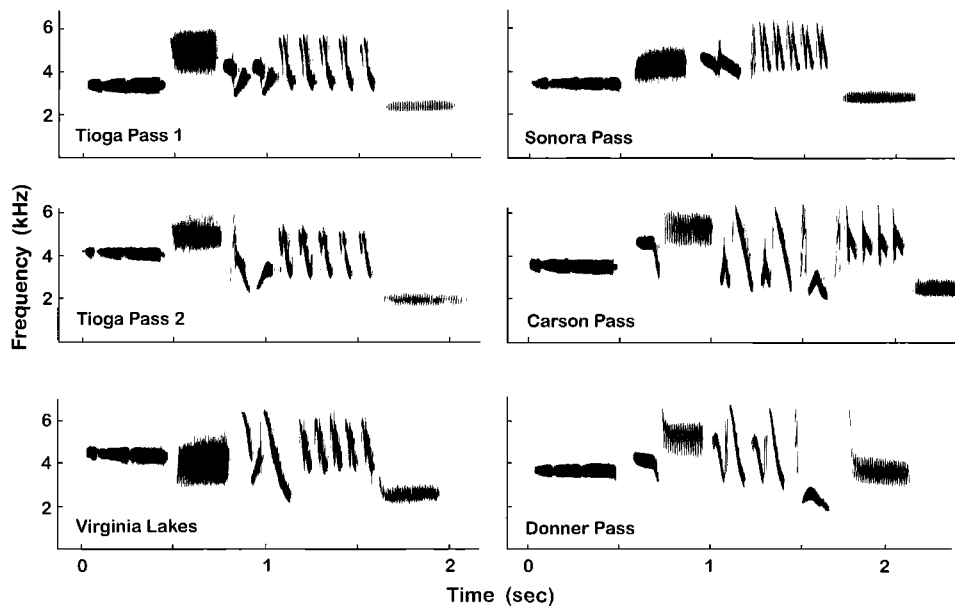
FIGURE 3.4.   Audiospectrograms of *oriantha* songs recorded at five different breeding areas in the Sierra Nevada. Two song types were encountered at Tioga Pass. The various notes have been described as whistles, buzzes, complex and simple syllables, and trills (Baptista and Morton 1982, 1988; Nelson et al. 1996). Audiospectrograms provided by Douglas A. Nelson.

tinctively from one geographic region to the next (Blanchard 1941, Marler and Tamura 1962; Baptista 1975, 1977). The possible function of these dialects in mate choice by females or as potential barriers to gene flow has been probed extensively, but results have been equivocal (Chilton et al. 1990, MacDougall-Shackleton 2001). Still they, and other features of White-crowned Sparrow vocalizations, have been the focus of many contemporary studies of song learning and sociality (Petrinovich and Patterson 1981; Baptista and Morton 1982, 1988; Baker 1983, Baker and Thompson 1985, Baptista 1985, Kroodsma et al. 1985, Chilton et al. 1990, Lampe and Baker 1994, Nelson and Marler 1994; Nelson et al. 1995, 1996; MacDougall-Shackleton 2001, MacDougall-Shackleton et al. 2001).

Non-song

The various vocalizations of *oriantha,* other than song, including their description, context of use, and possible functions, have been reported for a population in the Rocky Mountains of southwestern Alberta by Hill and Lein (1985). They found nine vocalizations expressed by adults that could be reliably identified. All nine were used by males and five were used by females. The five most commonly used calls were given the descriptors of *pink, whine, trill, flag,* and *sip.* The *pink* was a mobbing or scolding note used by both sexes when a disturbance or intrusion occurred on the territory (in our study this note was described as *chip*). The *whine* was used by both sexes and was associated with conflicts and with locomotor activity. The *trill* was also used by both sexes, but in quite different contexts. It was uttered by females when soliciting copulations and by males when

they were involved in same-sex attacks and territorial disputes. *Flag* was used only by males and was associated with agonistic behavior. *Sip,* a quiet call, audible to the investigators only from close range, was given by males during non-agonistic encounters and by incubating females while flying back to their nests.

The non-song vocalizations in this Rocky Mountain population, and their social contexts, are mostly familiar to us, but they may be employed in a slightly different manner in Sierra Nevada populations. For example, the *sip* call (*seep* to us) was used at Tioga Pass by incubating females when leaving the nest, as well as when entering it. If the call was not given by the departing female, the male appeared not to recognize her and would pursue her quite aggressively in an aerial chase until both birds finally landed, whereupon hostilities ceased. The *sip,* therefore, appears to function as an identification or contact call between mates. In both wild and captive *oriantha* we have heard numerous calls or notes, often of low volume and given at close range to other birds, that were not mentioned by Hill and Lein (1985). Given the microgeographic variation present in the songs of *oriantha* (see below), it seems clear that additional studies of inter-populational variation in their non-song vocalizations should yield interesting comparative data.

Song

In 1969, during a search for *oriantha* populations to the north of the study area, it was discovered that males singing in meadows at Sonora Pass and at Carson Pass sounded quite different than the ones at Tioga Pass (Fig. 3.4). The following summer Jorge Orejuela recorded more than 1,000 songs from 142 males at 14 locations over a distance of 500 km along a north-south axis of the Sierra Nevada. Songs had a duration of about 2 sec in all populations, but substantial variation in their structure was evident, and 10 distinctly different patterns or dialects were identified. Furthermore, variation in song within populations was inversely related to habitat area, being less variable in large meadows than in small ones (Orejuela and Morton 1975). Twenty-six years later, in 1996, males were again recorded at some of the original sites and it was discovered that the local dialects had been retained except for some drift at the smallest, most fragmented of the habitat areas (Harbison et al. 1999)

In another study of geographic variation in song types of *oriantha,* Baptista and King (1980) recorded songs from 18 populations scattered over six western states (California, Colorado, Idaho, Nevada, Oregon, Wyoming) and two provinces (Alberta, British Columbia). They found regional differentiation of song into types that shared elements in common with other subspecies (*nuttalli, pugetensis,* and *gambelii*). It is well understood that White-crowned Sparrows learn their songs by copying those that they hear early in life (Marler 1970), so some *oriantha* juveniles appear to learn at least portions of their songs while in contact with other subspecies, presumably during migration or on wintering areas. In their survey, Baptista and King (1980) also discovered that a recently established population in the San Bernardino Mountains of southern California was probably founded by birds from the central Sierra Nevada because their dialect was identical to the one at Tioga Pass. Note that this speculation gains support from Harbison et al.'s (1999) demonstration that dialects are retained in an area over a considerable period of time. Lein (1979) was also able to use the concept of dialect persistence in *oriantha* to address another zoogeographic question. He

found that birds in the Cypress Hills, a disjunct population (see Fig. 1.2), were probably not in contact with their closest neighbors, some 250 km away in the Rocky Mountains, because their dialects were quite different.

Singing by female songbirds, specifically the oscine passerines, is considered to be uncommon, but it does occur. The function of female song is unknown, but various suggestions have been made. For example, it may facilitate pair bonding in Northern Cardinals (*Cardinalis cardinalis*; Ritchison 1986), or signal intra-sexual aggression in Yellow Warblers (*Dendroica petechia*; Hobson and Sealy 1990). Among White-crowned Sparrows, captive *gambelii* females sing frequently while undergoing photostimulation (Morton et al. 1985) and *nuttalli* females sing year around in the wild, perhaps to advertise for a mate or to fend off other females from their territory (Baptista et al. 1993). Female *oriantha* were observed singing robust, male-like songs, but only at the beginning of the nesting season (Morton et al. 1985, Baptista et al. 1993). As yet, no adaptive value can be assigned to this behavior. It could be functioning in territoriality, but its apparent restriction to the early season in this subspecies suggests that it might simply be an epiphenomenon, the result of high, transient levels of sex hormones produced during a period of generally elevated steroidogenic activity.