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THE INFLUENCE OF HABITAT QUALITY AND GENDER ON THE VARIABLE MATING
SYSTEM OF A TERRITORIAL PASSERINE, THE SAVANNAH SPARROW

By

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ABSTRACT

THE INFLUENCE OF HABITAT QUALITY AND GENDER ON THE VARIABLE MATING SYSTEM OF A TERRITORIAL PASSERINE, THE SAVANNAH SPARROW

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Factors influencing territorial spacing, reproductive successes and pair bonds of male and female savannah sparrows were examined using data from a behavioral, observational study of an individually-marked southern Michigan population of a migratory passerine, the savannah sparrow (Passerculus sandwichensis). Behavioral observations were made, territories were mapped and measured, nests were mapped and fates determined, and pair bonds were assessed. The significance of an unexpected finding of a female territorial system was examined relative to historical definitions of territoriality and mating systems and in contrast to the assumptions of the polygyny threshold model.

The majority of mated pairs were monogamous, with polygynous pair bonds occurring among five to twenty-four percent of the mated pairs. Using data on the reproductive successes and spacing systems of both genders, explanations were sought for variances in territory sizes as well as for the predominance of monogamy and the low, but regular incidence of polygynous pair bonds.

A significant inverse relationship existed between territory area and an estimate of habitat quality based on the measurement of a stable habitat feature. Female territories showed more overlap of boundaries

in areas of higher quality. Nest spacing of nearest neighbors was negatively correlated with the proportion of overlap, with this relationship appearing mid-season, when resident females faced a trade-off between territorial defense and parental demands.

In certain years, the ability to engage in multiple nests resulted in significant differences in reproductive success. Re-nesting ability on the part of the female was linked to early nest initiation dates, habitat quality and male age.

Polygynous pair bonds occurred when a male could expand and secure two female territories or, more commonly, when two females nested within the space defended by one male. Male expansion was limited by male-male competition for space. Spacing of nesting females appeared to be influenced by habitat quality and by the conflicts faced by the resident female between territorial defense and nesting demands. In this population, the time limitations of the breeding season and same sex territorial interactions result in a predominance of monogamous pair bonds, even in a habitat which varies in quality.

IN MEMORY OF:

Ethel K. Read
Irene F. Jorae **Loretta Locher**
Janice D. Johnson Cooper

**Curiosity about the natural world combined with a spirit of wonder -
these are their legacies to me.**

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CHAPTER I

INTRODUCTION

The savannah sparrow is a small (18g), monochromatic passerine (Emberizidae; Emberizinae; Passerculus sandwichensis) which breeds throughout much of northern North America in open country habitats such as coastal dunes, salt marshes, bogs, tundra, hayfields and pastureland. It is migratory throughout the vast majority of its range with some resident populations in the salt marshes of Baja California, Mexico. Nests are placed on the ground and both parents usually participate in the care of the young.

Studies of migratory populations of savannah sparrows in several locations have revealed a primarily monogamous mating system centering on a resource-based territorial system (Potter 1972; Stobo and McLaren 1975; Welsh 1975; Dixon 1978; Weatherhead 1979a; Bedard and LaPointe 1984b). Yet, in some of these populations, from five to forty percent of the pair bonds were reported as polygynous, involving one male simultaneously pair bonding with two females.

The polygyny threshold model (Verner and Willson 1966; Orrians 1969; Emlen and Oring 1977) attempts an explanation for the occurrence of polygyny in species with both resource-based territories and bi-parental care of the young. These traits are typical of most birds in the order Passeriformes, including the savannah sparrow. Thus, the polygyny threshold model has been the model of choice in previous explanations of varying proportions of monogamy and polygyny in populations of this species. Models which involve considerations of territory area and quality, such as the polygyny threshold model, are

strongly assumption dependent (Hixon 1987). Since many of these assumptions in the polygyny threshold model are implicit, caution must be exercised not to forego an initial examination of their validity before testing predictions of the model.

The presence of a mixed mating system combined with a resource-based territorial system made the savannah sparrow a good species to study for an understanding of the interface of resource distribution, spacing systems and mating systems. The open grassland habitat facilitated the visual observations of male and female behaviors, the delineation of territorial borders and the locating of nests; all factors crucial to building an understanding of the mating system.

In this study, I attempted an understanding of the underlying causes of the predominance of monogamous pair bonds and the low, but regular, incidence of polygynous pair bonds in part of a breeding population of savannah sparrows, using qualitative and quantitative data from a behavioral observational study of individual males and females. Upon detecting a female territorial system, I hypothesized that the observable mating patterns of individuals could be explained as the result of the spacing patterns of males relative to other males and females relative to other females. These spacing patterns, in turn, could be understood as resulting from a balance of the costs and benefits of all activities each gender undertook throughout the breeding season in an effort to maximize his or her reproductive success. Following standard practice in behavioral observational studies, quantified data are complemented in this study by the inclusion of data that cannot currently be quantified. The data were

also used, where applicable, to examine the validity of the assumptions of the polygyny threshold model. The methods of data collection as well as the types of data collected were determined by the following rationale and conceptual approach.

A system can be defined as "a regularly interacting or interdependent group of items forming a unified whole" (Webster's New Collegiate Dictionary 1977). A mating system, then, seems an appropriate way to describe the overall pattern which emerges as a composite of mating patterns exhibited by a population of individuals. Natural selection acts most strongly at the level of the individual (Williams 1966). Therefore, an understanding gained through study of the factors which potentially influence the reproductive success of individuals will result in a solid evolutionary basis for any understanding of the origin of a mating system.

Any study of individuals must recognize that both males and females will experience selection for differential reproductive success, although often not in the same manner or with the same intensity. Females, with their larger gametic investment in eggs, have been termed the limiting sex (Trivers 1972). It is assumed that with a higher gametic investment, females should be selected to exhibit a stronger choice relative to a potential breeding situation but exhibit less variance in the resultant reproductive success. By contrast, it is usually assumed that males will exhibit more variance in their reproductive success, and often stronger selective pressures with respect to phenotype, as they compete for opportunities to be chosen as mates by the limiting sex. Even if male reproductive success does vary more than that of females, this does not mean that variability in

female reproductive success is unimportant (Hrdy and Williams 1983). An understanding of mating systems must include consideration of factors which affect the reproductive success of both genders considered both separately and together. This results in a view of a mating system of a species which is a composite of the mating patterns of both genders. Gender mating patterns are, in turn, a composite of the patterns of individual males and females.

More concretely, the initial difference in gametic investment in an anisogamous species may fundamentally influence the variety of ways that individuals of each gender attempt to maximize reproductive success. Costs and benefits of parental care, spacing relative to the same and the opposite sex, and potential for and advantage of multiple breeding opportunities may differ between the genders as their importance to individual reproductive success differs. Thus, gender may be viewed as the primary source of behavioral variation between individuals in a sexually reproducing species. Because of this, a concerted effort was made at every juncture not to use either gender's behavior as the standard by which the other gender was measured. Rather, gender was used as a lens through which the questions about options regarding reproductive success were viewed in turn for both males and females (Figure 1). The consideration of female reproductive success relative to that of other females is not yet prevalent in avian studies in general, most particularly in those dealing with passerines, (but see Hannon and Zwickel 1979; Hannon et al. 1982; Hannon and Smith 1984; Hannon 1984; Davies and Lundberg 1984; Davies 1985; Eliason 1986; and Breiehagen and Slagsvold 1988). This lacuna in data has far-

reaching repercussions in the realms of definitions and theory. These implications are considered in some detail in the chapter entitled "Background."

Time is inherently a component of the variance in extrinsic environmental factors as well as in intrinsic physiological factors. Therefore, time was another lens used to view the factors influencing reproductive success of each gender (Figure 1). Particular emphasis was placed on the time constraints which are inherent in the limited breeding season of a migratory species.

The ultimate objective of such an approach is an understanding of the mating patterns of individuals of a population which is based on a consideration of the factors influencing the spacing of males relative to other males, females relative to other females and the genders relative to each other. A beginning understanding of spacing, in turn, arises from the consideration of factors which have the potential to influence the reproductive success of males relative to other males and females relative to other females. Finally, the mating system of the population is seen as a composite of the gender-based mating patterns of the individuals in that population.

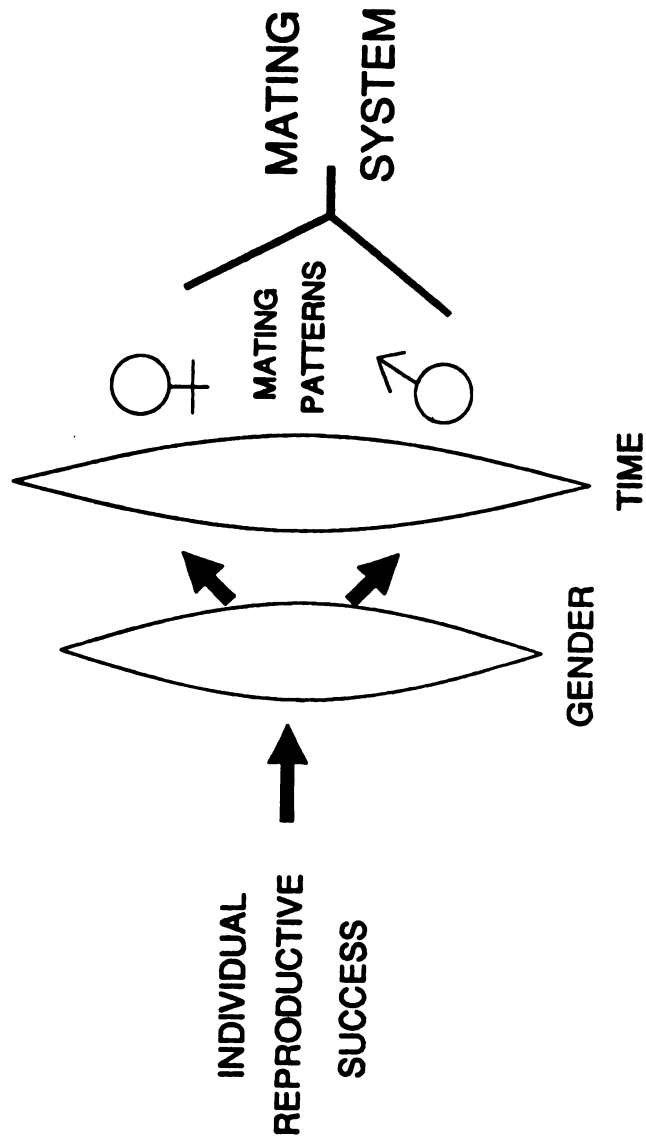


Figure 1. Analytical approach to the study of mating systems

CHAPTER II

BACKGROUND

Definitions of territoriality

Problems in defining territoriality

Since mating systems are widely considered to result in some fashion from the spacing of individuals (Verner and Willson 1966; Orians 1969; Emlen and Oring 1977; Kleimann 1977; and others), a definition of territory is crucial to a discussion of mating systems. The following discussion on territoriality owes much to Kaufmann's (1983) excellent review article.

The concept of territory was originally defined by looking at the behavior of a male bird defending an area against conspecific males for the purposes of acquiring access to a female for breeding (Howard 1920; Dewar 1920; Tinbergen 1936; Noble 1939; Lack 1944). The definition of territory as a "defended area" (Noble 1939, Hinde 1956, Brown and Orians 1970) has its origins in these studies. As the study of territoriality has expanded to include diverse taxons of animals, definitions have also become more inclusive (Pitelka 1959; Ralls 1977; Waser and Wiley 1979; Kaufmann 1983; Stamps 1983, 1988; Stamps and Buechner 1985). Kaufmann (1983) summarized and critiqued the current state of thought on this topic and set forth a definition of territory as "a fixed portion of an individual's or group's range in which it has priority of access to one or more critical resources over others who have priority elsewhere or at another time. This priority of access must be achieved through social interaction." This definition has the advantage over previous definitions in that it can be applied in an

unbiased fashion across taxons and genders. It has the advantage of taking the focus off the degree of exclusivity of use of space (Pitelka 1959), which is on a continuum, not an all or nothing phenomenon. Male territories frequently show varying degrees of boundary overlap and fluidity of boundaries in both birds and mammals (Stenger and Falls 1959, Weeden 1965; MacDonald 1983; Arcese 1987; Dyrce 1989). Since critical resources have implications for the reproductive success and ultimately the fitness of the organism, this definition is also one that functions well in the consideration of the evolution of mating systems. Thus defined, territory subsumes other spacing terms such as home range when these basic criteria are met. Kaufmann's (1983) definition of territory will be the standard throughout this discussion.

Defining dominance

In principle, territoriality defined as a spatial form of social dominance appears to be eminently functional. In practice, the measurement of dominance is not always so clear, particularly in studies involving captive versus free-living organisms or in studies which span taxons or genders (Gauthreaux 1978; Bernstein 1981; Fox et al. 1981; Eckert and Weatherhead 1987; Dixon 1988; and others). The main difficulty in assessing dominance with reference to territoriality in birds has been the historical emphasis on aggression as the primary measure of the degree of territoriality (Howard 1920; Tinbergen 1936; Noble 1939; Lack 1944). Recent work has emphasized the tandem and equally important role played by the subordinate in a dominance situation (Marler 1971; Kaufmann 1983). Displays which convey the

dominance or subordinateness of a territory holder can be extremely subtle and may be missed by the human observer if they result in the fleeing of the subordinate opponent before any interaction can be quantified. Yet, such behaviors accomplish the function of dominance in a territorial system; that of priority of access to resources in a defined space. Both dominant and subordinate components are necessary to produce, and hence to document, a spacing system.

Measurement of aggression

Aggression is often quantified using male agonistic behavior as the implicit standard of measurement. In birds, song, chases, fights and various postures may be the most frequently occurring male agonistic behaviors as well as the most visible and easily quantified. Using such criteria, the male may be assigned a larger role than the female in territorial defense (Baeyens 1981a). Female aggression may also be more variable over the length of the breeding season as she faces other demands on her time and energy associated with egg production and care of zygotes and young (Breiehagen and Slagsvold 1988). This temporal component of female aggression is a potentially important variable. In some situations female spacing behavior has been completely ignored because of the emphasis on defining territory based on male agonistic behaviors (Searcy 1986). Wilson (1975) even stated that typical territorial behavior is "most fully developed in adult males." All such conclusions are circular if male agonistic displays were initially chosen as the definitive standard of measurement.

Biases of gender in current literature

The difficulty not only lies in assessing a comparative degree of territoriality between genders, but also in even detecting and labeling

territoriality where it exists. In mammal species with known territorial systems, females are often described as occupying home ranges where they are dominant, particularly in terms of bearing young, over other females (Yeaton 1972; Bailey 1974; Jarman 1974; Powell 1979; Holmes 1984; Gipps et al. 1985; Ramsay and Stirling 1986; Kawata 1987; and others). Varying degrees of spatial overlap for foraging may exist (Fuller 1978) but with only one female raising young in the same space. A male territory may encompass one to several female home ranges (Kleiman 1977; Ralls 1977). Similar situations have been documented in lizards (Manzur and Fuentes 1979; Huey et al. 1983; Stamps 1983; Bull 1988). Although the terminology "home range" is used in accordance with the policy of using the restricted definition of a territory as a defended area, the home ranges in these examples agree with the definition of territory set by Kaufmann (1983). In contrast, as mentioned in the introduction, avian female territorial behavior is rarely considered except as part of the male system, while territorial behavior in avian males is commonly both anticipated and found. In the majority of bird species during the breeding season, males hold territories in order to gain access to females. Female birds have been consistently described in the majority of literature as selecting the male's territory and perhaps selecting the male as well, rather than competing for and selecting resources relative to other females. In conjunction with this male oriented interpretation, any territorial behavior that she might exhibit has been viewed as participation with the male in the defense of his territory.

Variation in female reproductive success. A limited definition of territory may be viewed as symptomatic of a more fundamental bias. This bias is that of assuming that the greater variation in male reproductive success results in the male's having more important influences on the social structure of the species than the female. This approach, in turn, may result in the complete dismissal of the effect that female reproductive variation may have on the social system of the species. While it is true that a lower gametic investment and a concomitant potential for greater reproductive variation may lead to male territorial and mating patterns which differ from those of the female, this does not make the male patterns more important in an understanding of the territorial and mating system of the species (Hrdy and Williams 1983; Wasser and Waterhouse 1983). Sources of variation in male reproductive success should not be allowed to subsume those of females.

Hrdy and Williams (1983) have outlined fundamental sources of variation in female reproductive success. Genetic differences, female mate choice, female elicitation of male support and protection, mothering styles and skills, competition with other females, and cooperation among females may all contribute to reproductive success. In the treatment of female-female competition, the authors note that "a female's competitive status relative to other females may be the single most pervasive influence on her reproductive success...influencing diverse aspects of her life." Both competition by females for the resources critical to reproduction, as well as cooperation in utilizing such resources, implies some sort of spatial priority of access to the resources which potentially excludes other females. Male support and

protection may also be a resource that is the object of female competition, and one that can be secured by means of territorial behavior.

Components of a complete territorial definition. If a territory is defined by "priority of access to resources over others", a complete description of a territorial system will include a identification of the "other" (the subordinate). If "social interaction" is another component of the definition, then a complete territorial description will include the types of social interactions used to secure the access. These could vary from song and visual cues employed by birds to olfactory cues which have been documented in mammals and amphibians (Gosling 1987; Horne and Jaeger 1988; Smith et al. 1989).

The same geographical space may thus be viewed as a part of two distinct territorial systems. Not only might the types of social interactions vary qualitatively and quantitatively between the two genders, so might the resources which are being acquired. In a typical avian passerine territorial system, the main object of male territoriality is believed to be priority of access to females. To this end a male may exclude all other males from the territory, but allow access to his territory to any female and, in some cases, to non-breeding males. The concern of the male does not appear to be with the sequestering of the maximum amount of food resources on the territory but rather, with competition for mating opportunities. In contrast, the female is typically more concerned with attaining priority of access to the food or nesting resources as well as to potential male parental care. To this end, she may exclude all other females and

sometimes males other than her pair bonded mate. Along the same lines, Hixon (1987) used Schoener's (1971, 1983) terminology to predict that the male would be an area maximizer and the female an energy maximizer.

Evidence for female territoriality

The historical lack of emphasis on female territoriality, particularly evident in avian ethology, stems in many cases from this lack of attention to female-female competition. It is exacerbated by measurement techniques which often employ male standards, or simply fail even to consider the possibility of the existence of female territoriality. Nevertheless, some evidence for female territoriality does exist for a variety of species across taxons, sometimes directly documented by spatial measurements and other times evidenced by indirect measures such as the presence of female-female aggression in a defined space. The following brief review provides a sampling of the taxonomically widespread evidence for female territoriality. It is meant as a preliminary review, not an exhaustive treatment.

Insects

In insects, female territorial behavior is often undocumented. Yet, even a cursory selected reading hints at the presence of such systems. Bartlett (1988) found that female carrion beetles (Nicrophorus vespilloides) were likely to fight with other females upon meeting upon a carcass used for the incubation of eggs and provisioning of the parents and the young. By contrast, males, in the absence of females would cooperate in burying a carcass, establishing a dominance hierarchy in competition for a mate only after a female arrived. If the carcass were exceptionally small, the usual biparental care was

disrupted by female aggression directed toward driving off her mate, perhaps in order to conserve the limited resource for herself and her young. Female dragonflies appear to actively choose oviposition sites, but here there is actually evidence in some species for the aggregation of females rather than spacing by dominance (Waage 1987). A study of water striders (Limnoparus dissortis and L. notabilis by Spence and Wilcox (1986) described courtship and territorial water surface ripple signals employed by the male and implied that females also have a signaling repertoire associated with courtship. Such a signaling repertoire could also be potentially used to communicate with other females, but female responses and possible competition were not examined in this study.

Amphibians

Studies on amphibians show a similar dearth of information on female behavior, yet some exceptions do exist. The first territorial work done on red-backed salamanders (Plethodon cinereus) dealt with male pheromonal and behavioral advertisement and defense of territories (Jaeger and Gergits 1979; Jaeger et al. 1982, 1986). In line with the recently placed emphasis on subordinate behavior, they found that 26% of the contests ended with the fleeing of the intruder in response solely to pheromonal signals, in lieu of overt aggression (Jaeger et al. 1982). Additional studies revealed the existence of a similar female territorial system. Additional experiments with pheromones indicated that the females show an even more aggressive response to the presence of intruder pheromones than do the males, and bear the scars of previous fights (Horne and Jaeger 1988). Spatial studies on anurans

have tended to focus on male breeding territories. Although female bullfrogs actively seem to select the best oviposition sites, no data were presented to indicate whether females compete for such sites or non-competitively aggregate in certain locations (Howard 1978).

Reptiles

Documentation of female territoriality in reptiles is most frequent in studies of lizards, perhaps because of their high visibility and diurnal habits. Although female spacing is usually referred to in terms of home ranges, it appears to meet Kaufmann's (1983) functional criteria for a territory. Thus defined, female territoriality has been documented in Sceloporus jarrovi (Simon 1975), Liolaemus tenuis (Manzur and Fuentes 1979), Uta stansburiana (Fox et al. 1981), Trachydosaurus rugosus (Bull 1988), and others (Brattstrom 1974; and Stamps 1983). In reptiles other than lizards, often even the spacing of the males is poorly known and the question of female spacing has not been broached (Galbraith et al. 1987).

Mammals

Female territories in mammals are also recorded as home ranges, but once again meet the criteria set forth in this paper for territory. Due to the secretive habits of many mammals, much of the evidence stems from radiotelemetry or trapping studies. Examples of spacing systems involving solitary females include bobcat (Bailey 1974), tiger (Smith et al. 1989), gray fox (Fuller 1978), selected mustelids (Powell 1979), selected antelopes (Jarman 1974), bank vole (Clethrionomys glareolus) (Gipps et al. 1985), and red-backed vole (Clethrionomys rufocanus) (Kawata 1987). An elegant experimental study involving playbacks of vocalizations, similar to work done with male birds, revealed a female

territorial system associated with a monogamous breeding system in the agile baboon (Mitani 1987). In addition, group female territories, sometimes with female dominance hierarchies, have been documented in such diverse species as fallow deer (Clutton-Brock et al. 1988), red-necked wallaby (Johnson 1986), gelada baboon (Dunbar and Dunbar 1977), and selected ground squirrel species (McLean 1984), to mention but a few.

Birds - Direct evidence.

Because female spacing in birds has rarely been examined apart from male spacing, documentation of female territoriality may most effectively be searched for using indirect as well as direct evidence. Such data are available because of the strong tradition of behavioral and territorial studies in ornithology. Table 1 summarizes some of the evidence for the existence of female territoriality in thirty families. One must often search for anecdotal mention of females since they are rarely the focal point of the studies. Because of these limitations of the literature, an exhaustive list of species with evidence of female territoriality cannot be produced at this time. The present review does, however, provide an idea of the scope and variety of evidence which already exists, albeit in a disguised form, in support of female territoriality in birds. This lends credence to the view of this study that female territorial behavior in the savannah sparrow is not peculiar to this species; that perhaps mating systems of other avian passerines should be examined with the same gender perspective.

Observations of spatial dominance involving priority of access to resources on the part of the female provide direct evidence of female

territoriality. Most commonly, if aggression is involved, it has been observed as directed toward competing females. It may also be directed toward males other than her mate or mates, or even interspecifically. The space and the resource may be one and the same as is the case when nest sites are restrictive and food resources are not economically defensible. In such cases the female or the pair may defend the nest site (often a cavity) from either take-overs or conspecific brood parasitism. Examples are certain alcids (Dulude et al. 1987), tree swallow (Stutchbury and Robertson 1987), and white-fronted bee-eaters (Emlen and Wrege 1986). Male and female buffleheads appear to defend a territory which may encompass several nesting cavities, thus preventing close settlement by conspecifics (Gauthier 1987; Gauthier and Smith 1987). In other species with aggregated nest sites, such as red-winged blackbirds, females may attempt to prevent nesting by later settling females and thus aggressively limit the number of females potentially sharing resources and paternal care of young (Hurly and Robertson 1985; Lenington 1980). A female of a species whose territory provides both nest sites and food resources (Type A territory, sensu Nice 1943) may also aggressively attempt to limit settlement by additional females and thus maintain priority of access to nest sites, food resources, and male parental care. Documentation of this type of female territoriality exists for the tree sparrow (Weeden 1965), swamp sparrow (Willson 1966), the dunnoek (Davies 1985), the great tit (Bjorklund and Westman 1986) and the savannah sparrow (Stobo and McLaren 1975; This study).

The clearest examples of female territoriality in the literature, to date, tend to come from species where the male has no role or a

limited role in parental care. Examples of female territorial behavior associated with fledged young have been documented in the ducks (Young 1970; Savard 1982; Haland 1983). Female territories have also been reported in various species of grouse (Herzog and Boag 1977; Maxson 1978; Hannon et al. 1982; Hannon 1984; Bergerud and Butler 1985; and Wegge and Rolstad 1986), brown-headed cowbird (Dufty 1982; Teather and Robertson 1985; and Yokel 1986), hummingbirds (Wolf 1969), lyrebirds (Kenyon 1972) and birds of paradise (Pruett-Jones and Pruett-Jones 1988). This more than likely does not reflect a unique association of female territoriality with uniparental care but rather the human observer's freedom from the confounding factor of male territorial behavior associated with the nest. In many of these species copulation occurs on male display territories which are distinct from the female territories.

Other direct evidence for female territory comes from cooperatively breeding birds, particularly those involving one breeding female with auxiliary male helpers. Examples include the acorn woodpecker (Joste et al. 1985) and Galapagos mockingbird (Curry 1988). In these species the dominant female drives off all competing females while allowing extra males to remain on the territory.

In the non-breeding season, territorial behavior may secure access to vital food resources. Competition may be both between and within genders in some species. The Townsend's solitaire, a thrush, (George 1987) and the hooded warbler (Morton et al. 1987) have both been reported to have single bird feeding territories, sometimes with habitat distinctions between genders.

Table 1. Evidence for the existence of female territoriality in birds

FAMILY - Subfamily Genus species	Literature Citation	FT	FA	NA	SF	ND	XF	BI	FB
ANATIDAE									
<i>Tadorna tadorna</i>	Young 1970	X	X						
<i>Anas platyrhynchos</i>	Halland 1983	X							
<i>Bucephala albeola</i>	Gauthier 1987								
	Gauthier and Smith 1987	X	X		X				X
<i>Aythya valisineria</i>	Anderson 1985		X		X				
<i>Bucephala islandica</i>	Savard 1982	X	X		X			X	
ACCIPITRIDAE									
<i>Circus cyaneus</i>	Picozzi 1984a,b		X	X			X		
<i>Accipiter nisus</i>	Newton et al. 1977								
	Newton 1988		X		X	X		X	
<i>Buteo galapagoensis</i>	deVries 1975						X		
<i>Aquila chrysaetos</i>	Faaborg & Patterson 1981		X						
	Tjernberg 1985					X	X		
PHASIANIDAE									
<i>Dendragapus canadensis</i>	Herzog & Boag 1977	X	X						
<i>Dendragapus obscurus</i>	Bergerud & Butler 1985						X		
	Hannon et al. 1982	X	X			X			
<i>Lagopus lagopus</i>	Hannon & Smith 1984	X	X						
<i>Tetrao urogallus</i>	Wegge & Rolstad 1986	X			X				
<i>Bonasa umbellus</i>	Archibald 1975								
	Maxson 1978	X	X						
RALLIDAE									
<i>Gallinula chloropus</i>	Gibbons 1986		X					X	
JACANIDAE									
<i>Jacana spinosa</i>	Jenni & Collier 1972	X	X						X
<i>Jacana jacana</i>	Osborne 1982	X							

Table 1 (cont'd.)

FAMILY - Subfamily Genus species	Literature Citation	FT	FA	NA	SF	ND	XF	BI	FB
HAEMATOPODIDAE									
Haematopus ostralegus	Harris 1970						X		
CHARADRIIDAE									
Vanellus vanellus	Toft 1984	X	X						
Charadrius alexandrinus	Warriner et al. 1986	X							
Charadrius montanus	Graul 1974		X						
SOLOPACIDAE									
Actitis macularia	Hays 1973								
	Oving & Knudson 1973	X	X						
Calidris mauri	Holmes 1971				X				
Calidris temminckii	Hilden 1975		X						
Calidris alpina	Jonsson 1987		X						
LARIDAE									
Larus delawarensis	Dulude et al. 1987		X						
ALCIDAE									
Ptychoramphus aleuticus	Manual 1974	X	X				X		
STRIGIDAE									
Surnia ulula	Sonerud et al. 1987	X	X	X		X			
Aegolius funereus	Carlsson et al. 1987			X		X			
TROCHILIDAE									
Glaucis hirsuta	Snow 1973			X				X	
Phaethornis guy	Snow 1974		X						
Pantherpe insignis	Wolf 1969	X	X						

Table 1 (cont'd.)

FAMILY - Subfamily Genus species	Literature Citation	FT	FA	NA	SF	ND	XF	BI	FB
MEROPIDAE									
Merops bullockoides	Emlen & Wrege 1986	X	X						
PICIDAE									
Melanerpes formicivorus	Joste et al. 1985	X	X					X	
TYRANNIDAE									
Empidonax virescens	Kellner & Ritchison 1988		X (song)						
Empidonax traillii	Walkinshaw 1966								
	Prescott 1986								
	Sedgwick & Knopf 1989		X	X	X				
Empidonax minimus	Kellner & Ritchison 1988		X (song)						
MENURIDAE									
Menura superba	Kenyon 1972	X	X						
HIRUNDINIDAE									
Tachycineta bicolor	Stutchbury & Robertson 1985		X				X		
CINCLIDAE									
Cinclus mexicanus	Price & Bock 1973	X		X					
TROGLODYTIDAE									
Cistothorus palustris	Welter 1935								
	Picman 1977								
	Leonard & Picman 1987a,b		X	X		X		X	
Troglodytes troglodytes	Garson 1980	X							
Troglodytes aedon	Freed 1986		X					X	

Table 1 (cont'd.)

FAMILY - Subfamily Genus species	Literature Citation	FT	FA	NA	SF	ND	XF	BI	FB
MIMIDAE									
Nesomimus parvulus	Curry 1988	X	X						
Mimus polyglottus	Derrickson 1989	X	X	X				?	
PRUNELLIDAE									
Prunella modularis	Davies 1985	X	X	X	X			X	
MUSCICAPIDAE									
Sialia sialis	Gowaty & Wagner 1988		X					X	
Myadestes townsendi	George 1987	X							
Saxicola torquata	Johnson 1961		X		X				
Oenanthe oenanthe	Brooke 1979		X	X					
Turdus migratorius	Young 1951		X						
Turdus merula	Dewar 1920							X	
Cettia cetti	Bibby 1982	?				X			
Acrocephalus scirpaceus	Catchpole 1971, 1972		X						X
Acrocephalus arundinaceus	Dyrce 1986		X						
Phylloscopus sibilatrix	Temrin & Jakobsson 1988		X						
Phylloscopus trochilus	Howard 1920								
	Lawn 1982		X						X
Ficedula hypoleuca	Alatalo & Lundberg 1984								
	Harvey et al. 1985		X	X			X		
Sylvia communis	Howard 1920		X						
PARIDAE									
Parus major	Krebs 1982								
	Bjorklund & Westman 1986	X	X				X		
SITTIDAE									
Sitta europaea	Matthysen 1986, 1987	X	X						

Table 1 (cont'd.)

FAMILY - Subfamily Genus species	Literature Citation	FT	FA	NA	SF	ND	XF	BI	FB
MELIPHAGIDAE									
Manorina melanocephala	Dow 1979		X						
EMBERIZIDAE - Parulinae									
Dendroica kirtlandii	Mayfield 1960			X					
	Radabaugh 1972				X	X			
Dendroica fusca	Morse 1976		X						
Dendroica magnaolia	Morse 1976		X						
Dendroica discolor	Nolan 1978		X		X	X			X
Dendroica striata	Eliason 1986		X		X				
Dendroica petechia	Reid & Sealy 1986								
	Hobson & Sealy 1989	X	X						X
Setophaga ruticilla	Ficken 1962		X						
Geothlypis nelsoni	Morton et al. 1987	X							
EMBERIZIDAE - Coerebinae									
Coereba flaveola	Wunderle 1984	X	X	X					
EMBERIZIDAE - Cardinalinae									
Pheuticus melanocephalus	Hill 1986		X				X		
Passerina cyanea	Payne 1983		X	X	X				
Spiza americana	Zimmerman 1966		X	X					
EMBERIZIDAE - Emberizinae									
Emberiza citrinella	Andrew 1956		X						
Emberiza schoeniclus	Bell 1967								
	Bell & Hornby 1969			X				X	
Calcarius lapponicus	Seastedt & MacLean 1979					X			X
Melospiza melodia	Knapp & Krebs 1974		X (song)				X		
Zonotrichia georgiana	Willson 1966	X	X						

Table 1 (cont'd.)

FAMILY - Subfamily Genus species	Literature Citation	FT	FA	NA	SF	ND	XF	BI	FB
<u>EMBERIZIDAE - Emberizinae (cont'd.)</u>									
<i>Passerculus sandwichensis</i>	Weatherhead & Robertson 1980a,b								
	Stobo & McLaren 1975								
	Welsh 1975								
<i>Ammodramus maritimus</i>	Rogers, this study	X	X	X	X	X	X	?	X
	Post 1974								
	Post & Greenlaw 1975		X						
<i>Ammodramus caudacutus</i>	Post & Greenlaw 1982		X						
<i>Spizella pusilla</i>	Best 1977		X		X		X		
<i>Spizella arborea</i>	Weeden 1965	X	X				?		
<u>EMBERIZIDAE - Icterinae</u>									
<i>Xanthocephalus xanthocephalus</i>	Lightbody & Weatherhead 1987		X						
	Blakley 1976								
<i>Aegialius phoeniceus</i>	Hurly & Robertson 1984, 1985								
	Beletsky & Orians 1987a,b		X	X	X		X		X
	Duffy 1982								
<i>Molothrus ater</i>	Teather & Robertson 1985								
	Yokel 1986	X	X						
<i>Icterus galbula</i>	Flood 1985		X						
<i>Euphagus cyanocephalus</i>	Williams 1952		X						
<i>Dolichonyx oryzivorus</i>	Martin 1974								
	Gavin & Bollinger 1985								
	Wootton et al. 1986		X	X	X				X

Table 1 (cont'd.)

FAMILY - Subfamily Genus species	Literature Citation	FT	FA	NA	SF	ND	XF	BI	FB
FRINGILLIDAE									
Carduelis tristis	Drum 1939		X						
Carpodacus mexicanus	Thompson 1960		X						
Fringilla coelebs	Howard 1920								
	Saether & Fonstad 1981								
	Mikkonen 1985	X	X				X		X
Fringilla montifringilla	Mikkonen 1985	X	X						
PLOCEIDAE									
Euplectes hordeacea	Lack 1935		X						
PARADISAEIDAE									
Paradisaea rudolphi	Pruett-Jones & Pruett-Jones 1988	X							
CORVIDAE									
Pica pica	Baeyens 1981a,b		X						
Corvus monedula	Roell 1979	X	X				X		
Gymnorhinus cyanocephala	Marzluff and Balda 1988		X						

Table 1 (cont'd.)

Key to types of evidence: X = evidence exists for this species
? = incomplete observations in literature

FT Female territoriality: Spatial priority of access to resources directly observed

FA Female aggression: Female-female aggression observed. Sometimes female-male aggression

NA Nesting asynchrony: If two females nest in one territory then second female does not nest until first female is incubating.

SP Site fidelity: A greater than random probability of returning to the same territory to breed in the ensuing year.

ND Nesting density: Concurrent nests in the population are dispersed in a pattern which differs from random.

XF Extra females: Floating or non-breeding females are present in a population, indicating that some females are prevented from breeding.

BI Breeding interference: One female is directly or indirectly able to destroy the nesting attempt of another, usually spatially competing, female.

FB Female boundaries: Females are recorded to regularly use space that falls outside the male's original borders for feeding or nesting.

Birds - Indirect evidence

Female aggression. While the observational data do not always clearly associate female dominance with a geographical space, there are numerous references to female aggression and in a few species, song by the female. The early writings on avian territoriality of Howard (1920) detail female-female aggression in the willow warbler, whitethroat, reed warbler, and the chaffinch. The object of the female's aggressive behavior was assumed to be the male's territory. The examples listed in Table 1 include mainly records of aggression directed toward conspecific females although in some cases aggression was also directed toward conspecific males. In any case, the phenomenon of female-female aggression is widespread. A preliminary reading of the literature lists 79 species in 27 families (Table 1). In most cases, the presence of female-female aggression is strongly suggestive of female territoriality. This is particularly true when it is linked with the presence of non-breeding or floating females (Hill 1986). Many studies may simply lack more careful observations of the spatial component of the dominance behavior from the female's perspective.

Site fidelity. Site fidelity or philopatry in male birds is frequent in occurrence and considered an integral part of territorial behavior. The significance of site fidelity in females has been confounded by the question of whether she is choosing to return to the same geographical location or to the same mate. In species which suffer a high mortality on wintering grounds and migration, returning to a specific territory may be very unlikely to reunite a pair from the previous season. For some species, there are also records of a female

returning to the same territory but pairing with a new, neighboring male even if her previous mate was present (Weatherhead and Robertson 1980a; Eliason 1986; Picman 1987; This study). In such cases, the faithfulness appears to be toward the territory. In a marked bird study of canvasback, a diving duck, Anderson (1985) found that females exhibited significantly greater percentages of site fidelity between years than did the male. Other studies have indicated a lesser degree of site fidelity on the part of the female (Blancher and Robertson 1985; Ueda 1986). In some cases this may be fact, but in others it may be artifact. It could result from a greater difficulty in banding females for observation. Or, in other cases, the initial territory which was used for the subsequent comparison may have originally used the male boundaries for mapping, which may not have matched the female boundaries. Nonetheless, even if females can be shown to be less site faithful, it may argue for more between-season flexibility in site faithfulness, in response to factors such as nest predation or a higher rate of mortality, not for a decreased degree of female territoriality as a whole. In spite of the ambiguities of interpretation, female site fidelity does seem at least to indicate a female territorial perception. Table 1 documents its presence in such diverse species as bufflehead (Gauthier 1987), Barrow's goldeneye (Savard 1982), canvasback (Anderson 1985) European sparrowhawk (Newton et al. 1977), western sandpiper (Holmes 1971), wheatear (Brooks 1979), stonechat (Johnson 1961), Kirtland's warbler (Radabaugh 1972), prairie warbler (Nolan 1978), blackburnian warbler (Eliason 1986), field sparrow (Best 1977), savannah sparrow (Bedard and LaPointe 1984b; This study), red-

winged blackbird (Beletsky and Orians 1987a,b), and bobolink (Gavin and Bollinger 1985; Wooten et al. 1986).

Non-breeding females. If resources are limited and some females maintain priority of access to these resources via territoriality, then it is likely that some females would be prevented from breeding and exist as a floating population (Faaborg 1988). This is analogous to the interpretation of male floaters in a breeding population (Brown 1969). A bird which does not acquire a territory may be prevented from breeding temporarily or for all of its lifetime. Other individuals may lose ownership of a territory and become floaters after having bred. A floating population of non-breeding birds is viewed in either case as a result of a territorial system which prevents some individuals from breeding at a particular time. Since male birds, as the sex with the lower gametic investment, can be expected to attempt to attract as many females as possible for insemination, not exclude them from breeding, a floating female population provides indirect evidence of monopolization of resources by female territorial behavior. The existence of floaters has been historically demonstrated by the removal of a territorial bird and documentation of its replacement (Hensley and Cope 1951; and Stewart and Aldrich 1951). These two early removal experiments focused on male territory holders in a variety of wood warbler (Parulinae) species because of the male's high visibility to the human experimenters. Still, some female replacements for removed females were documented by Hensley and Cope. Other removal experiments which specifically included females have provided some evidence of a floating female population in the oystercatcher (Harris 1970), the blue grouse (Hannon

and Zwickel 1979), the song sparrow (Knapton and Krebs 1974) and the chaffinch (Saether and Fonstad 1981). Some removal experiments have shown an absence of female floaters as was the case with Holcomb's (1974) red-winged blackbird study. Timing, however, may be essential to female replacements. In Holcomb's study the females were removed after the starting date of the latest nest. There may be a time after which a female no longer chooses to settle if there is not sufficient time left in the breeding season for her to raise a brood successfully. Surplus females or, alternately, females from suboptimal habitats, were reported in a removal study by Hurly and Robertson (1985). In some field studies, observation alone has revealed a floating female population, either through a ready replacement of any female which leaves her breeding position, by seeing female intruders investigating the territory, or by documentation of individuals which do not breed until they are greater than one year old. Such observation has revealed a floating female population in field sparrows (Best 1977), rufous-collared sparrows (Smith 1978), red-winged blackbirds (Dolbeer 1976), Cassin's auklet (Manuwal 1974), pied flycatcher (Harvey et al. 1985; Slagsvold et al. 1988), and savannah sparrow (This study).

Nest spacing. Female birds incubate their eggs externally in a nest which is placed in a particular habitat. Food availability for the young and protection from predation are the two main factors influencing nest location. If feeding is done on territory, near the nest, then competition with other females for resources near the nest may exist, resulting in dispersion of nests. If male parental care is important to female reproductive success, this too might result in

competition between females for nest location, in order to avoid the sharing of paternal care (Seastedt and MacLean 1980). If nest sites are not so limited as to produce aggregated female nesting such as that described for the red-winged blackbird, then this competition may produce a hyperdispersed pattern of nest placement in the population. Such patterns have been observed in the European sparrowhawk (Newton et al. 1977), the blue grouse (Hannon et al. 1982), the Kirtland's warbler (Radabaugh 1972), the prairie warbler (Nolan 1978), the savannah sparrow (Stobo and McLaren 1975), and lapland longspur (Seastedt and MacLean 1980). The clearest data are those which deal with nests that exist concurrently since females that settled concurrently were free to interfere with the settling of their neighbors and thus influence each other's nest spacing. Populations which breed in a highly synchronous pattern are good candidates for obtaining these data. If the breeding season is prolonged, nest spacing may change when the early nesting females are incubating and limited in their time for aggression, allowing the closer spacing of later settling neighbors.

Nesting asynchrony. Female aggression toward other settling females may also result in asynchrony of nesting cycles by multiple females in a restricted space. Aggression at the beginning of the nesting cycle may succeed in temporarily preventing settlement by a competing female. Nevertheless, ensuing demands of egg laying, incubation and brood care on the resident female may raise the cost of such territorial exclusivity, resulting in her eventual inability to prevent settlement by another female. The result can be nesting of the two females which is staggered in time (Crawford 1977; Oring 1982).

Nesting asynchrony between females is frequently mentioned,

particularly in studies involving multiple females nesting with one male (Table 1). It is possible that nesting asynchrony could result from a pattern of intentional delay on the part of the later settling female rather than from aggression on the part of the primary female. But in many of the cited species, female-female aggression has been noted, suggesting that females are trying to settle earlier and are prevented from doing so. In addition, evidence from a variety of species shows that females which breed earlier have a higher lifetime reproductive success (Clutton-Brock, 1988). This early breeding advantage also argues against an intentional delay in nesting on the part of the later settling females since doing so could be detrimental to their reproductive success.

Male and female territorial borders. Female borders may differ from male borders. These discrepancies between male and female borders may be observed directly by observation of use of space by both sexes or indirectly through the placement of the nest by the female.

In most species, females appear to make the final selection of the nest site. Occasionally, a nest is located outside of the male territorial borders (Gavin and Bollinger 1985; This study). In many such accounts the nest is described as being outside of or at the edge of the territory, with territory being measured using the male's perception. It is also plausible that the female has placed her nest within her borders and that her borders differ from those of the male.

The observation of the actual territorial borders of the female provides more direct evidence. Descriptions of female snow buntings by Tinbergen (1939), described the females as frequently walking outside

the male borders and even fighting there. His interpretation was that a female had not yet learned the male borders. A similar interpretation was offered by Mikkonen (1985) in describing the movements of female chaffinches and bramblings. Dewar (1920) described a female blackbird (Turdus merula) who began a pairbond with a male on one territory, then, before nesting, moved across the street to a new, unclaimed territory. The male subsequently joined her there for nesting. More restricted shifts in male territorial borders upon the arrival of a female have been observed in ovenbirds, a new world warbler, (Stenger and Falls 1959) and savannah sparrows (Stobo and McLaren 1975; This study). Additional observations of discrepancies in male and female borders have been recorded in bufflehead (Gauthier 1987; Gauthier and Smith 1987), Lapland longspur (Seastedt and MacLean 1979), red-winged blackbird (Dickinson and Lein 1987), bobolink (Gavin and Bollinger 1985). There are also records of a female selecting a territory that was not occupied by a male. A male subsequently moved into the area and claimed the female as his mate by claiming her territory (Dewar 1920; Stobo and McLaren 1975). In these cases, it appears that the female is primarily selecting a territory, which may be superior to any areas occupied by males. Thus, a female boundary or nest site which differs from that of the male may provide more indirect evidence of a female spacing system which differs both quantitatively as well as qualitatively from the male system.

Breeding interference. Finally, female aggression toward competing females may even extend to nest disruption, ovicide or infanticide. Nest disruption may be subtle and hard to detect as is the case when direct harassment of a female leads to failure or

abandonment of her nest (Catchpole 1971; Davies 1985). It may involve stealing of nest material from a would-be neighbor's nest as is the case with the hairy hermit, a tropical hummingbird (Snow 1973). Egg dumping or conspecific nest parasitism might also be viewed as a form of competitive nest disruption which has been documented in the common Moorhen (Gibbons 1986), and eastern bluebird (Gowaty and Wagner 1988). Egg dumping may be performed by non-territorial females without a nest or by neighbors seeking to increase their reproductive success. Female aggression may also involve actual destruction of eggs and young. This may be in conjunction with a take-over of a neighboring territory as has been reported for the northern jacana (Jenni and Collier 1972) and tropical, residential populations of the house wren (Freed 1986). In other cases, female aggression results when resident females attempt to exclude an intruding female, as has been reported for Barrow's goldeneye (Savard 1982), acorn woodpeckers (Joste et al. 1985) and northern mockingbirds (Derrickson 1989). Sometimes both egg dumping and egg removal occur. Newton (1988) reported finding extra eggs in the nest of the normally monogamous European sparrowhawk and subsequently finding some eggs pushed out of the nest and eventual desertion of the nest. He suspected that two females were competing for one nest and one male. Because of the unpredictable nature of these events, documentation is difficult. Nevertheless, their very existence provides evidence of female dominance centering on a spatial priority of access to resources associated with nesting demands and thus meet the criteria for territory.

The validity of the use of indirect evidence. The highly visible nature of male territorial behavior has made documentation of male territoriality almost a foregone conclusion. The subtle nature of many dominant-subordinate interactions as well as the difficulty of simply observing female behaviors in many species mean that initial documentation of female territoriality may have to make use of indirect evidence. Certainly the case is stronger when a species exhibits several pieces of indirect evidence. When I focused an observational behavioral study on females of the savannah sparrow, I was able to acquire abundant direct and indirect evidence for female territoriality in this species. Although some behaviors, taken alone, could potentially be misleading as evidence for territoriality, they should not be dismissed until disproven by an observational study which directly addresses the question of female spacing. Particular combinations of indirect evidence such as female aggression, site fidelity and nesting asynchrony taken together provide even stronger evidence for female territoriality. Females should be expected to engage in behaviors which will increase their reproductive success. With that basis of investigation, and more careful collection of data which document direct and indirect evidence for female territoriality, females which do not exhibit territorial behavior may well prove to be exceptional cases.

Definitions of mating systems

Problems in defining mating systems

Duration of the pair bond. The term used to describe the mating system of a species is a composite. Contained within are mating

patterns of both individuals and genders. Any definition of a mating system should therefore be one which facilitates investigation of its collective genesis.

Historically, terms describing avian mating systems have been designated based on the duration of the pair bond (Lack 1968; and Selander 1972). Kleimann (1977) and Wickler and Seibt (1983) have pointed out that this confounds social systems and mating systems at the outset. The confusion which may result from such an approach becomes obvious with a term like promiscuous. It has been used to mean "no preferential pair bonds" (Wiley 1974). It is unclear whether the word "preferential" refers to the lack of mate selectivity or the lack of a sustained pair bond. Without a clearer definition, the interpretation is left to the reader's discretion. This reliance on the reader's interpretation can create ambiguity when the term is applied, as it often is, to an avian lek system. In that situation, a lack of sustained pair bonds on the part of the male may exist concurrently with high female selectivity among males (Wrangham 1980; Bradbury 1983; Borgia et al. 1985; Beehler and Foster 1988). Thus, a contradiction exists between the two equally valid interpretations of the term. To add to the debate, Wickler and Seibt (1983) have further suggested that mate selectivity across diverse taxons may need to be discussed apart from both social and mating systems, thus removing this component from the definition of a mating system.

Another criticism of this approach which relies on the duration of the pair bond is that the genetic effects of mating outside the pair bond are not fully considered (Gowaty 1980). Extra-pair copulations or

conspecific brood parasitism may also be components of the mating system (Gladstone 1979; Pierotti 1981; Roskaft 1983; Gowaty and Karlin 1984; Flood 1985; Gavin and Bollinger 1985; Emlen and Wrege 1986; Frederick 1987; Westneat 1987a,b; Birkhead et al. 1988; and Brown and Brown 1988). Although these behaviors are not always easy to observe and quantify, it seems preferable to employ a definition which does not exclude their consideration.

In birds, the duration of the pair bond is usually a function of parental care. The degree of parental care may in turn be influenced by the accessibility of resources for the young, phylogenetic developmental constraints (altriciality or precociality of the young), avoidance of predation, and opportunities by the male or female for additional copulations or broods. Using pair bond duration as part of the integral classification scheme may obscure variables that potentially have other direct influences on the mating system.

Resource distribution and number of mates. Emlen and Oring (1977) classified mating systems based on the potential for males or females to control access to mates either directly, or secondarily through control of resources. Differences in the degree of resource monopolization and hence, monopolization of mates, are used to subdivide mating systems which are fundamentally defined on the basis of the number of mates possessed by an individual. In all their resource-based classifications of monogamous and polygynous systems, females are assumed to settle in males' territories in direct response to the abundance of resources held by the male. Female-female competition for these resources or for parental assistance from the male is not a component of this scheme. The result is a classification

of mating systems from a male perspective. Oring (1982) expanded on these definitions and stated that female-defense polygyny results when females are aggregated for reasons unrelated to reproduction. If males are aggregated during the breeding season, the usual interpretation is that the aggregation is related to reproductive goals. Similarly, I submit that if females are behaving gregariously during the breeding season, one could safely assume that the reasons are not "unrelated to reproduction." In contrast, Wrangham and Rubenstein (1986) misrepresent the role of the female in the opposite manner when they describe female-female relationships as "unimportant" in resource defense polygyny in contrast to ascribing a critical role to female sociality in female defense polygyny. In their interpretation, dispersion of females in space is viewed as evidence against female social interactions while female aggregation is viewed as evidence for female social interactions. This view of female dispersion is tantamount to using male territoriality as evidence against male social interactions.

Another fundamental problem of a classification scheme for monogamy and polygyny such as that of Emlen and Oring (1977) is the confounding of the descriptive element (ratio of the number of breeding males to the number of breeding females), with a secondary causal element (male potential to spatially monopolize resources or females). Male spacing is viewed ultimately as a function of female spacing, either indirectly by sequestering resources critical to females or directly by defending access to females. Factors which ultimately influence female spacing are not considered except through the intervening variable of male

spacing. The implicit assumption of this scheme is that both genders are assessing the same resources and doing so in the same manner, yet it is certainly possible that females are not using the same criteria for spacing as are the males. Making the causal mechanism an integral part of the definition makes it more difficult to examine the underlying assumptions of the explanatory model and search for possible differences between the genders.

Gametic contribution ratio

Thornhill and Alcock (1983) defined insect mating systems based on the number of mates individuals have, rather than focusing on territories or pair bonds. Wiley (1974) elaborated on this principle when he defined mating systems based on the relative contribution of gametes by the two genders, or the breeding sex ratio. Gowaty (1981) used the term gametic contribution ratio to mean the same thing. A mating system exhibiting a gametic contribution ratio which differs from one is termed polygamy. A ratio of males to females less than one is termed polygyny. Polyandry is a male to female ratio greater than one. The difficulty in using this definition lies in assessing the gametic contribution ratio (Ralls 1977, Gowaty 1981). Gowaty (1980) argued that apparent mating patterns that can be observed are probably strongly correlated with the actual mating patterns leading to the gametic contribution ratio. The actual contribution ratio is also affected by mortality of nests. Only those individuals who produce young in a season actually contribute gametes to the population. In the absence of perfect observational data, one must rely on a description of the apparent mating system and refine this with knowledge of nest mortality. The result is the distinction of two

types of gametic contribution ratios. The observed ratio corresponds to a ratio of the number of breeding males to the number of breeding females, regardless of the outcome of the effort. The actual ratio refines the observed ratio by excluding those individuals who failed to produce any offspring in the season under consideration. Being aware of the distinction between apparent and actual mating patterns and observed and actual gametic contribution ratios can keep the researcher aware of limitations in the data with the result being a more complete understanding of the evolutionary significance of mating patterns.

There are also definite advantages associated with a classification scheme based on the gametic contributions of the sexes. First, it describes the mating system in an evolutionarily relevant way in terms of genetic contributions to future generations. It does so without taking one gender as the implicit vantage point. In fact, it makes it possible to focus explicitly on intersexual conflict in the evolution of mating systems (Gowaty 1981). Individual mating patterns can then be described as components of the whole system. For example, in a polygynous system a male may mate with multiple females while the female chooses to mate with only one male. The system is termed polygyny because of the breeding sex ratio, but the individual and gender patterns that comprise the system as a whole can still be examined for a greater understanding of the underlying causes of the system. Secondly, such a classification does not make causal mechanisms an integral part of the definition. This allows the investigator to postulate and investigate various pathways which may result in genetically equivalent mating systems. Mock (1985) suggested

that monogamy is so diverse that it should not even be considered as a single mating system. If mating systems are first defined using their common denominators, then they may be descriptively subdivided using modifying adjectives in a fashion similar to the schemes of Emlen and Oring (1977) or Oring (1982). Such schemes should, however, balance both male and female perspectives.

The interface of territorial systems and mating systems

The mating system and territorial system of a species are inextricably linked (Brown 1964, Verner 1977). The number of mates an individual can acquire in time and space will always be influenced in part by the spacing of genders relative to one another. A mating system defined by a gametic contribution ratio can only be understood by looking for the factors which influence the spacing of each gender separately and then examining the interaction of the two genders' territorial systems.

Spacing of individuals in a population is influenced by the advantages and disadvantages of aggregation versus dispersal, relative to critical resources (Waser and Wiley 1979). The costs and benefits of spacing are not only influenced by the distributions of the critical resources but also by the density of the population. Both the pertinent resources as well as population demography may differ between males and females.

A male, with a smaller gametic investment, can usually best increase his reproductive success by obtaining copulations with additional females, thus contributing gametes to more zygotes. Females, with their larger gametic investment, are viewed as the

limiting sex for whom the males compete (Trivers 1972). Males can be expected to try to maintain priority of access to females as their critical resource since the number of fertilized gametes has the greatest influence on male reproductive success. Thus, the male territorial system needs to be examined relative to access to females (Wickler and Seibt 1981). This requires knowledge of the factors which influence the spacing of females.

A female can best increase her reproductive success by successful production and nurturance to adulthood of the maximum number of fertilized eggs. Given the male motivation described above, she is not usually limited by getting her eggs fertilized, but rather in maintaining priority of access relative to other individuals, particularly females, over depletable or non-sharable resources such as food, shelter, and paternal care of young. Female territoriality can be expected to be most strongly influenced by the factors which have the strongest influence on her reproductive success.

Thus, males can be expected to compete spatially with other males for access to females for copulation. The form this male-male competition will take as well as the variation in reproductive success between males will consequently be influenced by the spacing of the females. In turn, the females can be expected to space themselves relative to other females in a pattern which increases each female's chance of obtaining the resources critical to the production of a maximum possible number of independent, successfully reproductive young. Wasser and Waterhouse (1983) have pointed out that the emphasis on the former type of competition (for fertilizations) "has resulted in

a conspicuous absence of theoretical and empirical work on female-female competition."

Mating system theory in birds and mammals

As has been discussed, the gametic investment difference inherent in anisogamy results in a situation of intersexual conflict. This conflict of interests between genders is particularly pronounced in species that exhibit some degree of male nurturance of the young. Historically, the dominant presence of male parental care in birds and its relative absence in mammals has resulted in the formulation of mating system theories which seem to differ fundamentally from one another with regard to this factor. In this section, I will examine the validity of using male parental care as the basis for a split in approaches to mating system theories.

The basis for mating system theory in birds

In birds, monogamy is the rule, occurring in approximately 90% of all species (Lack 1968). Also in birds, oviparity (coupled with nurturance demands of the young) has made possible male parental investment in the care of zygotes and young (Mock 1985). Combined, the result has been theories of avian mating systems which arise from an interface of the advantages of bi-parental care and the distribution of critical resources (Verner and Willson 1966; Orians 1969; Wittenberger 1976; Oring 1982; Mock 1985; and others). Bi-parental care is assumed to be especially important to the nurturance of altricial young of passerines, with their dependence on the parents for an extended period. In these cases, polygyny is assumed to be disadvantageous to a female and her young because of the potential loss in male assistance

when his assistance is shared with other females. In a graphical representation of the polygyny threshold model with reproductive success plotted on the y axis and habitat quality on the x axis, it is this sharing of male parental care which results in the reproductive success curve for polygynously-bonded females being drawn below that of monogamously-bonded females (Orlans 1969). In turn, it is the distance between the two curves which determines the size of the polygyny threshold relative to habitat quality.

The basis for mating system theory in mammals

By contrast, monogamy in mammals is rare, estimated to occur in less than 3% of the species (Kleiman 1977). Because females bear young viviparously and nourish them initially through lactation, opportunities for male parental care are more limited than they are for birds. With the exception of bringing food for young, other paternal contributions of mammals show a debatable effect on reproductive success (Kleiman 1977; Kleiman and Malcolm 1981). As might be expected, mammal mating system theory has focused on the advantages of female spacing and mobility as factors more important in the shaping of mating systems than male parental care (Ralls 1977).

The role of male parental care

Obligate monogamy. Although the emphases differ, male parental care is still a component of both mammal and bird mating system theory, either by its presence or by its absence. In reference to mammals, Kleiman (1977) distinguished between two types of monogamy. Facultative monogamy occurs solely when the distribution of resources results in a spacing of males and females in a one to one ratio.

Obligate monogamy results when male assistance in rearing the young is needed by the female. These categories are analogous to the exclusive and biparental monogamy of Barlow (1988). Male assistance can take the form of increased vigilance against predators as has been reported for certain African antelope (Wittenberger 1979) or provisioning of the young or the female with food. Even in a social species, if resources are not sufficient on the territory for the breeding of more than one female, a female dominance ranking may prevent all but the top female from breeding, thus resulting in a monogamous pair bond.

For monogamy to be truly obligate with respect to male parental care, male care must be critical to the raising of his offspring. It is not enough merely to look for monogamous species which exhibit direct male care of the young. In support of this point, Kleiman and Malcolm (1981) pointed out that the percentage of mammals manifesting direct paternal care is higher than the percentage exhibiting monogamy. Neither is it enough to demonstrate that male parental care is beneficial. One must show that the male cannot do better by attempting to secure additional matings at the expense of decreasing parental care (Dunn and Hannon 1989). What evidence is there for the existence of monogamy that is truly obligate with respect to male parental care?

Wittenberger and Tilson (1980) provided a listing of bird species for which bi-parental care is an apparent necessity. In some desert and tropical species the possibility of nest overheating can only be prevented by continuous nest attendance by two parents. Conspecific attacks on the young by neighbors may force bi-parental nest attendance in certain gull species. And in some alcids and terns which must travel to offshore feeding grounds, it has been documented that two

parents are necessary to raise even a single chick. Recently, the necessity of bi-parental care in the magpie (Pica pica) has been documented (Dunn and Hannon 1989). A male may still attempt extra pair copulations in some species (Pierotti 1981), but devote parental care only to his pair-bonded female.

The evidence for mammals is less clear. Obligate monogamy in Kleiman's (1977) original classification seems to include components of resource distribution and female dominance, suggesting that factors other than male parental care are important. Again, in order for monogamy to be truly obligate with respect to bi-parental care, it must be clearly demonstrated that a male cannot do better with multiple mates than with one. The male can be seen as choosing between an option of attempting to secure additional fertile females and an option of concentrated paternal care for one set of offspring. He is predicted to attempt the option which gives him the greatest reproductive success. If securing additional females would increase his reproductive success, yet monogamy still persists, one must look for further constraints on the male's access to fertile females. A good place to look for such constraints is in the factors which influence dominance and spacing of females.

Male parental assistance as a defensible resource. In most mammal species, as has been noted, male parental care is relatively unimportant to the female's reproductive success. In most bird species, however, paternal care has been assumed to be a factor that has the potential to be important to the reproductive success of the female and the male as well. It may influence the longevity of the

female, her ability to produce multiple broods, as well as the survival of her young. When female savannah sparrows were experimentally deprived of male assistance in a high arctic population, their young suffered decreased growth (Weatherhead 1979a). This type of data provides an argument for continuing an examination of the importance of male parental care in monogamy, even when the mating system is not obligate with respect to this factor. The following discussion is derived from the bird literature.

If male assistance is an important factor in female reproductive success, then females would be expected to evolve means to secure this aid. Most passerine or songbird species hold territories that provide both food and nest sites. In such species, female aggression which is directed toward maintaining priority of access to those resources may also increase the female's chances of attaining priority of access to male parental care (Yasukawa and Searcy 1982; Derrickson 1989).

Females may thus be spaced out in a pattern which maximizes their chances of monopolizing male parental care, as well as resources. Any attempts made by the male to expand the size of his territory relative to that of the females will carry the cost of competition with other males. Thus, a male might be constrained from being a polygynist both by competition with other males as well as by the dispersal of females. If he is thus constrained into monogamy and has the option for paternal care, then he can be expected to choose the next best option of rendering assistance in the nurturance of the young that he has fathered.

Ralls (1977) rejected male parental care as the key variable influencing the mating systems of mammals. Because of the close

theoretical link between avian monogamy and paternal care, she also rejected passerines as a good model for the evolution of monogamy and polygyny in other vertebrate taxa, specifically in mammals. In contrast, I submit that the essentials of mating system theory between the two taxa are the same. In both taxa, the spacing of females relative to the spacing of males determines the number of mates a male can acquire. In passerines, male parental care may be viewed simply as yet another resource, perhaps among many, to which females can maintain priority of access through territorial behavior. There is no convincing evidence that male parental care is deserving of a position as the key resource influencing female spacing in species where male assistance is not critical. These similarities between mating systems in mammals and birds further indicate that any foundation to an understanding of a mating system must attempt a thorough understanding of all the factors which influence the spacing of individuals of both genders.

Primary factors influencing the spacing of individuals

To understand the factors exerting the strongest influence on a territorial system, it is necessary to look at the factors which have the greatest influence on the reproductive success of the individual. These factors, as has been noted, differ between the genders. They may also change through time.

Factors influencing spacing of males. Male spacing is expected to be most strongly influenced by his ability to contribute gametes to potential offspring. This translates into securing access to multiple fertile females or sometimes access to the same female for repeated

broods. In short, the spacing of males is expected to be related to the spacing of females. The degree to which paternal care is an option or a requirement may also influence the ability of a male to territorially secure multiple mates. This has already been noted in the comparison of mammals and birds. In addition, factors which influence the spacing of males may also exhibit temporal variation as they change in importance with regard to other factors which have the potential to influence male reproductive success.

Factors influencing the spacing of females. Female spacing may be influenced in varying degrees and combinations by such factors as access to male assistance in raising young, the timing of breeding, the availability of quality sites for bearing and rearing young, and the abundance and distribution of food resources for herself and the young. Some of these factors may be interrelated, such as male parental care and the abundance and distribution of resources. The problem becomes one of assessing how these factors influence female spacing through time, based on their importance to female reproductive success. It is possible that a particular factor could have so great an importance to female reproductive success that it overrides other factors. An example of such a situation may be species where the most critical resource to the female's reproductive success is the procurement of a nest site.

Aggregation of breeding sites of females, stemming from either environmental constraints or from advantages of clustering, can lead to a situation where one male can maintain priority of access to multiple females. This is documented in a highly exaggerated fashion by a species such as the elephant seal where the aggregation of females on

parturition and lactating sites enables a minority of bulls to secure the majority of the copulations (LeBoeuf 1974). The lack of paternal care of young further enhances polygynous tendencies in this and any other species exhibiting this pattern.

In bird species, the clearest examples of the influence of nest site spacing on the mating system involve those where food resources are not acquired on the male's territory. Although females may still compete for proximity of access to foraging grounds, defense of food resources is indirect. If the possibility of paternal care exists, females may also be competing for a share of that resource. Thus, females may be competitively aggregated if nest sites are limited or cooperatively aggregated if some benefit accrues to clustered nesting (Altmann et al. 1977; Wittenberger 1979). Female aggression is almost always predicted in the first case as later settling females compete with earlier settling females for an opportunity to breed. Early female settlers may aggressively exert some influence on the number of females who settle subsequently (Williams 1952; and Lightbody and Weatherhead 1987). But the amount of intrusion pressure from later settling females, coupled with other time and energy demands associated with nesting, may limit the degree to which additional females can be totally excluded from a nesting area (LaPrade and Graves 1982).

If nest sites are aggregated, a male may have the opportunity to secure multiple females through the holding of a larger space than that of several individual females. His territorial potential, however, may be constrained by both competition from other males as well as parental care requirements. In a species such as the red-winged blackbird,

paternal care requirements are such in a resource-rich marsh that a male can do better by securing the nest sites of several females than by giving full parental attention to one brood. In other species with aggregated nests such as western gulls (Pierotti 1981), bee-eaters (Emlen and Wrege 1986), ibises (Frederick 1987) or egrets (Gladstone 1979), the parental care demands and intra-gender competition may be such that territorially controlling access to multiple females is not a viable option. A male may still attempt extra-pair copulations, but resistance on the part of the female results in a reduced probability of successful insemination.

An examination of two existing mating system hypotheses

There are currently two main hypotheses which seek to explain the variation in monogamous and polygynous mating systems both comparatively between species as well as within a species or even within a population. These are described in some detail below, with a special effort made to clearly distinguish between the two. In addition, the importance of male parental care to the female is one of the major assumptions of the polygyny threshold model, thus making it potentially the most relevant model for any avian species exhibiting male parental care of young. Since savannah sparrows fall within this classification, I have critically considered the assumptions which are an integral part of the polygyny threshold model. Hixon (1987) advocated testing the assumptions as hypotheses in their own right or testing multiple secondary predictions of models before undertaking any test of the primary predictions of a model.

Resource distribution hypothesis. In the majority of bird and mammal species, sites used for raising young cannot be considered apart

from the distribution of food or other critical resources. An understanding of how the spacing of individuals is directly related to the spatial distribution of both shelter and food has been the keystone of mammal mating system theory (Jarman 1974; Ralls 1977; Kleiman 1977; and others). The resource distribution hypothesis (Holmes 1984) describes the mating system of a population as a function of male spacing relative to female spacing which, in turn, is a function of the distribution of critical resources. The degree of both monogamy and polygyny in a population can thus be seen primarily as a function of the spacing of females (Case II of Hixon 1987). This model assumes that there are no or minimal parental care obligations on the part of the male. In the bobcat and the tiger, both species without male assistance in the raising of the young, females occupy separate territories which are part of a larger male territory, making him a polygynist (Bailey 1974; Smith et al. 1989). It is also assumed that hunting specializations of felids further promote a solitary existence in this family (Kleiman and Eisenberg 1973).

Marmot species are commonly polygynous (Downhower and Armitage 1971). The hoary marmot is unusual in that it exhibits monogamy in some populations. Holmes (1984) found that the females were too widely dispersed for a single male to maintain access to more than one mate. Female spacing was attributed to the locations of acceptable hibernacula (hibernation burrows) and the distribution and abundance of forage near each hibernaculum. In contrast to most birds, male parental care was unimportant in this species, but female dispersion still restricted male access to a single breeding female. The result

was a monogamous mating system. Other populations of marmots without the same habitat restrictions on females are primarily polygynous.

Parental care obligations may also affect the spacing of males but the resource distribution hypothesis does not directly address this concern. Mammalian monogamy, such as that found among canids such as wolves, is ascribed to a combination of male parental care and dominance hierarchies, usually without making a direct attempt to tie it in with the resource distribution hypothesis (Kleiman and Eisenberg 1973).

Polygyny threshold model. The polygyny threshold model was originally developed to describe the occurrence of polygyny in territorial passerines which exhibit male parental care (Verner and Willson 1966; Orians 1969; Emlen and Oring 1977). It fundamentally differs from the resource distribution hypothesis in the emphasis that is placed on the male. He is seen as the controller of resources that the female needs and a potentially important source of parental care and variation in quality of genetic contribution. Wittenberger (1976) has called this combination the "breeding situation." Females are expected to settle on the territory that presents them with the best breeding situation, of the options left open to them. This results in a settlement pattern in the same rank order as that of the territories ranked by resource abundance. Polygyny is hypothesized to result when the resources on the territory are sufficiently rich to compensate a secondary female for the potential loss in male parental assistance and depleted resources resulting from the prior occupation by another female. The female is thus presented with a choice between mating monogamously with a male on a marginal territory or mating as a second

female with a male on a good quality territory. She is predicted to choose the option which gives her the greatest reproductive success. This active female choice of both resources and the mated status of the male (unmated or mated) leads to the prediction that the reproductive success of a secondary female on a good quality territory should be greater than or equal to that of a monogamous female on a marginal territory.

In species which exhibit no parental care, the model assumes that female mate selection is based entirely on male genotype. In these cases, there is no difference predicted between the reproductive success of monogamously-bonded females and polygynously-bonded females. In the graphical representation of the model, the two reproductive success curves become congruent, resulting in a prediction of no polygyny threshold (Orians 1969). In this paper I will adopt the established usage of the polygyny threshold model which restricts its meaning to cases with demonstrated bi-parental care and predicted reproductive differences between monogamously and polygynously-bonded females. It is only in this case that the polygyny threshold has a concrete meaning.

Both the resource distribution hypothesis and the polygyny threshold model explain monogamy and polygyny based on the spatial distribution of females. Nonetheless, the assumption of the polygyny threshold model that male parental care of the young is a key variable in determining female spacing and ultimately, female reproductive success, delineates it as a restricted subset of the resource distribution hypothesis. It should only be applied to species where

male parental care can be shown to have the requisite level of importance, not as a loose synonym for the resource distribution hypothesis. Emlen and Oring (1977) included the polygyny threshold model as part of their discussion of resource defense polygyny, but do not make clear distinctions between it and other resource-based polygyny. Wittenberger (1979) referred to the polygyny threshold model specifically in an explanation of the highly polygynous pinniped mating system (LeBoeuf 1974) which has neither resource-based territories nor a component of male parental care. In such a case, it is not clear how the model is being applied. Such uncritical usage makes it even more difficult to distinguish valid predictions and tests of the model.

A better understanding of the applicability of and evidence for the polygyny threshold model comes from an examination of its implicit assumptions and the predictions which follow. The foremost underlying assumption is that female reproductive success is most strongly determined by some combination of the quality of the male's territory, the genetic caliber of the male, and the necessity of and quality of male parental assistance. Territorial resources and male parental care are viewed as predictable, continuous, depletable resources. Therefore, it follows that a female which mates monogamously will have a higher reproductive success than one which mates polygynously, on a territory of given quality. One would predict, then, that the primary female would aggressively attempt to maintain her privileged position, making female-female aggression and dominance an integral, unstated prediction of the model. Orians (1969) and Wittenberger (1979) recognized this prediction and the actual presence of female aggression, but did not examine the effect of female-female aggression

on the other assumptions and predictions of the model.

Given the evidence for avian female territoriality which has already been presented, an examination of the place of female aggression and territoriality in the polygyny threshold model seems a necessity. Female aggression may itself be an additional factor (not included in the model) which directly influences the reproductive success of other females. This may take the form of energetically costly and dangerous fighting between females or interference with nesting attempts. It is theoretically possible for female aggression to have a greater direct influence on female reproductive success than the quality of the male and his territory. An incoming female's selection of a breeding situation in such a system may be partially or predominately in response to the level of aggression that she encounters. A territory which lies above the polygyny threshold may remain under the dominance of a solitary female if her aggression makes the sharing of resources too costly for any incoming female (Oring 1982). Territoriality, by definition, is associated with the distribution of resources. If female spatial dominance of resources is documented in a system (female territoriality) then it is no longer accurate or realistic to discuss a polygyny threshold which is a function solely of male monopolization of resources that vary in quality. In turn, female-female aggression cannot be considered independent of the distribution of resources, which has been the tendency thus far (Wittenberger 1976, 1979).

Male parental care is an integral part of the model. In fact, postulating that a higher quality territory compensates a secondary

female for potential reductions in male parental care and resources assumes that the factor influencing reproductive success and male parental care are linked in some way. In some species, the factor with the greatest influence on reproductive success may have no link with a potential loss in male parental care. If this is the case, females would not be expected to actively select a territory based on the mated status of the male as well as territory quality, but rather, space themselves so as to acquire the resources vital to their success. The expected reproductive successes would differ across habitats of varying quality as would the density of nesting females. The mated status of the female would simply be a by-product of female spacing, not an active choice by the female. This, like the example of hoary marmots (Holmes 1984) matches the resource distribution hypothesis, but not the more restrictive polygyny threshold model. These models do not always differ in their predictions, but they do differ in the postulated mechanisms.

Competitive versions of the polygyny threshold model (Wittenberger 1979) assume that the existence of polygyny must depend on the advantages or disadvantages to the least advantaged individual of the breeding unit (Gowaty 1981). Thus, polygyny has not been predicted to occur unless the success of the secondary female on a good territory is at least equivalent to that of a monogamous female on a marginal territory. If females are territorial, however, some females may be excluded from breeding during the season and exist as floaters. In a species with a low survivorship from year to year, females should be selected to mate in their first year rather than intentionally delay breeding until a better opportunity arises (Murray 1985). Thus, female

floaters would be expected to attempt to breed as soon as possible, wherever they can enter the territorial system. This might result in their becoming secondary females which do more poorly than any monogamous female, yet still do better than females which fail to breed that year. Female territoriality thus calls into question the fundamental comparison of reproductive successes which has been a primary test of the polygyny threshold model.

As originally formulated, the polygyny threshold model predicted that females should settle on male territories in a rank order matching that of the quality of the territory. This prediction is based on the assumption that territory quality is the most important factor influencing the settlement and reproductive success of females. Mean reproductive success of the females is assumed to be "uncomplicated by density effects" (Orlans 1969).

Given this, it should be possible to use territory quality to predict which territorial males will remain unmated, which will become monogamists and which will secure multiple mates. Many studies have been unsuccessful in measuring the appropriate habitat variable which allows for a ranking of territories independent of the order of female settlement and density of settling females. This has made testing of the prediction impossible in these cases (Verner 1964; Dhondt 1987). In still another study (Zimmerman 1966), the researcher was able to use habitat variables to distinguish between territories which were acceptable and unacceptable to females, but was unable to distinguish any degree of attractiveness based on the same habitat variables. In other words, it was impossible to distinguish the territory of a

monogamist from that of a polygynist based on a measure of habitat quality which appeared to be relevant to the female's reproductive success. Wittenberger (1979) ascribed this lack of fit with the model to a low predictability through time of the quality of the territories from the perspective of the male. The conclusion was that females were settling in the predicted order, but that order was changing through time. The males' attempts to accurately assess territory quality at the outset were thus foiled. In the lark bunting, overexposure to heat from the sun is the main cause of nestling mortality (Pleszczynska (1978; Pleszczynska and Hansell 1980)). The eventual pair bond status of the male could be predicted based on an independent assessment of the amount of cover available on a territory for the nesting females. Still, territory quality alone did not accurately predict the order of settlement. Females chose to mate monogamously further into the season than predicted by the model. Pleszczynska and Hansell (1980) interpreted this as a decision on the part of each female which weighed the seasonal reproductive success (directly associated with habitat quality) against lifetime fitness (indirectly associated with the amount of paternal assistance rendered to a primary versus a secondary female).

Discrepancies in settlement times relative to the ranking of territories can, however, be simply explained in a mating system model which includes female territoriality. If site faithfulness is a component of a female territorial system, then returning females are more apt to return to previously held territories, either regardless of their quality or within a broad category of quality (Bollinger and Gavin 1989). The dominance advantage that is part of philopatry may

override any advantages of settling according to a rank order for both genders. The presence of site fidelity in a species automatically makes suspect any ranking of the quality of territories that was based on arrival times rather than an independent habitat variable. Females may also fail to settle in the order predicted by the quality of the territory if female aggression delays settlement of high quality sites by additional females. Eventual settlement of the higher quality sites can occur later when the first female has a nest to tend and is constrained from devoting as much time and energy to aggression (Oring 1982). Thus, a situation such as the one described by Pleszczynska and Hansell (1980) may still be a result of females simply choosing a territory based on habitat quality, without needing recourse to an explanation which weighs variables affecting both seasonal and lifetime fitnesses.

Holmes (1984) has pointed out that the polygyny threshold model, in contrast to the resource distribution hypothesis, has the disadvantage of treating monogamy as a default condition which exists whenever disparity in habitat quality is such that the polygyny threshold is not reached. Monogamy cannot be explained so simplistically when the existence of female territoriality is taken into consideration. In a monogamous species where female territoriality resulted in a floating population of females, a constant pressure would exist for territories to be settled by additional females. These females need only do better than zero reproductive success in that year and should be willing to settle as additional females even on territories which fall beneath the polygyny threshold. Such a situation demands an active causal

mechanism to explain the persistence of monogamy in the face of such pressure. The polygyny threshold model provides no explanation alternate to the default of not reaching the threshold. Female aggression has been proposed as an ad hoc hypothesis to explain the persistence of monogamy in populations where a disparity in territory quality equal to the polygyny threshold exists, but no attempt has been made to connect such female aggression with resource distribution, or to examine its implications for the assumptions and predictions of the polygyny threshold model (Wittenberger 1979; Oring 1982). The result is essentially two hypotheses passing under the guise of one; one hypothesis for polygyny and one for monogamy.

CHAPTER III

MATERIALS AND METHODS

Study Area

The study area was located in southern Michigan (42 degrees 47 minutes N, 84 degrees, 35 minutes W) on the Inland Lakes Study and Research Center, on the campus of Michigan State University, Ingham County, (T3N, R2W, Sec. 1).

Savannah sparrows bred on a site consisting of approximately 40 hectares of grassy fields. These fields surrounded four artificial ponds with an open shoreline and few emergents, each pond approximately 5 hectares in size. Four smaller (.4 to 1.5 ha.) ponds were completely bordered by emergent vegetation. The habitat occupied by the population was bisected north to south by a paved county road. Paved driveways, rapidly being subsumed by vegetation, crisscrossed each of these two sections. The dictates of pragmatism and efficiency restricted my study primarily to 20 to 25 pairs of sparrows occupying 18 hectares of land lying west of a paved county road. Approximately 8 to 10 hectares were actually occupied by nesting, territorial birds in any given year. A roughly equivalent number of birds nested on essentially similar land lying to the east of the county road. The next closest group of nesting savannah sparrows were a 1.6 km away in pasture land. One road survey per year at the height of the breeding season failed to locate any banded birds in suitable locations 1-3 km away from my study site.

The entire habitat had been disturbed with the exception of one small pond. Clay soil had been imported when artificial ponds were dug

as part of a sewage treatment system and the entire area had been planted in perennial grasses (Beaver 1988). At the time of this study the following grasses dominated the field: Agrostis gigantea, Bromis inermis, Fescue oviana, Fescue sp., Phalaris arundinacea, Phleum pratense, and Poa compressa. Forbs such as goldenrod (Solidago sp.), chickory (Cichorium intybus), sweet clover (Melilotus spp.), wild carrot (Daucus carota), thistle (Cirsium spp.), dock (Rumex), plantain (Plantago sp.), burdock (Arctium minus), and dandelion (Taraxacum officinale) also grew throughout the site. A few scattered woody plants had been planted (Crataegus sp., Pinus sp.). All non-woody plants exhibited a patchiness in their lushness of growth which appeared to vary with patterns of soil richness and drainage but which was stable from year to year. This pattern was particularly evident in the variation in growth of the grasses.

Duration of study

This study included the breeding seasons (April through the beginning of August) of the years 1984-1987, inclusive. In 1988, observations were limited to recording the identities of returning territorial males and females and banding unmarked birds. The data which follow are all from 1984-1987 with the exception of the frequencies of returning birds, which also make use of the 1988 data.

Banding

Male savannah sparrows arrive in southern Michigan from early to mid-April. Females usually follow by one to four weeks although a few females may arrive as early as the first males. If female arrival is exceptionally early or male arrival is delayed, then the majority of males and females can arrive simultaneously. Territorial males were lured into a mist nest using a taped song and a stuffed model. Gender was determined by reference to the cloacal protuberance (Wolfson 1952) and later confirmed by behavioral observations. Each male was banded with a U.S. Fish and Wildlife Service (USFWS) band on the left leg and a unique combination of one to two color bands on the right leg. Females were usually captured by flushing them off the nest into the nets during incubation or brooding although an occasional individual was attracted to the singing model for capture. Females were also banded with a USFWS band and a unique color code, on opposite legs from the male. In addition, a blue color band was placed over the USFWS band of females as an aid in gender identification. Other methods were attempted in order to band females before nesting. Simple treadle traps, baited with millet and waxworms (*Lepidoptera* larva), were used in 1986 with limited success. Monofilament snares were also tried in conjunction with a stuffed model, but were successfully avoided by the attacking birds. Later in the season, some nestlings and independent fledglings were banded with USFWS bands only, as time allowed. The totals of birds banded for the first time in each of the four years are listed in Table 2. Returning color-banded birds from previous years were always recorded and if possible, re-captured and examined.

Table 2. Summary of banded savannah sparrows

1984-1987				
Year	Color-banded adults		Nestlings	Independent juveniles
	Males	Females		
1984	29	22	41	15
1985	23	13	14	12
1986	42	20	0	0
1987	22	22	45	57
TOTALS	116	77	70	85

Standard measurements of tarsometatarsus, wing chord, and tail were recorded to the nearest .5 mm. Weight was measured to the nearest .5 g using a 50 g Pesola scale. The extent and intensity of the yellow coloration at the lores and supercilium was also qualitatively estimated and sketched as an aid in identification and for possible future reference. Age was estimated by assigning the age of one year to the new territorial birds in each year and by counting the years that each individual returned. For the majority of the birds, this was probably accurate. Still, some birds banded as juveniles did not attain territorial status until they were two or three years old. Thus, estimates of age for some individuals may be conservatively young.

Behavior

In this section I describe the behavior of male and female savannah sparrows both in general and in some detail, drawing from the literature as well as my own work. The literature lacks detailed descriptions of distinct territorial behaviors of male savannah sparrows and there are no detailed references to female behaviors. In my study, these behavioral observations were the means by which territories were mapped, pair bonds were recorded, nests were located and reproductive success was determined. They are important not only in their own right as qualitative data of the type which is standard in behavioral observational studies, but also as a portion of the procedures of this study. They thus represent a combination of background information that can be considered part of the methods and of observations that belong to the results of this study. Rather than report them in two locations, I have included them in detail in the chapter on methods.

The behavior of color-marked individuals was recorded by focusing on an individual for 30 minutes while making a written record of activities. Each territorial pair was observed at least once every other day, although inclement weather occasionally made this every third day or affected the amount of time an individual was able to be watched. Observations were made using a 25x60 power spotting scope and 8x40 binoculars. If a bird had not yet been color marked when observations began, I noted any plumage traits that might help me distinguish it until banding. Males were the focal observational animals for two years in 1984 and 1985; females were the focal animals

in 1986 and 1987. Since females had never been observed as focal animals in this species, I had to devote considerable effort in the first year to learning how to locate and follow them. Interestingly, in the years of male focal bird observation, very few incidences of female territoriality were observed. Because of the often subtle nature of female agonistic behaviors, a focal female study apparently was necessary before the extent of their behaviors could be appreciated. My experience causes me to question the validity of the report of an absence of female territoriality in other studies which have focused only on males.

Because this study sought to explore the mating system of this species, it was important to place behaviors of individuals into their social milieu. Thus, it was important to take observations on all territorial individuals in a designated contiguous area. The sample size of individuals, large by the standards of studies of this nature, thus precluded the collection of more detailed data, such as that required to establish rigorous time activity budgets. Such studies would be even more valuable as further research, building on the findings of the present study.

Observations began when the males arrived in early April and continued until the birds left their territories in late July or early August. Daily (six days a week) observation periods ranged from 3 to 10 hours, with an average of about 5 hours, resulting in over 500 hours of observation each season. Most observations were made in the dawn (0430 EST) to late morning (1100 EST). Morning was chosen because the observer already was at the site to do banding, which required low winds and dim lighting, and because the birds interacted more

vigorously in the morning hours, resulting in more efficient procurement of data. The majority of observations were taken by a single observer, making efficiency a critical issue.

Song

Only males have been observed to sing in this species. Song is restricted to territorial males or males who are making an attempt to acquire or expand a territory. Non-breeding (floating) males and breeding males which are off their territory behave in a furtive fashion and do not sing. The male usually ascends a perch to sing and assumes an upright posture. Before a female is acquired, a male sings with the head thrown back and the bill held open. The perch may be as low as a tuft of grass or weed stalk or as high as a 20 meter tree. Reid (1987) has shown that there is a conflict between feeding and song by male savannah sparrows. This conflict is sometimes resolved by engaging in what has been called feed-singing (Beaver unpub.) where the bird may perch up on a grass tuft to sing one or two songs interspersed with short feeding bouts on the ground. The rate of song delivery in feed-singing is greatly reduced from pure song bouts (Beaver unpub.).

When a female arrives in the vicinity of a male's territory, the amount of time spent in song decreases sharply; a finding reported for other passerines (Nice 1943; Wasserman 1977; Krebs et al. 1981) as well as for other savannah sparrow populations (LaPointe and Bedard 1984). If the male does sing, he does so with muted song, bill closed, perched in the vicinity of the female. This "whisper or muted song" has been reported for males of other species when a female is available for copulation (Armstrong 1973). A second increase in percentage of time

spent singing by individual males, coinciding with the initiation of nesting by females has been noted some savannah sparrow populations (McLaren 1972; This study). McLaren interpreted this as having the function of attempting to attract another female, making the male a polygynist, an interpretation with which I would agree. LaPointe and Bedard (1984) noted an increase in male song upon the loss of a mate but not in conjunction with the stage of the breeding cycle. In contrast to the McLaren study, their population exhibited no polygyny and a high percentage of unmated territorial males (designated as bachelors), leading them to suspect a shortage of females. My own behavioral observations have indicated that the male is not only influenced by the behavior of his own female but also by the presence of other unmated females in the vicinity of his territory. If a male is actively following and courting a neighboring female or if he is occupied with the feeding of nestlings, time spent singing decreases. Thus, in order to place a male's behaviors in context, it is necessary to have a description of all his potential social interactions, not just the activities of his mate. Statistical treatments which group males by the stage of their female's nesting cycle do not take into account the entire social milieu of the male. LaPointe and Bedard (1984) describe this as the "behavioral plasticity of the passerine breeding cycle," and insinuate that more information, of the type just described, is necessary for a thorough understanding of a time-activity budget.

Vigilant Perching

Vigilant perching is used to describe watchful behavior by a territory holder, performed from a highly visible perched position. The behavior may serve a variety of functions. The bird exhibiting this behavior usually selects a conspicuous perch in the territory. The selected location thus makes an individual obvious to any potential intruders and may serve as a passive visual advertisement of occupancy. The individual appears to be poised for flight, often with the neck slightly outstretched, and seems to be actively looking around its territory. The perch apparently affords a good view of the territory and the owner can fly to aggress any intruder in a matter of seconds. Both males and females exhibit this behavior throughout the season. It is most pronounced in a male during two time periods. The first is during the laying period when his female is feeding between laying bouts. In this case, vigilance may serve a mate guarding function. The second time is when his first female is incubating and other unmated females are still present in the immediate area. In this case it may also serve the male as a way to locate females for courting and copulation attempts. In contrast, non-territorial birds of either gender were rarely observed perching in conspicuous locations.

Aggression

The aggressive behaviors discussed below are associated with territorial and mate conflicts. Both genders exhibit the same basic repertoire of behaviors. Males direct aggression almost exclusively toward other males. Females are most often aggressive toward other females but may also direct limited aggression toward males other than her mate. She may even direct aggression toward her own mate if he

attempts copulations before she is receptive.

To the human observer, the aggressive postures range from the subtle to the very obvious. Upon sighting an intruder, a territory holder may erect its crest feathers and stretch out its neck. It may also open its mouth in a gape or perform unilateral or bilateral wing raises (Nice 1943, Post and Greenlaw 1975). A submissive bird will respond by sleeking its feathers, orienting its body horizontally to the ground and attempting to creep off the territory through the vegetation. An unobtrusive sparrow greatly resembles a rodent moving through the grass. Frequently, when territorial females encounter one another while feeding, the most subtle postures described above are the extent of the altercation. I learned to look for an intruding female whenever the focal bird raised her crest and frequently located her before she slipped off the territory. The dominant female usually resumes feeding after having asserted her territorial dominance.

Disputes at borders are more prolonged and involve individuals of the same gender. In these cases a parallel walk (Beaver unpub.) is performed. The contenders walk side by side along a perceived border, with each staying on its own side. Very often unilateral wing raises are performed toward the antagonist. Crests are usually erect and gaping may occur as well as buzzing notes. As the display continues, one or both birds may engage in displacement feeding motions or may pick up dead plant material and carry it in the bill. Often borders are selected on open ground, thus enhancing the visibility of the display. Parallel walks may also take place on vertical surfaces such as shrubs, adjoining plant stalks or fences. The behaviors of males

and females are identical in these displays with the only difference being the location of the borders.

Individuals often defend their borders on the ground. On foot, a territory holder may rush toward an intruder in an attempt to drive it off the territory. If the intruder stays, a parallel walk or fight might ensue. Females rush other females if they violate a territorial boundary and also rush males other than their mates, if approached by them.

Territories are also advertised and defended by flight displays. Males may approach an intruder in an exaggerated slow flight with shallow wing beats, legs dangling, and fluffed belly feathers. Any such slow flight, seen in several contexts, I have called a flutter flight. A series of musical chip notes, sometimes ending in a buzz, may accompany such an approach toward an intruder ("chip-buzz flight," Beaver unpub.). If the intruder takes flight, an aerial chase may ensue. If the intruder stays in place, the result may be a parallel walk or fight. Flight is also used by both males and females as a territorial display which is not specifically directed at an individual intruder. In this use, the territory holder performs a flutter-flight which may circle the borders of the territory or traverse one particular border. Males may also direct a similar slow flight at a male who is attempting to settle in a previously claimed area. The object in these situations seems to be to prevent settlement by the intruding male by keeping him constantly harassed and in continual flight. Such aerial displays between males are particularly evident when the birds first settle in the spring and again later in the season when non-breeders attempt to settle as invaders (described under "non-

breeding individuals"). The male which is attempting to settle may even sing during flight under these circumstances. Aerial chases using a normal speed flight seem to be the prerogative of males chasing other males from disputed areas. Additionally, multiple male aerial chases are often initiated when one male pursues a female in flight. This type of chase is described below under courtship.

Actual fighting is not common. Brief incidences may occur when a female fights to reject a copulation attempt by a male. Sustained fights are recorded for same sex interactions, particularly for females, when two females make simultaneous claims on a territory (Beaver pers. comm.; This study). In these fights, females may lock bills and feet and tumble on the ground, emitting buzz notes and occasionally drawing blood. Fighting bouts are punctuated by bouts of parallel walking and short flights throughout the contested territory. Male fights are rarely prolonged. They usually consist of the two combatants rising one to three meters above the ground with feet extended toward each other before returning to the ground where a parallel walk often follows. Nevertheless, later in the season, young males have been captured who are missing patches of feathers on the flank or head or who are bloodied around the mouth. They attest indirectly to the possibility of some fairly involved fighting on the part of the males.

Weatherhead and Robertson (1980a) used a model savannah sparrow and experimentally provoked aggressive responses from male savannah sparrows in their arctic population near Churchill, Manitoba. They specifically stated that females were not observed to react

aggressively to the models. But they also did not mention observing females as focal birds, indicating a possible lack of discernment on their part. They stated that they interpreted all unmarked birds which responded aggressively as being males, introducing another possible source of error. On two occasions, early in the observation of focal females, I presented a territorial pair with a stuffed savannah sparrow mount, perched in an upright singing position. In both cases, both genders responded aggressively. The male typically performed chip-buzz flights and unilateral wing raises. With no response from the model, he eventually flew approximately to another portion of the territory and began singing. In one case, the female was visibly more persistent in her agonistic displays than the male. She stayed off her eggs and performed the typical border displays associated with a parallel walk. When the model did not respond, she flew at it with feet dangling and knocked it off the perch. She then proceeded to peck at it as it lay on the ground. She did not cease these displays until the model was removed nearly an hour later. She gave the same responses to a model that was placed on the ground in a crouched position, mimicking a female. These were trial presentations only, not performed with experimental rigor. They do, however, reveal the presence of a female aggressive response during the breeding cycle.

Pair formation and nesting

Upon selecting a territory and prior to egg laying, a female feeds assiduously throughout the territory and rebuffs any copulation attempts on the part of the male by buzzing and gaping at him when he approaches. Female weight significantly increases during this period, prior to egg-laying (Weatherhead 1979b). The male follows her

throughout his territory and into adjacent territories where he may provoke aggression from the resident male. During this time, neighboring male's often intrude on the resident's territory and approach the female. If a neighboring male approaches the resident's female near the border, the resident has been observed to place himself between the female and contesting male or attempt to herd her away from the border. These behaviors seem to match other descriptions of mate guarding (Nice 1937; Fitch and Shugart 1984; Birkhead et al. 1988).

Upon first locating a female, males were observed performing a "pointing" behavior. In this posture, the male perches above a female and remains immobile, feathers sleeked, with his bill directed toward her. She makes no visible response. Males were observed to hold this posture for as long as a minute. Eventually, he joins the female and she responds either by rebuffing his advances or by soliciting copulation. The function of this pointing posture is not apparent and because of its infrequent occurrence (perhaps occurring only at the first encounter with a female) and its brief duration, it was only recorded three times during this study.

Multiple male aerial chases occur when one male, in a rapid flight pursuit of a female, flies over other males' territories. The owners who have been trespassed against join the chase until three or more birds are participating in a rapid flight which moves throughout the area. Upon the cessation of the chase, the birds all return to their respective territories and the returning males usually begin to sing. In some cases, the initial chase pair leaves the study site entirely, flying well above the defended air space of all the territories, and

precluding the development of such a relay.

A territorial male responds to an intrusion by a new female by attempting courtship, making no efforts to exclude her from the territory. In contrast, a territorial female exhibits aggression toward any detected female intruders, attempting to drive them from the territory.

Once the pair bond is formed, either gender may lead or follow as they move around the territory on the ground and in flight. By this time the female may have retracted some of her original borders and the male may have altered some of his borders to conform with hers. Females did not visibly change their borders further once nesting had begun, in contrast to males who sometimes reduced the size of their territory in response to aggression from intruding males. Females respond to copulation attempts by intruding neighboring males during this time with aggression, including actual fighting if the male actually pounces on her. When the female is ready to copulate, she often does a flutter flight for several meters giving a call which begins with a musical chipping and ends with a series of notes which can be described as a descending "tew, tew, tew, tew..." notes. The male flies to where she has landed and the female solicits copulation by quivering her drooped wings, giving soft mewing calls and holding her tail cocked up at an angle. A female was never observed to solicit copulation from a male other than her mate and in fact always was observed to fight vigorously when pounced on by a strange male. During egg laying, copulations continue and the male is particularly attentive, flying to his female whenever she leaves the nest. Females are solely responsible for nest building, incubation and brooding of

young. I only recorded one incident of possible male brooding in four years. This conforms with Weatherhead's (1979a) findings of only two cases of male brooding in a two year study. It conflicts, however, with Bedard and Meunier's (1983) finding of seventy-five percent of males engaging in brooding behavior. In the study population, a male would resume singing, at a rate similar to his pre-female rate, once his female was incubating (Beaver unpub.; This study). This resurgence in singing is also an observation of another savannah sparrow population (LaPointe and Bedard 1984). Both parents contribute to the feeding of the young. I have no quantitative measures of time investment of both sexes in this activity, but qualitatively have the impression of more variability among males in feeding of young. Males may also be engaged in defending their territory against invading males or courting an available female, instead of devoting all energy toward care of young. Females do not appear to respond the same way to conflicting demands on her time. In the case of the loss of either partner, the sole remaining parent is capable of raising the young to fledging. This study has recorded incidences of both males and females successfully raising broods alone.

Foraging and diet

Observations of diet and foraging habits correspond with those in the literature. Arthropods comprise the major portion of the diet of savannah sparrows during the breeding season (Baird 1968). This was certainly true of the diet of this population as qualitatively assessed from foraging observations. Savannah sparrows in this grassy field habitat foraged around the edges of grass clumps, gleaning arthropods

from the foliage. This same behavior was reported by Wiens (1973) for a Wisconsin population and Bedard and LaPointe (1984a) for a population at Isle Verte, Quebec. Occasionally, early in the season, the sparrows would probe in the moist, soft earth and procure insect pupae (possibly Diptera: Tipulidae). It was not uncommon to see birds with soil on their bills in the early part of the breeding season. Later in the season, individuals were also observed occasionally feeding on dandelion seeds in between bouts of insect foraging.

Birds of both sexes were almost always observed foraging on their territories in the morning observation hours. The only exceptions occurred early in the season during prolonged cold, wet weather. Territory holders were then occasionally observed to leave their territories and forage along the shoreline of the ponds where they could feed on seeds or emerging aquatic insects and be sheltered from the wind. It is possible that individuals foraged off their territories more frequently at other times of day, but such an intensive time activity budget was beyond the scope of the study.

Territory

Initial territorial behaviors

Upon arrival on a territory, females fed almost continuously, with the feeding punctuated by brief territorial interactions with other females or aggressive rebuffs of the advances of a male. During the period preceding and immediately following pair bonding, females moved throughout their territory. These movements often took them through portions of territories of several males, resulting in aggressive

disputes between those males. Half of the nesting females were recorded as ranging through more than one male territory. A pair bonded male who was closely following a female in consort would attempt to change his borders through aggressive interactions with neighboring males, in an effort to secure the space that the female was occupying. When feeding nestlings, females remained within the territorial borders that were established during the initial period of intensive feeding. Early territorial shifts by a female to an area occupied by another male were uncommonly observed. Two observations in the four years involved females which began the pair bonding process with one male, but before any copulations were observed, moved and nested with a neighboring male.

Prior to the arrival of females, males devoted their time to singing and agonistic interactions with other males. They did not engage in the same intense feeding upon arrival as did the females. Instead, male feeding behavior was frequently combined with song in the feed-singing behavior or in shortened feeding bouts (Beaver unpub.; This study).

Delineation of male territories

Territory boundaries of male sparrows were delineated in all four years by observing the locations of singing perches and agonistic interactions with other males. Only males who held territories for time periods equal to or greater than five days were included in mapping efforts. When no neighbors were present to provoke interactions, boundaries were assessed first by observing singing perches and reversal of direction of movement by the bird at his borders and further clarified using the technique of flushing the bird

towards its border (Weins 1969). For the analyses involving frequencies of returning males, territorial males were also considered to be any male found singing on a territory for a time period of at least five days.

Delineation of female territories

Territories of nesting females were measured in 1986 and 1987. The most complete measurements come from 1987 after gaining experience in observing females in 1986. For this reason, detailed analyses of female territories employ the more complete 1987 data. Boundaries were delineated by observing the space the female used for foraging and by observing agonistic encounters between females. Females would stop and reverse direction, either on foot or in flight, at their perceived borders. As with males, the observer could often clarify borders with a flushing technique. The more secretive nature of females did not make it possible to estimate territory size for females which did not persist long enough to nest. Also, females did not sing, making them considerable less conspicuous to the human observer. Some late-settling females were extremely secretive in their activities, with few obvious interactions with other individuals, making an accurate map of their territories an impossibility. Because of these limitations, territories were not mapped for three females in 1987 who became second mates of polygynous males. In addition, I could not map the territories of the male and female of one pair because they had no neighbors and did not clearly define their borders by their behaviors. These limitations fall within the ranges of the other territorial studies cited in this manuscript. In a few cases, a female spent at

least a week on a territory, consorting with a male, but did not nest. These females were included in the analyses involving frequencies of returning territorial females, but not in the mapping efforts.

Mapping and measurement of territories

Boundaries were marked using surveyors' stakes (a wire .75 m long with a plastic flag on the top). The birds would occasionally use these as perches, as they did with all other elevated objects.

Territories were mapped using a scale map of the site which included landmarks which could be located relative to an individual's territory. Territories were measured by using a compass and tape measure to sight and measure between the surveyor's stakes. A polygon was then drawn to scale (Odum and Kuenzler 1955) and the territory area estimated in square meters by calculating the sum of areas of included triangles. In 1987, the study site was gridded with numbered stakes in a 20 X 20 m pattern. This facilitated mapping of the territories. It also made it possible to measure them by making reference to the grid superimposed on the scale map by estimating the proportions of occupied grid squares. The two measure techniques produced essentially the same result. Also in 1987, I used the map to estimate the proportion of female territories which overlapped with neighboring females. These measures were used in the nest spacing analysis.

Other studies (Dixon 1978; Stobo and McLaren 1975; Bedard and LaPointe 1984b) have shown territorial male savannah sparrows to be strongly site faithful. The territories of individually banded males and females were drawn on a map of the study area in each year for visual comparison of territory location of the same individuals between years.

The result of all these inter- and intra-gender territorial interactions is a territorial system which is not static. Measuring the daily changes in territories would be a complete study in itself and as such was beyond the scope of this one-person study. For my numerical analyses I used one estimate of territory size and location for each individual. The borders that were selected for measurement were those which existed after pair bonds were formed and the first nests were begun, but before floating males attempted settlement. In all years except 1984, a second measurement was taken on male territories which changed visibly in size later in the season following the late settlement of floating males or the disappearance of a male.

A range of territorial sizes for other savannah sparrow populations is reported in the literature. Stobo and McLaren (1975) reported a size range of .39-1.25 hectares for dunes and pastures on Sable Island, Nova Scotia. Territories in lightly grazed pasture in Wisconsin ranged in size from .16-1.09 hectares (Wiens 1973). Potter (1972) reported values of .06-1.2 hectares for old field and pasture in southern Michigan. Smaller territory sizes of .17-.21 hectares have been documented by Welsh (1975) for a dune beach in Nova Scotia and .12-.28 hectares by Bedard and LaPointe (1984a) for a tidal marsh-abandoned field ecotone in Quebec. Dixon (1978) reported extremely small average territories (.11 hectares) for a population inhabiting a grassy meadow on Kent Island, New Brunswick. Her study, however, focused only on a particularly dense population in a core (1.38 ha) portion of a larger breeding area on the island and thus might not have reflected the true range of territory sizes for this population.

Non-breeding individuals, or floaters

If the number of breeding age adults is greater than the number which can be accommodated on territories suitable for breeding, non-breeding birds or floaters (Brown 1969) should exist in the system. The length of time that a bird exists as a floater may vary (Arcese 1989). Individuals may be territorially excluded for their lifetime, for one to several breeding seasons of their life, or for a portion of one breeding season. During the time an individual is territorially prevented from breeding, it can be considered by definition to be a floater. The existence of territorial systems for both males and females in savannah sparrows leads to a prediction of the existence of floaters of each gender. Observational assessment of a floating population required identification of birds as unique individuals as well as the determination of their gender. Male floaters which attempted settlement could be sexed by their song. In this monochromatic species, all other gender identifications depended on behavioral observations. All nesting, territorial individuals were identified as individuals through color bands or, rarely, through unique plumage characteristics. Therefore, any unbanded individual who suddenly appeared in the system and particularly those who stayed for times of hours to days could be assumed to be a floater. Keeping track of floaters as individuals required individual color marking of the floaters unless an individual possessed a distinctive plumage trait. Color banding was only possible for the male invaders since only they came in readily to the lure of the model and taped song.

It is possible to argue that any of these unbanded floaters have attempted to breed elsewhere and failed. The fact that neither males

nor females were observed to relocate even in the face of predation losses of multiple nests, argues against such relocation as a general rule. Only one female was recorded as relocating on the study site after the loss of her first nest. Yet even if this relocation occurs very occasionally, a bird who has left its original territory after a breeding attempt must locate another vacancy before it can breed again. Thus, it is, at least temporarily, a floater who is attempting to enter the territorial system.

Some researchers (Potter 1972; Stobo and McLaren 1975; Weatherhead 1979a; Bedard and LaPointe 1984b) have reported these late male territorial claimants as late arrivals. They present no argument in favor of such a label, however. Rapid entry into a territorial system would seem to require advance knowledge of potential openings or weak spots. Weatherhead and Robertson (1980b) report male replacement after experimental removal within 24 hours. Such rapid replacement seems to argue in favor of a floating population which has been present in the area, continually assessing the potential in the system for possible entry. Thus, these birds may be later in settling on a territory but not necessarily late arrivals.

Nesting

In all years, all nests on the study site were located as early as possible and followed to termination. The intense behavioral observations of the parents made it unlikely that nests were completely missed. No more than two nests were known to have been missed during their active period in any year. These were later located as empty

nests. No nest on an observed territory remained unlocated through fledging, as the parental feeding of young would reveal their position. Locating the nests early in the breeding season facilitated the banding of females. This, in turn, made it easier to take behavioral observations on individual females. Early location and complete follow-through of nests also enabled me to obtain accurate records of the nest timing in order to make accurate determinations of any incidences of polygyny.

Dates of nest building, start of egg laying, start of incubation, and start of hatching were recorded for each nest. The nest was monitored until fledging, predation or abandonment occurred. Predation was identified by the complete loss of eggs or of young under fledging age or the presence of chewed or bitten dead young in the nest. In the case of mammalian predators, the nest was often torn apart as well. With the exception the rare disappearance of individual eggs or small young early in the nesting cycle (probably due to avian or reptile predators) predation was an all-or-nothing event. Potential nest predators on the study site included domestic cat, red fox, striped skunk, thirteen-lined ground squirrel, badger, weasel, garter snake, common grackle and common crow. If building or laying dates were not observed for a nest, they were estimated using a back calculation from the hatching date of the first egg and the assumption that one egg was laid per day. If hatching did not occur, commencement of nest building was estimated as occurring two days before the start of laying, unless behavioral observations gave an indication that the nest building period had been prolonged.

Nests were marked with a surveyors' stake placed one meter north of the nest and were monitored every other day. Because the 18 hectare plot was continually being completely traversed by the researcher, it is unlikely that trips to the nest served as a beacon for predators. Care was taken, however, to vary the direction of approach and minimize the creation of a human trail.

In 1987, the distances between the most closely spaced concurrent nests of females were measured in the field. Each female's nest had one nearest neighbor measure associated with it. A correlation analysis was performed to examine the relationship between the territory area, nearest neighbor nest spacing, foraging index and proportion of territorial overlap for females in 1987. Further analysis involved partial correlation analysis of these variables holding constant territorial area and the proportion of overlap, in turn. Following the results of the partial correlation analysis, the proportion of overlap was plotted against the foraging index and examined with a linear regression model.

Concurrent nests in 1987 were placed into two time periods by their nest initiation date. These time periods were separated by a week of no nest initiations. Time 1 included all nests which were initiated before the first nest began hatching. These were first nesting attempts for the season. Rarely, a very early re-nesting attempt was included as well. Time 2 included all nests which were initiated after the first nest of the season hatched. These nests included the majority of re-nesting attempts of females who lost a nest in the first time period, as well as first attempts of later settling females. Two females had third attempts which were exceptionally late and did not

commence until the neighboring nests had finished incubation. These two nests were not included in the analysis since they had no neighbors on contiguous territories who were still nesting when they initiated their final nest of the season.

In addition to the effects of habitat quality, the spacing of incoming females might also be affected by the level of aggression of the neighboring females who were already nesting. This, in turn, could be affected by the stage of the nesting cycle and the parental care demands faced by the female. There were four main stages: pre-nesting and building, laying eggs, incubating, and caring for young. These four stages, in turn, could be lumped into two main categories which reflected an increasing degree of investment in the nest and, concomitantly, a reduction in the time and energy available to the resident female for territorial exclusion of additional females. Nest building and laying constituted the category of nest initiation and care of eggs or young constituted the category of care of young. I then asked the question: "What was the activity category of the nearest neighbor when the focal female was nest building?" Each focal female had one nearest neighbor, and thus had only a single activity category of that nearest neighbor associated with her. The relationship between time period and the activity category of the nearest neighbor was examined using a 2 x 2 contingency table.

Finally, the relationship between the spacing of nearest neighbor's nests and the proportion of overlap of the female's territories were compared for the two time periods by means of linear regressions.

Habitat

Difficulties have existed in obtaining an accurate and biologically relevant direct measure of resource abundance for a species in both space and time. A study of the territorial system of savannah sparrows in Quebec (Bedard and LaPointe 1984a) did not reveal a significant relationship between arthropod abundance and territory size. Seastedt and MacLean (1979), studying male Lapland longspurs (Calcarius lapponicus) failed to find the expected inverse relationship using one year's data, but did see a relationship when an average of several years was examined, suggesting support for habitat quality as a proximate determinant of territory size. A previous study of the population that is the focus of this present paper (Beaver unpub.) found an inverse relationship between arthropod abundance and male territory size, when both were averaged by spatial subgroups over three years, but found no consistent relationship on a yearly basis. One difficulty of any study which attempts a direct measurement of food abundance lies in linking the sampling technique to the actual prey availability to the animal. For example, Meunier and Bedard (1984) found that the arthropods in the diet of nestling savannah sparrow did not match the proportions of arthropod taxa sampled in the habitat.

Such results suggest that the relevant measure that is needed is not merely one of prey abundance but one of prey availability; a composite of prey abundance and efficiency of procurement. The efficiency of procurement, in turn, may be directly related to the animal's style of foraging and the structure of the habitat. Odum (1945) has suggested that species of birds are frequently adapted to

the structure of the vegetation rather than to the species composition of plants. In addition, structural vegetative features in many habitats exhibit less variability than actual food resources, making them a useful tool for studies spanning multiple years. Food abundance may still vary between years if they do so in response to such factors as weather, but the structure of the habitat may remain stable. Thus, in some cases, such as the present study, a structural feature of the habitat may actually be a better estimate of habitat quality, for both the animal and the researcher, than a direct measure of prey biomass.

Savannah sparrows show a clear preference for foraging around the edges of vegetation, in a variety of geographical locations (Quay 1958, Wiens 1969; Bedard and LaPointe 1984a; This study). They walk on the bare earth or areas of reduced litter and glean arthropods from the edges of vegetation. As mentioned above, the vegetation on the site varied in growth patterns, producing quantitative differences in the density of foraging edge available to the birds which were visibly stable from year to year. Using these observations, I hypothesized that the density of such foraging opportunities was a factor influencing territory quality through its influence on foraging efficiency. It thus had an indirect influence on territory size.

In 1987, I developed a scheme to sample and measure this stable habitat feature of vegetation clumps. The 20 X 20 m grid was used in order to provide a basis for transects that was independent of the territorial borders of the individual birds. Within each grid square (400 m^2) I could visually distinguish patches of vegetation which differed primarily in the size of clumps of grass and forbs. The

sampling scheme was designed so as to produce a measure of the number of vegetation clumps within a patch as well as a map of the incidence of these patches on the study area. To this end, transects were located so as to sample one visually distinguishable patch. They did not cross patches and were 10 meters in length; one-half the length of a grid square. The location of transects within a homogeneous vegetation patch was fixed by use of a random number table, with loci at meter intervals numbered 1-20 on a map of the grid square. An initial random number selection (even or odd) determined the orientation of the transect (N-S or E-W). Most grid squares were sampled with two 10 meter transects. Occasionally, a square was comprised of more than two patches. In these cases, the additional patches were sampled using additional transects that were contained within the patch borders. In this fashion I sampled 7.6 hectares using 417 transects. This represented the majority of the 8 to 10 hectares used by nesting sparrows for the duration of each breeding season.

A clump was defined as live vegetation which was separated by bare earth or litter from the adjacent live vegetation by a space large enough for the unimpeded movement of a walking sparrow. The number of clumps which fell under a ten meter transect tape were recorded with their diameters, measured along the tape. From these samples, a mean number of clumps and a mean diameter of clumps per patch were calculated.

Most of the clumps of grass and basal rosettes of the common forbs had a nearly circular growth form. For analysis, all clumps were treated as if they were circular, enabling me to use the circumference of the clump to estimate the edge distance available for foraging by

the bird. I assumed that the biologically relevant measure was the density of foraging opportunities available in a defined area, such as a territory. I used the area of a 10 X 10 m square for standardization and calculated a foraging index for each patch using the total number of clumps per patch and the perimeter per clump. This was expressed in units of m/m^2 . The index values for each patch were then plotted on a gridded map of the study site. A map of the bird territories for each was superimposed on this map allowing the calculation of a mean value of the foraging index for each territory and thus the association of a single foraging index with each territory.

Statistical analysis

Most parametric and non-parametric tests were performed using software from SYSTAT, Inc. (1985). Some non-parametric tests on small data sets were completed by hand using procedures found in Sokal and Rohlf (1981) or Zar (1984). Data were examined for normal distributions using probability plots. Homogeneity of variances was tested using F_{max} tests. Where the requirements of normality and homogeneous variances were met, parametric tests were employed. This was true for data on territory areas, habitat quality, nearest neighbor nest spacing for 1987, and the proportion of overlap. Areas of territories were transformed by means of natural logs to achieve a best fit to a normal distribution. Proportions of territorial overlap were similarly transformed with an arcsine transformation. The analyses used included linear regression, and correlation. Where applicable, means were reported with sample sizes and standard deviations.

Other data which failed to meet the assumptions for parametric models were analyzed using non-parametric tests such as Chi-square analysis, Mann-Whitney U (two-tailed), and Kruskal-Wallis (two-tailed) and Spearman rank correlation. For non-parametric tests the foraging index (FI) was categorized into categories which were equal in size. The maximum number of categories (two or three) depended on constraints imposed by sample size and the type of statistical test. Contingency tables were analyzed by means of the log-likelihood ratio Chi-square test using the G statistic which is approximately distributed as Chi-square (Zar 1984).

CHAPTER IV

RESULTS

Territorial System

Sizes of territories

Size ranges of territories. Mean territory area for territories of all nesting males and females for all four years was .41 hectares ($n=121$, $SD=.28$). The territories ranged in size from a low of .07 to a high of 1.53 hectares. The largest magnitude of difference between large and small territories in any year was sixteen fold.

Factors influencing territory size. A regression analysis revealed a significant inverse relationship between the territory area of nesting individuals and habitat quality as estimated by the foraging index for all years (Figure 2). The negative slope is significant ($P<.001$). This matches the expected inverse relationship between territory area and resource abundance that is reported in the literature (Pitelka 1959; Stenger 1958; Holmes 1970; Miller et al. 1970; Simon 1975; Zach and Falls 1975; Salomonson and Balda 1977; Seastedt and MacLean 1979; Catterall et al. 1982; and others). One observed result of this relationship of territory area to a perennial habitat feature, combined with strong site fidelity, was a remarkable stability from year to year in the sizes of territories in each portion of the study site.

The data from 1986 and 1987 were used for a further examination of the relationship between territory area and foraging index broken down by gender and by three categories of age (1 year, 2 year and greater

than 2 years). These were the years with the most complete data on both gender and age. There was no difference between slopes of regression lines for males and females ($t=.234$, $P>.50$). Likewise, there were no differences between the slopes of regression lines for all three age categories ($F=.05$, $P>.5$).

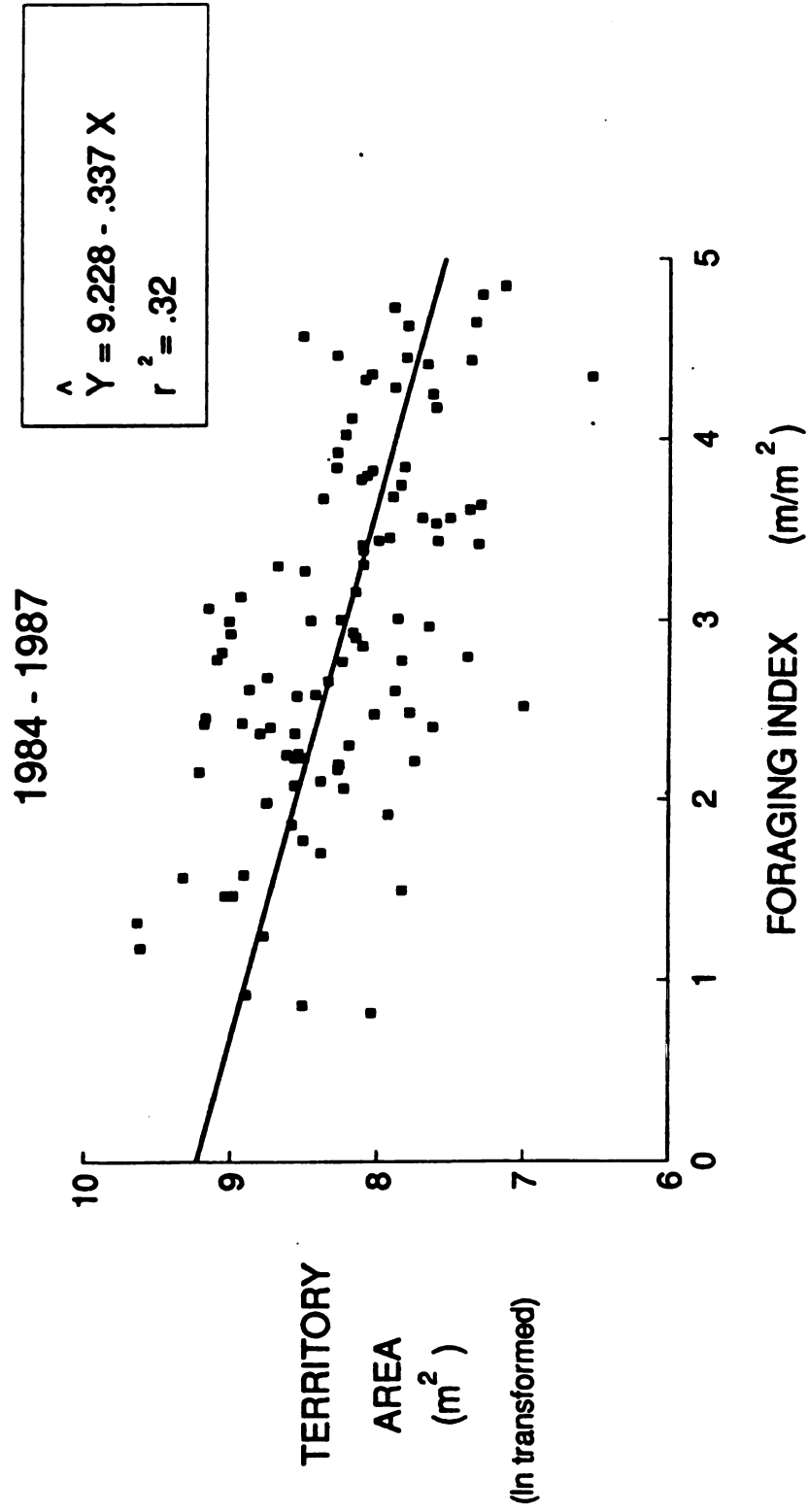


Figure 2. Relationship between territory area and foraging index for nesting, territorial savannah sparrows

Habitat selection by territorial birds was examined. Three categories of foraging index were used to classify the occupied territories. This was the highest number of categories that could be used without creating sparse cells in the contingency table. The observed frequencies of territories in these categories were compared to expected frequencies. These expected frequencies were calculated by multiplying the total number of recorded territories of nesting birds times the proportion of habitat available on the study site in each category. The null hypothesis was that these two distributions would be equal if the birds were exhibiting no habitat preference. The data do not support the null hypothesis ($\text{Chi-square}=41$, $\text{df}=2$, $P<.001$, Table 3). Individuals appear to have chosen territories in the two highest categories of quality in preference to low quality areas. This habitat selection is not surprising when viewed in conjunction with the larger size of territories in areas of low foraging index. The sizes of territories and the density of birds in a particular area are inextricably linked, with fewer birds occupying a low quality area.

Table 3. Observed and expected frequency distributions of nesting territory holders by foraging index category

1984-1987			
Foraging index category	Percentage of total area	NUMBER OF TERRITORIES	
		Observed	Expected
FI \leq 2	42.1	16	42.9
2 < FI \leq 3	19.2	41	19.6
FI > 3	38.7	45	39.5

Although male and female territory areas showed no differences in their relationship to the foraging index, they did appear to differ in the exclusivity of borders. The mapping of female territories revealed a higher percentage of them showing overlap of boundaries than male territories (Table 4). Nesting males rarely allowed any shared space with other males. The overlap of female territories was estimated from the mapping of the territories and hence, like the territorial area measures, was a one-time measure made at the time of first nests. When this proportion (arcsine transformed) of the territory which was shared with another female (proportion of overlap) was plotted against the mean foraging index, a significant positive relationship emerged ($r=.664$, $df=33$, $P<.001$, Figure 3). As a visual examination of the map had indicated, the females seemed to be less exclusive in their use of space, tolerating more ambiguity in boundaries and hence, more territorial overlap, in the areas of highest foraging opportunities.

Table 4. Observations of selected behavioral events

Male feed-singing behavior 1985

Thirteen out of seventeen territorial males exhibited this behavior for one to three days during the period before they acquired a female. Two males also engaged in one bout of feed-singing while their female was incubating.

Female serial monogamy 1984-1987

1985. Female YEL/RD had one nest with a male who did not feed the fledglings and eventually failed to defend his territory against two invaders. The female had a second nest on the same territory, with one of the invaders.

1986. Female BLU-BLK raised her first nest alone after her first male disappeared. A new male, RD/BLK, took over her territory and attempted copulations while she made feeding trips. She eventually had a second nest with him which was predated. After the failure of the second nest, the female shifted to a neighboring territory that was higher in quality and whose female was no longer present. There she attempted a late and unsuccessful nest with a third male, BLU/ORG. Her second male was still present on her old territory at this time.

1987. Female ORG/PUR had a successful nest with her first male, RD/WT. He continued to feed the fledglings and she mated with a neighboring male who was successfully usurping RD/WT's territory. RD/WT disappeared after the fledglings from the first nest were raised.

Overlap of territorial borders for males and for females 1987

Number of male territories showing overlap of borders with neighboring male = 6

Total number of male territories with mapped borders = 23

Number of female territories showing overlap of borders with neighboring female = 12

Total number of female territories with mapped borders = 18

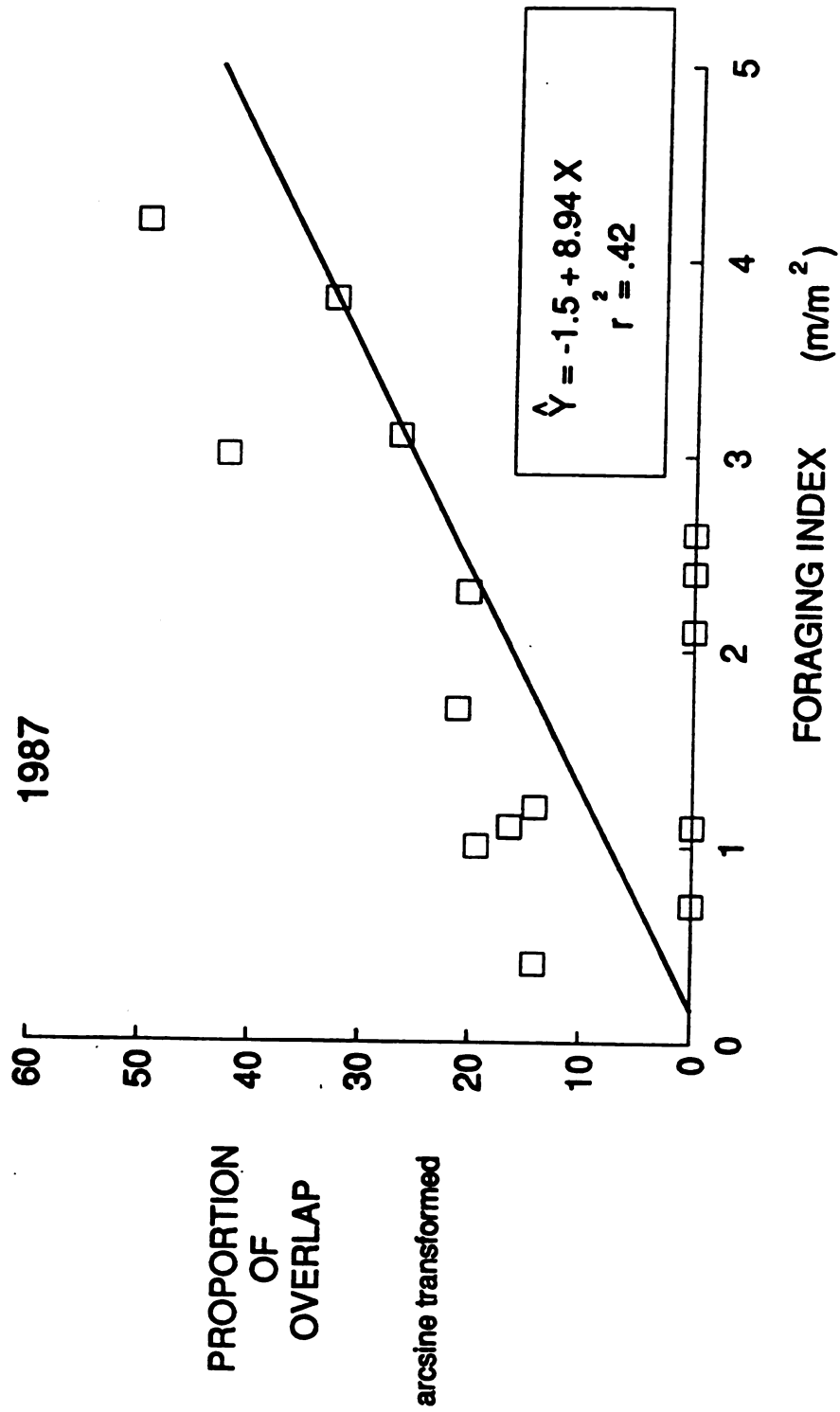


Figure 3. The relationship between the proportion of overlap of female territorial borders and habitat quality estimated by foraging quality

I recorded 17 incidences, from 1985-1987, of males who changed the size of their territory later in the season as the pressure from competitors changed (Table 5). In all but four cases, the males reduced the size of their territories in response to competition from late-settling male floaters. The four remaining cases involved territorial expansion when a neighboring male disappeared or shifted the position of his territory, leaving an available female (Table 5). I observed no similar changes in the size of female territories once nesting had commenced.

Table 5. Changes in areas of male territories in response to fluctuations in territorial competition.

Color code of male	Year	Original size of territory (hectares)	Altered size of territory (hectares)	
ORG	1985	.33	.14	
ORG/BLK	1985	.27	.03	
RD/WT	1985	.26	.15	
WT	1985	.21	.07	
BLK/ORG	1986	.24	.17	
BLU/RD	1986	.38	.60	Expanded
ORG	1986	.24	.68	Expanded
ROY	1986	.31	.16	
YEL/BLU	1986	.36	.23	
BLK/ORG	1987	.25	.19	
FUS-GRN	1987	.35	.63	Expanded
ORG/PUR	1987	.82	.73	
RD/BLK	1987	.86	.72	
RD/BLU	1987	.50	.29	
RD/WT	1987	.81	.53	
ROY/ORG	1987	.22	.31	Expanded
WT-GRN	1987	.28	.17	

Arrival times

Mean arrival dates. The mean arrival date of males was fairly constant, varying two weeks between early and late years. An average male arrival for all four years was the third week in April. Females arrived from one to five weeks after the males, with a four year average arrival time of the second week of May (Table 6). This unexplained variation in female mean arrival times resulted in varying degrees of asynchrony between male and female arrivals, between years. In a year such as 1985, the males arrived during the average time of the third week in April and the females arrived exceptionally early, in the last week in April. As a result, only 10 days separated the mean male arrival date from that of the females. That year, many individual males and females arrived simultaneously on the breeding grounds. Late arrivals for both genders occurred in 1984. There were also observable differences in the synchrony of arrivals of females as a group. In 1985, female arrivals were scattered, with approximately two thirds of the females arriving within a 32 day span. Only one day had records of arrivals of more than one female. By contrast, in 1987, two thirds of the females arrived within 22 days and four days had records of multiple arrivals. In 1984 and 1986, birds arrived with a warm front from the south, indicating that arrival from migration may be influenced by conditions along the migration route. This possible influence of regional weather patterns is well documented (Welty 1975) and has been previously reported for this population by Beaver (pers. comm.). In turn, arrival dates may influence the nesting dates and ultimately the reproductive success of the individuals.

Table 6. Mean dates of arrival of males and females and first nests of females

1984-1987

Year	Mean arrival date (n) (SD in days)		Mean date of building of first nests	Days from mean male arrival to mean female arrival.
	Males	Females		
1984	04/27 (11) (6.5)	05/21 (11) (15)	06/03 (18) (17)	24
1985	04/20 (17) (4)	04/30 (14) (12)	05/09 (17) (9.5)	10
1986	04/13 (17) (8)	05/15 (21) (15)	05/23 (20) (9.5)	35
1987	04/14 (28) (4)	05/05 (17) (5)	05/14 (20) (4)	24

The males included are those who have settled before the first nest is begun.

The females included are those engaging in a first nest of the season. Excluded are females who have replaced a female on a territory, females nesting with invading males, or females which do not settle until the majority of the females are fledging young or re-nesting.

Female order of settlement and territory quality. No relationship was found between the dates of female settlement on a territory and the quality of that territory for either of the focal female years of 1986 or 1987 (Spearman's rank correlation; $r=.265$, $n=16$ for 1986 and $r=.236$, $n=14$ for 1987, Table 7). This is not an unexpected finding in a system that exhibits pronounced site fidelity, described below. Females and males appeared to return to their territories of the previous year if they were available, irrespective of quality.

Table 7. Ranks of females by arrival dates and territory quality

1986 and 1987			
1986		1987	
Arrival Date Rank	Foraging Index	Arrival Date Rank	Foraging Index *
1	3.0	1	2.4
2	1.6	2	3.1
3	2.8	3	4.0, 2.7, 1.2, 3.0
4	3.3	4	2.8
5	2.8, 3.3	5	4.7, 4.2
6	2.2, 4.1	6	2.4, 3.2
7	1.8	7	3.5
8	3.3	8	2.4
9	3.7		
10	3.7		
11	2.7, 3.4		
12	4.4		
13	1.6		

* multiple foraging index entries = tied arrival ranks

Site fidelity

Faithfulness to location. My observations show strong site fidelity on the part of the males, with only occasional minor (< 50m) contiguous shifts in territory location. Only one male was ever observed to move to a new non-contiguous territory between years when he moved approximately 200 meters and relocated his territory on the opposite side of the pond. Interestingly, he did move from an area with a low foraging index to an area higher in quality. Another male which began on a lower quality site as an invader was able to shift approximately 40 meters to the neighboring territory of higher quality when it became vacant in the following year.

Female savannah sparrows also appeared to exhibit site fidelity in

my population, although, again, some minor contiguous (< 50 m) territorial shifts did occur. Two incidences were recorded of a female making a territorial shift greater than 50 m between years. In both cases, the female arrived after her territory of the previous year, and the territories contiguous to it, had been occupied by other females. I also recorded one instance of a female making a non-contiguous territorial move within a season. She left a territory which she initially shared with another female after the failure of her nest and moved to a territory where the male had lost his female. The initial territory had a foraging index associated with it that was approximately seven times higher than the index of the second territory. The new site had an unmated male present on it when she arrived. Thus, it is likely that the new site was not chosen because of its quality but rather because of its vacancy in terms of other females or because of the presence of an unmated male, or both.

Return frequencies of males and females. There was a non-significant trend for a higher percentage of territorial (both nesting and non-nesting) males to return in any one year than territorial females (Table 8). This trend was most pronounced in 1986 and 1987 when the females experienced their lowest rate of return and the males, their highest. Only in 1987 was there a significant difference between the return rates of males and females ($G=3.92$, $df=1$, $P<.05$).

Table 8. Returns of territorial males and females

1985-1988

Year	MALES			FEMALES		
	Number banded *	Number returned	Percent returned	Number banded	Number returned	Percent returned
1985	22	10	45	19	7	37
1986	28	15	53	19	5	26
1987	27	15	55	22	6	27
1988	29	12	41	25	9	36

* Number banded = total number of marked birds present in the year previous to the year of return

As an indirect estimate of longevity, I compared the tendency for males and females to return for more than one year. To do this, I compared the frequencies of returning territorial male and female sparrows categorized by the number of years each individual was sighted on territory (Table 9). The number of years a bird returned was not independent of gender ($G=9.78$, $df=3$, $P<.025$) with more males returning for a greater number of years. With no observed difference in site fidelity between the two genders, this would translate into a tendency for territorial males to live longer than territorial females, a result known from other species (Smith 1988). It would also result in fewer vacant male territories at the beginning of the breeding season.

Table 9. Frequencies of returning territorial males and females by the number of years they were sighted

1984-1988

Number of years sighted	Males	Females
One year	39	47
Two years	12	15
Three years	15	5
Four and five years	6	1

Non-breeding individuals or floaters

Time did not permit rigorous documentation and quantification of all non-breeding individuals. Nevertheless, observations made during the focal bird studies provide good direct observational and circumstantial evidence for the existence of floaters of both genders in this population. These data include the presence of unbanded birds on breeding territories, the continual sighting of a former territory holder which had abandoned its territory and the rapid filling of territorial vacancies by unbanded birds. More detailed descriptions of these findings for each gender are given below.

Non-breeding females. After a nest loss due to predation, some females did not re-nest but did remain on the edges of their territory for a day or two before disappearing. Four such females were recorded in 1986 and five in 1987, the two years of focal female studies. This enabled me to see that they had not been killed in the predation event, yet their disappearance from the territory indicated that they may have

joined the floating population. In fact, only one female was ever known to have been killed during a predation event. Other than death, possible reasons for territorial abandonment by females include injury or illness, energy depletion with regard to re-nesting demands, aggression by other females or various combinations of these factors. Vacancies in the female territorial system that occurred during the initiation period of first nests were filled by unbanded females. Seven such vacancies and subsequent replacements were recorded in the four years (9% of the total breeding pairs). In 1987, two probable floating females settled as second females of already mated males, later in the season. This phenomenon will be addressed in detail under the discussion about pair bonds.

In 1986, intensive behavioral observations of each banded female and her territory resulted in sightings of unbanded females which consorted, but did not nest, with already mated territorial males on territory. The estimated length of stay of eleven recorded females on ten different territorial areas varied from 1 day to 37 days (Table 10).

Table 10. Sightings of probable non-breeding female savannah sparrows

1986

Male territory	Foraging Index	Date first sighted	Date last sighted	Days present on territory
WT	4.85	05/01	05/03	3
RD/BLU, ROY & BLK/ORG	4.08	06/04	07/10	37
BLK/RD	2.68	06/19 07/12	06/19 07/14	1 3
BLU/PUR	2.30	07/01	07/11	11
ROY	3.83	07/02	07/02	1
ORG/GRN	1.59	07/02	07/26	25
RED/PUR	1.92	07/09	07/09	1
ROY/YEL	2.30	07/14	07/18	5
BLU/RD & YEL/GRN	3.08	07/15	07/23	9
MAG/YEL	4.40	07/23	07/23	1

These non-breeding females were observed on male territories which encompassed the range of foraging indices. I tested the null hypothesis that these floating females showed the same frequency distribution relative to the three categories of the foraging index as the distribution of existing female territories relative to the foraging index. The alternate hypotheses propose that females either attempted settlement preferentially on the higher quality territories where foraging was better or on the lower quality territories where competition might be less. I generated the expected frequency

distribution by multiplying the proportion of female territories in each foraging index category times the total number of floaters. When these distributions were compared, no significant difference was found between the observed and expected distributions of floating females (Chi-square=.46, df=2, $P>.75$, Table 11). Female floaters did not appear to attempt settlement preferentially either on the highest or lowest quality territories.

Table 11. Frequency distributions of floating females and available territories relative to habitat quality

1986

Foraging index category	Frequency of non-breeding females	Expected frequency based on the number available territories
1	2	3.0
2	4	3.5
3	5	4.5

Floating females were usually unbanded and any identification had to depend on observations of subtle plumage characteristics. Thus, it is possible that more than one female could have been involved in the longer residencies on territories. The main point at this juncture is not the length of stay by non-nesting females but, rather, that fact that some unbanded females were present, for varying lengths of time without nesting, on territories that were already occupied by nesting females. All but one of these appearances occurred after nesting was

well underway. It is possible that permanent settlement and nesting of the floaters were prevented in these cases by aggression of the resident female since, as has been noted, actual vacancies were readily filled by non-breeding females. I have one observation of a resident female's behaving aggressively toward an unbanded bird (who was identified as a female by her behavior) who stayed several days but never nested. In some cases, the lateness of the season probably also contributed to the failure to nest by unbanded females. The ages of these floaters were unknown in most cases, although one observed floater was a yearling which had been banded as an independent juvenile in the previous year. Another observation in this study involved a female which was banded as an independent juvenile and not resighted as a nesting territory holder until she was two years old. It is possible that she also was a floater as a yearling.

Non-breeding males. Non-breeding males may be unmated for all or part of the season and they may be territorial for all or part of the season. The highly visible manner with which males acquire a territory, using singing as part of the display, made it easier to procure evidence for male floaters than for females. Some specific evidence for male floaters follows.

Depending on the year, one to three banded males held territories at the beginning of the season but did not acquire a female and eventually left the territory. As the season progressed, these same individuals were re-sighted in other areas of the study site that were unoccupied by nesting females, often singing. In three instances, two males held territories in a low quality area concurrently occupied by

only one female. Only one male was able to nest with the female, leaving the other male unmated. Other males were without a female for varying lengths of time even after all their neighbors had mates in medium to high quality areas. They eventually acquired a female after the neighboring females had begun nesting. This phenomenon was not restricted to the same territories or the same males from year to year. Replacement of vacated male territories during the main portion of the breeding season was the rule. Males who abandoned territories with females or simply ceased active defense and display while remaining in the vicinity were, like females, quickly replaced in a matter of hours to days.

Three records exist for males (3 years or older) whose appearance and behavior suggested an inability to marshal the energy to continue territorial defense. They sat on the ground or lay on the ground, often near the margin of their territory. Their plumage was fluffed and they sang weakly and infrequently. Two such males lost their territory completely, while one (ORG/BLK, Table 5) had the size of its territory dramatically reduced.

Welsh (1975) reported unbanded birds throughout the season, chased from territories by the resident birds. I also continually sighted unbanded birds, sometimes assessed as males by their behavior, who were pursued before having a chance to settle permanently. These sightings suggest a floating population which continually search for vacancies, perhaps by testing the behavioral response of the territory holder.

As the breeding season progressed, mated males were involved in feeding their young. During this period, they appeared to devote less time and energy to territorial defense. New males took advantage of

this window of opportunity and inserted themselves into the interstices of the territorial system. Sometimes these later-settling males also took advantage of low aggression, older males such as those described above. I have called all of these late-settling males "invaders" since they invaded a territorial system that was already well-established (Table 12).

Table 12. Invading adult male savannah sparrows

1984-1987

	1984	1985	1986	1987
Number of Invaders	7	9	3	5
Number of Invaders which nested that year	3	1	0	1
Average invasion date	06/30	06/11	07/05	06/17
Percent of invaders which returned the following year	/	43%	67%	33%
Percent of invaders which returned the the following year and nested	/	29%	44%	33%

A ranking of years by the mean nesting initiation date (Table 6) is identical to a ranking of years by the mean invasion date (Table 12). In a late female arrival and nesting year, male invaders were also late in settling. In fact, they settled on the average of more than a month after the initiation of nests. Thus would place their

settlement in a time period when resident males were occupied with nests or had completed all nesting attempts. This might be due to reduced aggression on the part of the resident male.

The frequency distribution of thirteen male invaders from the four years relative to the foraging index was compared to the distribution of male territories relative to the foraging index, in the same manner as was done for the female floaters. Again, the distribution of floaters did not differ from the expected distribution based on the availability of territories (Chi-square=.046, df=2, $P>.95$, Table 13).

Table 13. Frequency distributions of invading adult males and available territories relative to habitat quality

1984-1987

Foraging index category	Frequency of non-breeding males	Expected frequency based on the number available territories
1	3	3.3
2	5	4.7
3	5	5.0

Invading males sometimes managed to procure a floating female who was also entering the territorial system when resident females were occupied with nesting duties. These invaders thus managed to nest, albeit late, that year. Others did not nest in their invasion year but did return to breed the following year on the same territory that was

acquired by the invasion. Thus, these males acquired a position in the territorial system as invaders that gave them a potential reproductive advantage over floaters the following year. The percentages of invaders which returned and those which returned and nested are listed in Table 12. Such late settlement in the year prior to the year of breeding may be very important in a site faithful territorial system since males returning to a territory usually have an advantage in holding that territory. This advantage of site fidelity is as yet unexplained in the literature except in a general way invoking the advantages of previous familiarity with the site.

For both genders I recorded late-settling individuals who appeared well after the mean date of the first nests (Tables 6, 10 and 12). This suggests that both genders may be employing the strategy of entering the territorial system when the resident territorial holders face conflicts of demands on their time and energy which stem from nesting demands. It is possible that late settlement might also spring from a late arrival from migration. There are, however, no data which indicate a prolonged spring migration in this species. In 1986, the date of invasion was almost at the end of the initiation of all nests (Tables 6 and 12). Such an extremely late date makes it unlikely that late-settling birds can be explained as late arrivals from migration.

Some males held a territory but did not secure a female and nest. In other studies these birds are referred to as bachelors. They have been used as evidence of a shortage of females in another population of savannah sparrows (Bedard and LaPointe 1984a). This explanation is refuted in my population by the presence of floating females. These non-breeding territorial males can be placed into two categories.

First, some males acquired a territory fairly early in the season and held it for varying lengths of time without ever securing a mate. These accounted for an average of 9% of the territorial males in the years 1985, 1986 and 1987. The invaders, described above, which entered the system late and did not acquire a female, made up the second category. When both categories of non-breeding, territorial males were considered together, percentages of males of both categories ranged from 19% in 1987 to 43% in 1985. They accounted for an average of 27% of all territorial males across the three years of the study.

Independent juveniles. At a time in the season when the fledglings of the first nests became independent, there occurred an influx of independent juveniles (hatching year or HY birds) from outside the study site. These juveniles often stayed together in small flocks and spent considerable time at the edges of territories in weakly contested areas such as road edges or lakeshore. They interacted aggressively with each other and with the adult territory holders. A few juveniles from nests on the site were also present, but for the most part they, like these juveniles, seemed to have dispersed to another location. Some of these dispersing juveniles were banded in all but one year (Table 2). Two of the males had small cloacal protuberances, perhaps indicating some hormonal activity. A total of four male juveniles returned in following years and became territorial breeders as yearlings. Another juvenile returned as an invader as a yearling and subsequently as a successful nester for two additional years. Intriguingly, one male banded as an independent juvenile was not sighted again until he became a nesting territorial bird at the age of

three years. One female juvenile was not re-sighted until she returned and bred as a two year old. Another female banded as a juvenile was observed as a yearling consorting with an invading male late in the breeding season, but did not nest that year. These data from the banded juvenile returns indicate that at least some portion of the floating population may be older than one year. A similar influx of independent juveniles has been reported for dunnocks (Davies and Lundberg 1984). In addition, younger birds have been documented as floaters in other species (Hannon and Zwickel 1979; Baeyens 1981a; Stutchbury and Robertson 1985; Hunter 1987; Arcese 1989). The dispersal of independent juveniles to appropriate habitat has been hypothesized as one way for an individual to increase its chances of procuring a territory early in life (Brewer and Harrison 1975).

Nesting

Nest initiation dates

The timing of arrival of females seemed to be related to the timing of nest building. When both the mean arrival dates of females and mean nesting dates of females were ranked for all four years, the rankings were found to be identical. Although there are individual differences, most females spent between one to two weeks after arrival (average of 10 days), before nesting, as if there were a minimum time requirement required after arrival from migration for provisioning in preparation for egg laying. Because of this, an early mean arrival date for the female population seemed to translate directly to an early date for nest initiation for the majority of females.

Within the framework of arrival times, however, the local weather could potentially exert an influence, particularly as it might affect the abundance of prey. Local weather data were available from a weather field station within .5 km of the study site. As mentioned, females arrived earliest of the four years in April 1985. The mean date of nest initiation in 1985 was earlier than the other years as well (Table 6). In 1985, the maximum daily temperature (averaged over five day blocks) had risen rapidly just prior to the onset of female arrivals, increasing 30 degrees in 15 days. A pronounced surge in temperatures could very well result in a surge in insect food. Ready access to abundant food upon arrival could, in turn, shorten the provisioning time and hasten the nesting of some of the early arrivals (Davies and Lundberg 1985). Nevertheless, the early arrivals in that year still waited the usual average of ten days or more before nesting. In fact, two early arriving individuals waited 19 and 25 days before nesting. Thus, it does not appear as if the rapid warming early in the season hastened the onset of nesting. No comparable rapid warming trends existed for other years.

The nest initiation pattern seems to have been most strongly influenced by the pattern of arrival from migration. Evidence comes from a comparison of the patterns of arrival and nest initiation dates of individuals through time in two particularly distinct years. Arrival of two thirds of the females in 1985 were spread over 32 days. Similarly, the nesting dates for ninety-four percent of the first nest attempts of the females were dispersed over a period of 35 days. There were only two recorded incidences of more than one female initiating a nest on the same day. The 1987 patterns of individual arrival and nest

initiation dates show a similar correspondence. In that year, over half of the females arrived within two weeks and a corresponding 80% initiated first nests within a span of 12 days. There were six incidences of more than one female beginning a nest on the same day.

At the present time, it seems that factors at some distance from the study site (such as regional weather patterns) have the greatest influence on the initiation dates of first nests through their influence on the timing of migration. Local weather patterns may still result in a fine-tuning of the system, but any current understanding of their influence is rudimentary at this time. Nesting patterns may also be influenced by physiological differences in individual females or aggressive interactions of females. I have no data to address the former, but will address the latter indirectly under nest spacing.

Nest mortality

A total of 153 nests were located and followed to termination during the study. Termination of the nest occurred with mortality of the eggs or nestlings if unsuccessful, or fledging of successful nests. The average nest mortality across all four years was 63.4%, with 36.6% of the nests reaching fledging (Table 14). There were no significant differences in the frequencies of successful and unsuccessful nests between years ($G=6.97$, $df=3$, $P>.05$, Table 15). When successful and unsuccessful nests were grouped by three categories of foraging index as a measure of habitat quality, nest mortality was found to be independent of the quality of the habitat ($G=.094$, $df=2$, $P>.05$, Table 16).

Table 14. Savannah sparrow nest mortality

1984-1987

Year	Total attempted nests	PERCENTAGE OF NESTS LOST			Percentage of nests fledged
		Deserted	Predated	Total	
1984	29	10.3	51.7	62.0	38.0
1985	30	6.7	43.3	50.0	50.0
1986	42	14.3	64.3	78.6	21.4
1987	52	9.6	50.0	59.6	40.4

Table 15. Frequencies of successful and unsuccessful nests by year

	Year			
	1984	1985	1986	1987
Successful	11	15	9	21
Unsuccessful	18	15	33	31

Table 16. Frequencies of successful and unsuccessful nests by habitat quality

	1984-1987		
	Foraging index of territory		
	FI \leq 2	2 < FI \leq 3	FI > 3
Successful	10	21	21
Unsuccessful	16	37	39

Predation accounted for the vast majority of all nests lost, accounting for 83% of all unsuccessful nests (Table 14). Thus, the results of the tests described above did not differ when only nests which failed because of predation were considered. Predation occurred throughout the season, at all stages of the nesting cycle and on territories of all categories of quality. In the remaining nests, embryos or nestlings died from exposure to the elements due to abandonment by the female. In some cases the female abandoned eggs for no discernible cause. An average of ten percent of the nests were deserted in all four years (Table 14). This percentage matches the 9.8% nests deserted that Dixon (1978) found for Kent Island, New Brunswick, savannah sparrows. Partial mortality of nests also occurred with deaths of individual embryos (non-viable eggs) and nestlings. Quantification of partial mortality from these causes fell beyond the scope and purpose of this one person study.

Multiple nesting attempts

The percentages of females engaging in multiple nesting attempts ranged from a low of 22% in 1984 to a high of 73% in 1987 (Table 17). It might be expected that females who began nesting earlier in the season would have more opportunity to re-nest, given the time constraints of the breeding season. There is a trend for the two years with the earliest mean initiation date of first nests to have the higher percentages of females engaging in multiple nesting attempts (Figure 4).

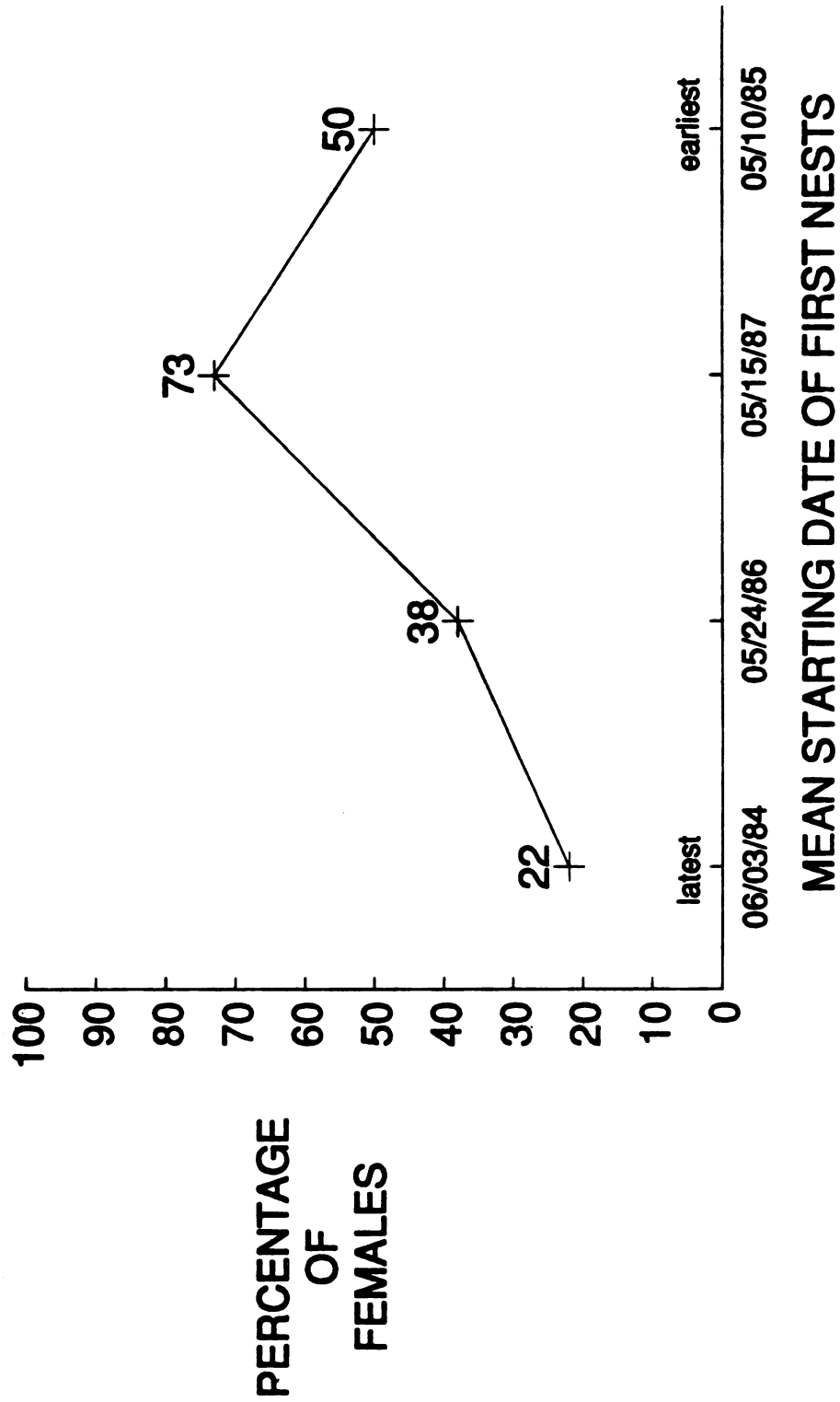


Figure 4. Percentages of females engaging in re-nesting attempts compared with the mean date of initiation of first nests, by year

The level and timing of nest mortality or the effects of other unexamined factors such as weather, may also influence the percentage of females which re-nest. For example, a higher mortality of early nests could precipitate more re-nesting attempts. Conversely, predation of nests with young later in the season might result in females that are unable to re-nest due to energy depletion associated with the care of the young (Nilsson 1983). Inclement weather occurring at the time of re-nesting might also tax an individual female's ability to secure the necessary resources for a re-nesting attempt that falls within the appropriate time frame. In 1986, for example, prolonged heavy rain coupled with below average temperatures, occurred during June at the height of the breeding season. Six females were recorded as having abandoned nests that were flooded or contained chilled eggs or young. This year also had the highest percentage of deserted nests in all four years (Table 14). Also in that year, many females did not re-nest, regardless of the reason for nest loss. They were quickly replaced on their territories by non-breeding females, resulting in the highest percentage (18.2%) of serial monogamous pair bonds of all four years (Table 18) and the lowest fledging success per female (Table 19).

Table 17. Multiple nesting attempts of female savannah sparrows

1984 - 1987

Year	Total nesting females	Percent multiple nesters	Percent double brooded
1984	23	22	13
1985	18	50	17
1986	26	38	8
1987	26	73	31

1984-1987.

1984-1987

Per nest = total young fledged/total nests initiated

All these factors could thus decrease the percentage of re-nesting females in a season. Not unexpectedly, the number of females engaging in single and multiple nests differed between years ($G=14.424$, $df=3$, $P<.005$, Table 20). This finding remained true when females with failed initial nests were excluded in an effort to control for the effects of the loss of the first nest ($G=8.689$, $df=3$, $P=.034$). The significance also held when data from 1984, 1985 and 1986 were each excluded in turn. When, however, data from 1987 were dropped from the set, no significant relationship remained ($G=3.734$, $df=2$, $P>.05$).

The tendency to engage in single versus multiple nest attempts was independent of quality of the territory, when three categories of habitat quality based on the foraging index were used and females were placed into the two categories of single nesters or multiple nesters ($G=4.332$, $df=2$, $P=.115$, Table 21). The actual number of nests attempted per female also had no significant relationship to the three categories of the foraging index (Kruskal-Wallis=2.88, $df=2$, $P>.05$, Table 22). The findings were the same when I again controlled for the effects of predation, by deleting cases with failed initial nests.

The ages of females for 1985, 1986 and 1987 were estimated from banding records by making the assumption that, beginning in 1985, unbanded females were first year birds. Some of these ages may be underestimates if the occasional female exists as a floater for one or more breeding seasons prior to nesting. To date, my data on floaters do not indicate that this is the general rule. Thus, these ages represent the best data available at this time. For the following analysis, the birds were placed into two age categories of one year and older than one year. When all females were considered, the tendency to

engage in multiple nests was independent of the age of the female ($G=2.474$, $df=1$, $P=.116$, Table 23). The actual number of attempted nests was also not related to the age of the female (Mann-Whitney $U=369$, $df=1$, $P>.05$, Table 24).

It requires more than 30 days for savannah sparrows to complete a successful nest and fledge independent young. The average span of time between the earliest and latest nest initiation across the four years was 67.25 days (Table 25), precluding the possibility of more than two successful broods at this latitude, even under ideal circumstances. In addition to the actual time required to complete the nest, females varied widely from days to weeks within a season in the amount of time that elapsed between nesting attempts, perhaps because of variations in the time required to get physiologically prepared for a second attempt. This adds to the total time necessary for double broods and may make their occurrence rare unless females begin nesting sufficiently early in the season. The tendency of females to re-nest after having had a successful nest (double brooding, + - and + +) was not independent of year ($G=9.103$, $df=3$, $P=.028$, Table 20). Double-brooding attempts ranged from a low of 8% in 1985 to a high of 31% in 1987. In 1985, one female successfully raised two broods of young. And in 1987, four females (15% of the nesting females in that year) raised two nests to fledging. In the cases of three of the double-brooded females in 1987, the male began attempting copulations while the female was feeding fledglings from the first nest. One male attempted to copulate with his own female while there were still young in the nest. The fourth female mated with a neighboring male and began a second nest while her

first mate continued to feed the fledglings from the first nest (female ORG/PUR, Table 4). Such serial mate acquisition and double-broodedness by the female has been demonstrated as a regular feature of a population of American goldfinch (Middleton 1988), but in this savannah sparrow population it appears to be a rare exception. Nonetheless, the potential for mate switching on the part of the female may account in part for the copulation attempts by the male, even when first brood young were still being fed. The frequencies of double-brooded females and females who only engaged in a solitary successful nest (+) within the season were compared across the three categories of habitat quality. There was no significant relationship between the tendency to be double-brooded and the quality of the habitat ($G=1.17$, $df=1$, $P>.10$, Table 21). The tendency to be double-brooded showed a significant relationship to the age of the female ($G=6.51$, $df=1$, $P<.025$, Table 23). One year old females were more likely to engage in a single nest than were females older than one year. DeLaet and Dhondt (1989) found the same relationship between age and the tendency to have double broods in their study of great tits.

The female may also engage in a re-nesting attempts following the failure of her first nest (- +, - -). This group of females with multiple nests was compared to females who did not re-nest following a failed nest (-). The likelihood that a female would re-nest following a failure was independent of the age of the female, considered in two categories ($G=.074$, $df=1$, $P>.10$, Table 23). This same tendency to re-nest following a failure was not independent of the quality of the territory ($G=5.502$, $df=1$, $P<.025$, Table 21). On a high quality territory, a female was more likely to re-nest following the failure of

her first nest than a female on a low quality territory.

In the tests comparing females re-nesting after a failure and females re-nesting after a success, small sample sizes made some of the significance tests suspect because of sparse cells in the contingency tables. This problem was solved in the cases of tests with the foraging index by redoing the test with the territories placed into two categories of $FI \leq 3$ and $FI > 3$. These two categories represented territories of poor to moderate quality in the first group and territories of high quality in the second group. The significance remained the same. There was no way to eliminate sparse cells in the case of tests involving age of the female, but these results were also confirmed by performing Mann-Whitney U tests using the actual age estimate as the dependent variable. These tests produced results nearly identical to the log-likelihood ratio Chi-square tests. In addition, age, considered in the two categories described above, is independent of the year ($G=.986$, $df=2$, $P=.611$).

Table 20. Frequencies of nesting attempts of female savannah sparrows

1984-1987

Year	Single attempts		Multiple attempts			
	-	+	+ -	++	- +	--
1984	10	8	3	0	0	2
1985	2	7	2	1	4	2
1986	10	6	2	0	2	6
1987	5	2	4	4	7	4

"+" = successful nest; "-" = unsuccessful nest

One symbol signifies a single nesting attempt per female, per year
Two symbols signify multiple nesting attempts, most commonly two

In the following cases with three nests, classification is based on the fate of the final nests.

"- - -" is counted as - -

"- - +" is counted as - +

"- + +" is counted as + +

The category of multiple nests includes all cases with more than one nest. The category of double broods only includes cases where re-nestings follow a successful nest, (+ -) or (+ +).

Table 21. Nesting attempts per female classified by number and fate, and tabulated by habitat quality

1984-1987

Nesting attempt type	Foraging index (FI) of territory		
	FI \leq 2	2 < FI \leq 3	FI > 3
Single nesting attempts			
-	4	15	6
+	0	10	7
Multiple nesting attempts			
++	0	2	2
+-	2	4	5
-+	1	5	7
--	1	5	8

For key to symbols, see Table 20

Table 22. Frequencies of actual number of nests attempted by all female savannah sparrows, grouped by habitat quality

1984-1987

Number of nesting attempts	Foraging index (FI) of territory		
	FI \leq 2	2 < FI \leq 3	FI > 3
1	4	24	13
2	2	11	15
3	2	6	6
4	0	0	1

Table 23. Nesting attempts per female classified by number and fate, and tabulated by age of female

1985-1987

Nesting attempt type	Age= 1 year	Age> 1 year
Single nesting attempts		
-	13	4
+	14	1
Multiple nesting attempts		
+ +	4	1
+ -	2	6
- +	9	4
- -	11	1

For key to symbols see Table 20

1984 data are not included as there were no age estimates for that year

Table 24. Frequencies of actual number of nests attempted by all female savannah sparrows, grouped by age

1984-1987

Number of nesting attempts	Age= 1 year	Age> 1 year
1	27	5
2	15	8
3	10	4
4	1	0

Table 25. Nest initiation spans for a population of savannah sparrows in southern Michigan

1984-1987				
NEST BUILDING DATES			NEST INITIATION PERIOD	TOTAL LENGTH OF BREEDING SEASON
Year	Earliest	Latest	Days between initiation of earliest and latest nests	Days between first nest built and last nest fledged
1984	05/14	07/22	70	80
1985	04/26	07/03	69	90
1986	05/08	07/12	66	90
1987	05/07	07/09	64	71

Clutch size

The sizes of clutches showed no significant differences between years (Kruskal-Wallis=2.31, $df=3$, $P>.05$, Table 26). To eliminate sparse cells in the following log-likelihood ratio Chi-square tests, the two smallest clutch sizes of 2 and 3 eggs were combined into one category. Clutch size was found to be independent of the foraging index of the territory ($G=1.403$, $df=4$, $P>.05$, Table 27). Furthermore, there were no significant differences in clutch sizes between first nests and re-nesting attempts of females ($G=.533$, $df=2$, $P>.05$, Table 28). Some females laid a smaller clutch of four in their first nesting attempt and five in their second nesting attempt. Other females reversed this sequence. There was also no evidence of an effect of female age on clutch size, when females were placed into two age

categories of one year old and older than one year ($G=.410$, $df=2$, $P>.05$, Table 29).

Table 26. Frequencies of clutch sizes for all female savannah sparrows, grouped by year

Number of eggs	YEAR			
	84	85	86	87
2	1	0	0	1
3	2	3	6	4
4	16	13	15	23
5	7	14	20	20

Table 27. Frequencies of clutch sizes by habitat quality

1984-1987

Number of eggs	Foraging index (FI) of territory		
	FI ≤ 2	$2 < \text{FI} \leq 3$	FI > 3
2	0	1	1
3	3	7	5
4	8	26	26
5	6	24	29

Clutches of 2 and 3 eggs grouped in one category for analysis

Table 28. Frequencies of clutch sizes of first nests and re-nests of female savannah sparrows

1984-1987		
Number of eggs	First nests	Re-nests
2	1	1
3	8	7
4	42	25
5	37	24

Clutches of 2 and 3 eggs grouped in one category for analysis

Table 29. Frequencies of clutch sizes by age of female

1984-1987		
Number of eggs	Age= 1 year	Age> 1 year
2	1	0
3	10	3
4	36	15
5	40	14

Clutches of 2 and 3 eggs grouped in one category for analysis

Reproductive success of females

Differences in reproductive success of females is examined in this section with respect to yearly variation, habitat quality, age of the female and the number of nesting attempts. Because male reproductive success has the greatest potential to be influenced by his pair bond status, male reproductive success will be reported under the section of reproductive success by type of pair bond. The section on pair bonds will also include results on reproductive success of females involved in polygynous pair bonds.

Reproductive success for both genders was estimated using the number of young known to have fledged from all attempted nests. Unfortunately, because the fledglings scatter throughout the territory while being fed for approximately a week after fledging, it was impractical to obtain an estimate of survival to independence. In addition, very few nestlings in this population return to the same site as adults. This study records two males returning in 6 years. Given these constraints, the number of young fledged was taken as the best available estimate of reproductive success. It ranged between 0 and 9 in nine categories. No individuals fledged 6 young (Table 30).

There was a significant difference among years in the number of young fledged per female (Kruskal-Wallis=12.78, $df=3$, $P=.005$, Table 30). When this test was repeated, with the deletion of females producing zero young, there was no longer a significant difference between years (Kruskal-Wallis=5.50, $df=3$, $P>.05$, Table 30). When females were placed into two categories of no young and some young, there was a significant difference between years in the frequencies of successful versus unsuccessful females ($G=8.522$, $df=3$, $P<.05$, Table

30). In 1985, only four out of eighteen females (22%) failed to produce any young. This contrasts with 52% in 1984, 62% in 1986 and 42% in 1987 of females failing to produce young. When the data from 1985 are excluded, there is no longer a significant difference between years ($G=3.929$, $df=2$, $P>.05$, Table 30).

There was a significant relationship between the number of young fledged and each female categorized in a composite fashion by number of nests she attempted and the success or failure of those attempts (Kruskal-Wallis=38.97, $df=4$, $P<.001$, Table 31). Single nesters were considered as one category and multiple nesters were given the four categories portrayed on Table 31. This categorization itself produced one category (- -) of females that always produced only 0 young. This could have been responsible for the significance of the test and so the test was repeated considering only females who produced some young. A significant finding remained (Kruskal-Wallis=16.07, $df=3$, $P=.001$). When the females with two successful broods (+ +) were removed from consideration in this latter data set, no significant difference in fledging success remained between the other categories (+, + -, - +) of nest attempts (Kruskal-Wallis=2.31, $df=2$, $P>.05$). The year 1987 had the greatest percentage of double-brooding females (Table 17). When this same test was repeated, excluding the data from 1987, no significance remained between the categories of nest attempts (Kruskal-Wallis=7.05, $df=3$, $P>.05$). When data from the year 1985, with one double brood, was excluded, a significant relationship remained (Kruskal-Wallis=12.65, $df=3$, $P=.005$).

Table 30. Frequencies of young fledged by single (S) or multiple (M) nesting females, by year

Number of young fledged per female	1984		1985		1986		1987	
	S	M	S	M	S	M	S	M
0	9	3	2	2	10	6	5	4
1	0	1	0	0	0	0	0	0
2	1	1	0	1	3	3	1	2
3	3	1	1	2	3	0	1	4
4	3	0	5	1	0	1	0	4
5	1	0	1	2	0	0	0	1
7	0	0	0	0	0	0	0	1
8	0	0	0	0	0	0	0	3
9	0	0	0	1	0	0	0	0

Table 31. Frequencies of number of young fledged by females categorized by type of nesting attempt

1984-1987

Number of young fledged	single nesters	Multiple nesters			
		++	+-	-+	--
0	27	0	0	0	14
1	0	0	1	0	0
2	2	0	3	4	0
3	8	0	2	5	0
4	11	0	4	2	0
5	2	0	1	2	0
7	0	1	0	0	0
8	0	3	0	0	0
9	0	1	0	0	0

For key to symbols see Table 20

The fledging successes of females on territories of differing quality were compared using three categories of the foraging index. The number of young produced per female was not related to the quality of the territory (Kruskal-Wallis=2.36, df=2, $P=.308$, Table 32). When only females producing some young were considered, the difference in the number of young fledged between the three categories of habitat quality approached significance (Kruskal-Wallis=5.33, df=2, $P=.070$, Table 32). An examination of Table 32 reveals a lower reproductive success for females on territories with a foraging index less than 2. If this foraging index category is removed from the analysis, no trend remained (Mann-Whitney $U=270$, df=1, $P=.199$).

Table 32. Frequencies of number of young fledged per female grouped by habitat quality

1984-1987			
Number of young fledged	Foraging index (FI) of territory		
	FI ≤ 2	$2 < \text{FI} \leq 3$	FI > 3
0	5	20	14
1	0	1	0
2	2	0	7
3	1	7	4
4	0	8	6
5	0	3	2
8	0	1	2
9	0	1	0

Females with one nest attempt, producing some young, were considered by themselves and tested for differences across habitats of varying quality (Table 33). No females with a single nesting attempt produced any young on territories with a foraging index of less than 2. Fledging success of females with one successful nest had no significant relationship to the remaining two categories of habitat quality (Mann-Whitney $U=39$, $df=1$, $P>.05$). Fledging success of females with successful multiple nests, considered separately from the single nesters, also showed no relationship to habitat quality (Kruskal-Wallis $=4.05$, $df=2$, $P=.132$, Table 33).

Table 33. Frequencies of number of young fledged by females categorized by type of nesting attempt and grouped by habitat quality.

1984-1987

Number of young fledged	Foraging index (FI) of territory FI ≤ 2			
	+	++	+-	-+
2	0	0	1	1
3	0	0	1	0
<hr/>				
<hr/>				
	2 < FI ≤ 3			
	+	++	+-	-+
1	0	0	1	0
3	4	0	0	3
4	5	0	2	1
5	1	0	1	1
8	0	1	0	0
9	0	1	0	0
<hr/>				
<hr/>				
	FI > 3			
	+	++	+-	-+
2	2	0	2	3
3	1	0	1	2
4	3	0	2	1
5	1	0	0	1
8	0	2	0	0

Only includes females producing some young

For key to + and - symbols, see Table 20. A single symbol means a single nesting attempt. Two symbols mean multiple nesting attempts.

There was no relationship between the number of young fledged and the age of the female. This was true when all females were considered together or when females failing to produce any young were eliminated from consideration ($P > .05$ in all cases, Table 34).

Table 34. Frequencies of number of young fledged per female grouped by age of female

1984-1987		
Number of young fledged	Age= 1 year	Age> 1 year
0	24	5
2	4	3
3	9	2
4	9	5
5	3	1
7	1	0
8	2	1
9	1	0

For illustrative purposes only, reproductive success was calculated on a per nest basis and a per female basis (Table 19). The calculation of reproductive success per nest gives an estimate of reproductive success for the year considered as if re-nesting did not occur. Reproductive success calculated on a per female basis includes the effects of re-nesting. Visually comparing these two figures makes it possible to gain an appreciation of the replacement value of re-nesting attempts to the reproductive success of the population. In all years, re-nesting was able to compensate in varying degrees for nest losses. In some years, such as 1987, re-nesting resulted in a doubling of the

average reproductive output of the population. A similar advantage for replacement clutches was reported by Nilsson (1983) for willow warblers in Swedish Lapland. In my population of savannah sparrows, males with monogamous pair bonds would experience the same reproductive success as success calculated on a per female basis. Males with polygynous or serial monogamous pair bonds would differ by having the potential to produce more than 5 young, just like the double-brooded females. Reproductive successes of males of the three pair bond statuses are examined below.

Nest spacing

Females nested within their own territories but sometimes placed their nest outside of the male's original borders. In such cases, the male modified his borders to include the female's nest site before nesting began by making minor (10 - 20 m) changes in his borders. Measurement of such day to day changes in territory size fell beyond the scope of this study. Nests were placed on the ground, often partially or completely under dead or live grass, which formed a roof over the nest. Some nests were placed within the grass tunnels of meadow voles (Microtus pennsylvanicus), forming an elongated tunnel entrance. All territories appeared to afford adequate grass litter for the camouflage of the nest indicating that nest sites were probably not limited in any absolute sense. Within a territory, areas avoided for foraging, such as exceptionally rank growth, were also not used for nesting. The nest sites were plotted on a map of the foraging index patches. From this mapped distribution, I then constructed a frequency distribution of nest sites for all four years relative to three categories of the foraging index (Table 35). This distribution was

tested against an expected frequency distribution of nest placement which was based on the proportion of the nesting area that was occupied by the three equal categories of habitat quality (the same as the test of habitat selection for territorial birds). The actual distribution of nests differed significantly from this expected distribution with the largest difference occurring in the foraging index category of less than 2 (Chi-square= 29.73, df=2, $P<.001$, Table 35). If the territorial space and eleven nests of females who had entire territories with no mapped patches of foraging index greater than 2 were excluded from the analysis, the same results held. It appears that females exert some selectivity in their nest selection even within their territory by avoiding patches with low quality foraging as nesting sites. Anecdotal evidence lends further support to this idea. One female, BLU-BLK, nested in 1985 in a territory of very low foraging index (approximately 1.4 m/m^2). In 1986, she nested in the same territory again twice, but on her third nest attempt that same year she moved to an adjoining territory when the resident female disappeared, mated with a new male and nested in a patch that had a foraging index greater than 3 (Table 4). In 1987, she returned to the higher quality site to nest again.

Table 35. Frequencies of nest placement relative to expected frequencies calculated from the distribution of patches of varying quality

1984-1987

Foraging index	Observed frequency	Expected frequency
FI \leq 2	19	47.62
2 < FI \leq 3	31	21.65
FI > 3	63	43.73

The nearest neighbor measurements from 1987 were examined in a correlation matrix that included territory area, nearest neighbor nest spacing, foraging index, and proportion of overlap. There were significant positive correlations between nearest neighbor nest spacing and territory area and between the proportion of overlap and the foraging index. All other pairwise combinations of variables showed significant negative correlations (Table 36). A partial correlation was then performed to examine the relationship between nearest neighbor nest spacing, foraging index, and proportion of overlap, holding territory area constant (Table 37). There was a significant positive correlation between the proportion of overlap and the foraging index ($t=5.26$, $df=29$) and a significant negative correlation between nearest neighbor nest spacing and the proportion of overlap ($t=2.21$, $df=29$). No significant correlation remained between nearest neighbor nest spacing and the foraging index ($t=1.88$, $df=29$). A second partial

correlation was performed to examine the relationship between nearest neighbor nest spacing, foraging index, and territory area, holding proportion of overlap constant (Table 38). There was an even smaller, non-significant correlation between nest spacing and foraging index and a small, non-significant correlation between nest spacing and territory area.. Thus, it appears that nest spacing is indirectly related to the mean foraging index through the placement of female territories relative to one another with this placement being assessed by the proportion of boundary overlap.

The relationship between the distance to the nearest neighbor's nest of each female and the proportion of territorial overlap for each female was examined for each time period using regression models (Figure 5). Only in time period II was there a significant and negative slope ($P < .001$) and a significant correlation coefficient ($P < .001$).

Table 36. Correlation of territory area (AR), foraging index (FI), nearest neighbor nest spacing (NN) and proportion of overlap (OV)

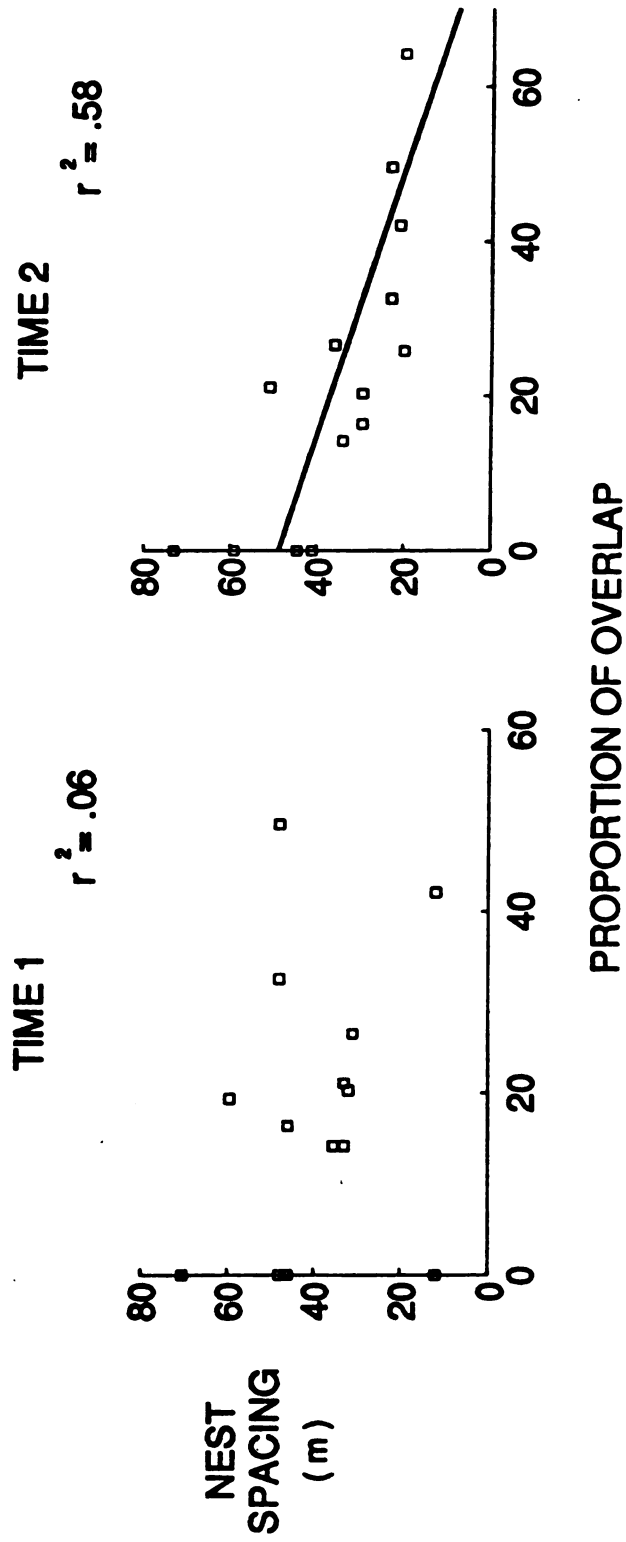
1987				
	AR	FI	NN	OV
AR	1.00			
FI	-.77 ***	1.00		
NN	.40 *	-.50 **	1.00	
OV	-.63 ***	.83 ***	-.53 **	1.00
* $P < .05$; ** $P < .002$; *** $P < .001$ N=33				

Table 37. Partial correlation matrix of nearest neighbor nest spacing (NN), foraging index (FI), and the proportion of territorial overlap (OV); holding territory area constant

1987			
	NN	FI	OV
NN	1.00		
FI	-.33	1.00	
OV	-.38 *	.70 **	1.00
* P<.05; ** P<.001		N=33	

Table 38. Partial correlation matrix of nearest neighbor nest spacing (NN), foraging index (FI), and territory area (AR); holding proportion of overlap constant

1987			
	NN	FI	AR
NN	1.00		
FI	-.14	1.00	
AR	.11	-.57 *	1.00
* P<.001		n=33	



$$\hat{Y} = 48.8 - .59 X$$

Figure 5. The relationship between distance to the nearest neighbor's nest and the proportion of territorial overlap for two time periods

The nature of the interaction of the time period and the nearest neighbor activity category was dissected further using a 2 x 2 contingency table (Table 39) which showed a significant lack of independence between the activity of the nearest neighbor and the time period ($G=17.48$, $df=1$, $P<.001$). Focal females are more likely in time period 1 to be building nests at the same time as their neighbors. In the second time period, the nearest neighbor was more likely to be caring for eggs or young while the focal female was nest building. Thus, the time periods are highly dependent on the activity of the nearest neighbors.

Table 39. Frequencies of activities of nearest neighbors when focal female is nest-building

1987		
Activity of focal female	Time period 1	Time period 2
Nest initiation	16	8
Nest care	1	16
nest initiation = nest building and egg laying		
nest care = incubation through nestlings		

To summarize, in time period II, most of the neighbors were occupied with the care of their nests while the focal female was nest building. Nearest neighbors were most closely spaced in the territories exhibiting the greatest amount of overlap. The territories showing the greatest amount of overlap, in turn, were directly related to the quality of the territory as assessed by the foraging index.

Mating patterns

Pair bond patterns

The majority of the birds formed monogamous pair bonds for the entire breeding season, with one male nesting with one female. A polygynous pair bond was assigned whenever two nesting females were found to be concurrently nesting with one male. When an individual male or female had more than one mate, sequentially, the pair bond was described as serial monogamy. Pair bonds, in this mating system context, refer only to those bonds which led to a nesting attempt. They do not include those situations where a female consorted with a male for a sustained period but never attempted a nest.

The percentages of total nesting males engaging in monogamous, serial monogamous and polygynous pair bonds are shown in Table 18. Monogamous males accounted for the majority of pair bonds for all four years with 70.6% in 1984, 88.2% in 1985, 72.7% in 1986 and 82.6% in 1987. Although polygynous pair bonds accounted for a minority of the breeding situations in all years, the percentages were always greater than the minimal 5% level that has been used to describe populations as regularly polygynous (Verner and Willson 1966). The following percentages of males were polygynous in the four years of the study: 23.5% in 1984, 5.9% in 1985, 9.1% in 1986 and 13.0% in 1987. This represented a total of 9 males in the population throughout the four years, accounting for 11 temporally distinct incidences of polygynous pair bonds involving 21 females. Two males formed polygynous pair bonds twice. One of these (ORG) kept the same primary female

throughout the season and managed to secure two other females sequentially when they were left as widows, thus forming two distinct polygynous pair bonds. The other male (BLU/ORG) formed polygynous pair bonds in two sequential years. Aside from these two males and one female, no individuals were a part of polygynous pair bonds more than once in the four year study. The remaining percentage of males in this population engaged in serial monogamous pair bonds.

From a female perspective, almost all females maintained a pair bond with only one male, thus making them monogamous. Resident females responded aggressively to territorial intrusions by additional females and thus limited their chances for settlement and nesting as part of a polygynous pair bond. Female-female aggression was observed for the duration of the breeding season, with 20 specifically recorded incidences in 1986, the first year of focal female observations (Table 40). In addition, aggression by individual females was observed throughout the nesting cycle, although more interactions were recorded when females were most mobile, either without a nest, laying eggs or with fledglings, in contrast to having eggs or nestlings ($G=3.89$, $df=1$, $P<.05$, Table 40). Small sample sizes of observed aggressive incidences precluded any more detailed analysis. No females had polyandrous pair bonds, maintaining two concurrent active nests with two males. Three females switched mates before re-nesting and displayed serial monogamous pair bonds (Table 4). One case involved a disappearance of the original mate and another the loss of the male's territory and his female to an invading male. In only one case did a female switch mates and nest with a neighboring male while her own original mate was still alive and in possession of a territory.

Table 40. Frequencies of observed incidences of female-female aggression, grouped by stage of the nest cycle

1986

Stage of nesting cycle	Number of incidences
Pre-nesting through egg-laying	7
Incubation	2
Feeding nestlings	2
Feeding fledglings	3
In between active nests or after last nest	6

Types of polygynous pair bonds

In a species where both males and females are territorial, a male can only be polygynous when his territory encompasses the majority of the space occupied concurrently by two females. Thus, polygynous pair bonds in any population may be both described and explained in terms of the spacing of both males and females through time. In this population, there appeared to be two distinct ways for a male to occupy the same space as two females. A male might successfully acquire two females by defending a territory which encompassed two distinct, contiguous female territories (Type I). He might accomplish this by aggressively driving away the neighboring competing males or by opportunistically acquiring the widowed mate of a male which was killed or otherwise unable to continue to hold his territory. Male territorial expansion to encompass two female territories accounted for three of eleven incidences in the four years of the study. In one of

these incidences, the male clearly drove away potential neighboring males early in the season. In two other cases, a male was able to secure a neighbor's female when the neighbor disappeared. In one of these cases the neighbor was killed while the cause of the disappearance of the third male was not determined. McLaren (1972) also reported a polygynous bond that arose in this fashion in his Sable Island population (Ipswich race) of savannah sparrows, as did Derrickson (1989) for northern mockingbirds. A male may also become polygynous when two females overlap their territories sufficiently so as to occupy the same amount of space as the male holding a territory in the same area (Type II). Without radically changing the size or shape of his territory, the male can thus become a polygynist. The remaining eight incidences were of Type II.

Females of polygynously-bonded males also differ in the synchronicity of their nesting attempts. Such temporal differences in the use of nesting space enable one to describe existing pair bonds with more precision relative to the activities of the females. Females may occupy the same space at totally disjunct time periods, resulting in the serial monogamy described above. Females occupying the same territory may enter the nesting cycle in nearly complete synchrony, building nests within a span of three days. Or, females may nest in the same territory, but do so asynchronously, with the second female initiating a nest only after the first female already is incubating or tending young. Of the eight incidences of females of polygynously-bonded males nesting in the same space, three did so in a synchronous pattern and five in an asynchronous pattern, with the second female not

beginning her nest until the first female had eggs or young. A summary of number of incidences of the types of polygynous pair bonds recorded for this study is found in Figure 6.

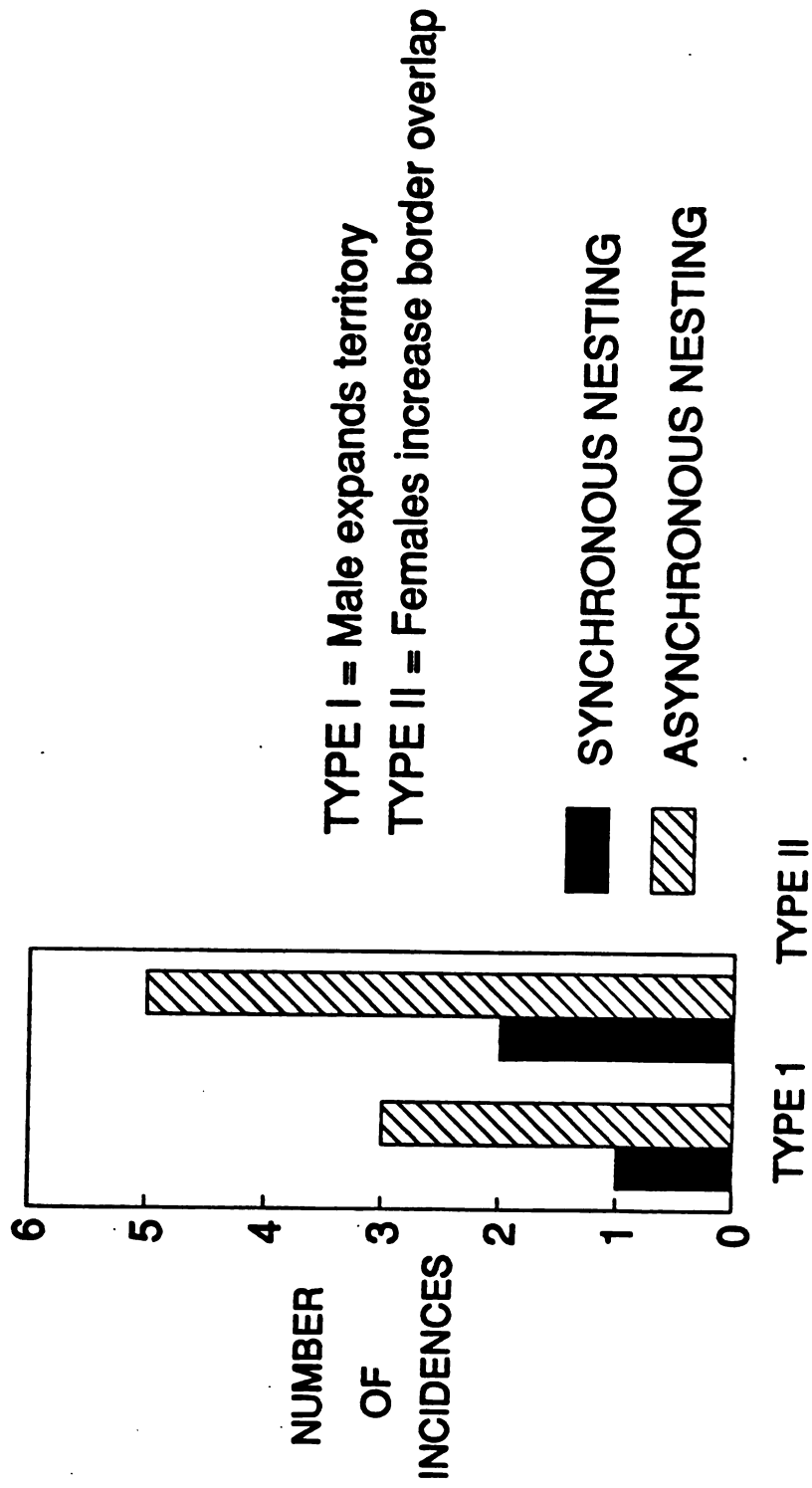


Figure 6. Number of incidences of polygynous pair bonds by territorial type and nesting synchrony

In each of the three cases of synchronously nesting females, one female abandoned both her nest with eggs and the territory before hatching took place. Again, McLaren (1972) reports a similar occurrence of synchronously nesting females with subsequent territorial abandonment by one of the females in his population. Female-female aggression may be responsible, at least in part, for the abandonment by one female. In this regard, one incident from my study, spanning several days, is worth reporting in some detail. The first female (PUR/WT) arrived on 29 April 1986 and was contested for by the three males whose territories she foraged within. She first copulated with the male (GRN/WT) who held the majority of the area that she was using for foraging and consorted with him for 10 days. On 12 May a second female (GRN/ORG) appeared on the same territory. Concurrently, the adjacent male (ROY) intruded on the territory and by the next day GRN/WT had disappeared from the territory and was not seen again. On 13 May I recorded the first incident of aggression between the two females and copulations between the male ROY and the first female, PUR/WT. The female PUR/WT was estimated to have begun nest building on this date. On that same day, female PUR/WT assiduously followed the newly arrived female around the territory, with both females displaying territorially and frequently fighting on the ground. This aggression continued unabated for several hours that day and was recorded for the following four days during which PUR/WT was laying eggs. No aggression was recorded when PUR/WT began incubation on 17 or 18 May. The second female, GRN/ORG began nest building on about 19 May. The next day the two females were engaged in sustained aggressive interactions again. When I checked PUR/WT's full clutch of eggs, they were found to be

damp, cold and apparently abandoned. Her male ROY copulated with her at least once after the loss of her nest. During the ensuing parallel walks between the two females, PUR/WT also displayed by picking up dead grass in her bill on at least three occasions. In between aggressive interactions, PUR/WT was observed on a favorite perching site, feathers fluffed, in a state of inactivity. Two days later she was still present and consorting with her male, ROY, but no longer engaged in aggressive encounters with GRN/ORG. Instead, she spent much time sitting on the ground, preening. Her actions and appearance suggested a bird who did not have the requisite energy for sustained interactions. As of 21 May, there were no further sightings of PUR/WT. At the time she deserted the area, all the neighboring males had bonded with females, leaving no vacancies in the female territorial system in the immediate vicinity of her original territory. Nearly three weeks later, PUR/WT nested with a male who had lost his female, on a territory that was approximately 300 meters away from her original territory, and considerably lower in quality. Another contributing factor to PUR/WT's nest and territory loss may have been seven days (16-22 May) of temperatures in the range of 50 degrees F, coupled with almost continuous driving rain showers. It may be that the physiologically demanding weather coupled with continuous aggressive interactions with the other female, rendered her incapable of staying on the territory and attempting a second nest. I am uncertain as to whether aggression played a role in PUR/WT's initial abandonment of her first nest, but it seems quite clear that the days of sustained aggression may have been responsible for her abandonment of the

territory even after she copulated with her male in preparation for a second attempt.

Factors influencing the occurrence of polygynous pair bonds

Polygynous pair bonds occurred on territories ranging in size from approximately .2 ha to .9 ha. When only Type II polygynous pair bonds were considered, the size range remained the same.

Values of foraging indices ranged between 2.1 and 4.6 m/m² for territories of males with polygynous and serial monogamous pair bonds. Polygynous pair bonds were not restricted to the same territories in subsequent years. In no year did males with polygynous pair bonds occur on territories with foraging indices less than 2. In contrast, 11 incidences of monogamy occurred on territories of such a low foraging index. When the number of males exhibiting the three types of pair bonds was compared across three categories of foraging index, pair bond type was not independent of foraging index ($G=15.035$, $df=4$, $P=.005$, Table 41). Sparse cells in the contingency table made this significance suspect. Therefore, I grouped males with multiple females (serial monogamous and polygynous pair bonds) together in one category and repeated the test. The pair bond status of the male was still not independent of habitat quality ($G=13.253$, $df=2$, $P=.001$). When the test was repeated with the category $FI < 2$ excluded, a significant relationship remained ($G=5.294$, $df=1$, $P<.025$). Intriguingly, however, an examination of the actual frequencies shows more males with multiple females in the medium quality category of habitat than in the highest quality category. For males with monogamous bonds the opposite situation prevailed (Table 41). Above a foraging index of 2, polygynous pair bonds are not occurring preferentially on the

territories of highest quality.

Table 41. Numbers of males classified by number of females and number of nests, grouped by habitat quality

1984-1987

Pair bond status	Number of nests	Foraging index (FI) of territory		
		FI \leq 2	2 < FI \leq 3	FI > 3
M	1	7	7	9
M	> 1	5	9	15
SM	> 1	0	7	1
P	> 1	0	6	4

M=Monogamous; SM=serial monogamous; P=polygynous

Males might have multiple nest attempts by nesting either with one female who re-nested or with multiple females. When males were placed into two categories of having one nest or multiple nests, the distribution was independent of the foraging index ($G=4.364$, $df=2$, $P>.05$, Table 41). Only males with seasonal monogamous pair bonds (one female per breeding season) were then subdivided by whether the female attempted one or multiple nests. The numbers of males with these two types of monogamous pair bonds were independent of the foraging index ($G=1.408$, $df=2$, $P=.495$, Table 41).

The age of the male was not significantly related to his pair bond status, when males were classified as having monogamous, serial monogamous, or polygynous pair-bonds and males were placed in two age

categories of 1 year and older than one year ($G=1.650$, $df=2$, $P>.05$, Table 42). Four out of nine polygynists were three years old with the remaining polygynists distributed among the 1,2 and 3 year old age categories (Table 42). The same finding held if males with serial monogamous pair bonds and polygynous pair bonds were considered together and compared to males with only one female ($G=.871$, $df=1$, $P>.05$, Table 42). When males were again classified by whether they had single or multiple nests their distribution was not independent of age ($G=4.741$, $df=1$, $P=.029$, Table 42). If males with monogamous pair bonds were considered and classified on whether the female had one or multiple nests, these two types of monogamous pair bonds were not independent of the age of the male ($G=3.871$, $df=1$, $P<.05$, Table 42). Older monogamous males were more likely to have females which engaged in multiple nesting attempts.

Table 42. Numbers of males classified by number of females and number of nests, grouped by age of male

1984-1987					
Pair bond status	Number of nests	Age			
		1	2	3	4
M	1	15	7	4	0
M	> 1	8	10	5	3
SM	> 1	3	2	2	0
P	> 1	2	2	4	1

M=monogamous; SM=serial monogamous; P=polygynous pair bond

Finally, the numbers of males engaging in the three different types of pair bonds were not significantly different between years ($G=7.185$, $df=6$, $P=.304$, Table 43). This finding held when males with serial monogamous and polygynous pair bonds were combined into one category and compared with males with monogamous pair bonds ($G=3.105$, $df=3$, $P=.376$). When the monogamous males were further subdivided into two categories based on whether the female had one or multiple nesting attempts, however, there was a significant difference between years ($G=13.37$, $df=3$, $P=.004$, Table 43). An examination of Table 43 shows that in 1986, a large proportion of the males nested with one female who produced a single nest. In 1987, a large proportion of the monogamously-bonded males had females who attempted multiple nests. Removing only the data from 1986 resulted in a difference in types of pair bonds between the remaining years which approached significance ($P=.07$). Removing only the 1987 data resulted in no significant

difference or even non-significant trend between the remaining years of 1984-1986 ($P > .05$).

Table 43. Numbers of males classified by number of females and number of nests, grouped by year

1984-1987					
Pair bond status	Number of nests	Year			
		84	85	86	87
M	1	9	7	11	4
M	> 1	3	8	4	15
SM	> 1	1	1	5	1
P	> 1	4	1	2	3

M=Monogamous; SM=serial monogamous; P=polygynous

Reproductive success by type of pair bond

Females. Reproductive successes of primary and secondary females of polygynously pair-bonded males for all four years were examined, with the primary female designated as the first to nest in an asynchronously nesting set of two females on a single territory (Table 44). Polygynous male bobolinks have been reported (Martin 1974) to favor the female who nests first by providing more parental care to her young, to the detriment of the secondary female's reproductive success. A lower reproductive success of secondary females could result directly from reduced food for the young by reduced parental care or through depletion of food resources on the territory. The temporal status of a

female can only be designated in the case of asynchronously-nesting females. And direct spatial competition for food resources is only expected when females share one territorial space. Therefore, using these criteria, I restricted the analysis to a small subset of ten polygynously-bonded females. No differences in reproductive success were detected between these females (Mann-Whitney $U=13$, $df=1$, $P>.05$, Table 44). When the females who produced zero young were deleted from the analysis, in order to eliminate the effects of predation on reproductive success, the difference between the two categories of females approached significance, with a lower success for secondary females (Mann-Whitney $U=6$, $df=1$, $n=5$, $P=.076$, Table 44). When the success of only the actual concurrent nests of primary and secondary female was compared, rather than the overall reproductive success of each female, there was no significant difference between the two (Mann-Whitney $U=23$, $df=1$, $P>.05$, Table 45). The same finding resulted when the nests which were predated or abandoned were deleted from the sample (Mann-Whitney $U=5$, $df=1$, $P>.05$, Table 45). Thus, it does not appear as if male assistance or resource availability varies enough between the two females to produce differing reproductive successes that could be detected at the level of fledging success of a single nest.

Reproductive success could also be lowered if secondary females were less likely to attempt multiple broods than were primary females, due either to increased strain on the female from reduced male assistance or delayed dates of nest initiation. Such a difference in ability to engage in multiple nests could be responsible for the trend of a higher reproductive success for primary females. A higher percentage of primary females than secondary females engaged in

multiple nesting attempts, but this difference was not significant (Mann-Whitney $U=17$, $df=1$, $P>.05$, Table 46). The small sample sizes in these analyses make it difficult to make any definitive conclusions at this time. If the preceding test of number of nest attempts and female status is repeated with a mock data set which uses the same proportions, yet triples the sample size, a significant difference emerges. Larger sample sizes may elucidate some of this but, for the present time, meaningful results demanded rigor in selecting the pertinent subset of data for analysis, even at the expense of sample size.

Table 44. Frequencies of number of young fledged for primary and secondary females of polygynously-bonded males

1984-1987		
Number of young fledged	Primary female	Secondary female
0	3	2
1	0	1
2	0	2
3	1	0
5	1	0

Table 45. Frequencies of number of young fledged for concurrent nests of primary and secondary females of polygynously-bonded males

1984-1987

Number of young fledged	Primary female	Secondary female
0	3	3
1	0	1
2	0	1
3	1	0
5	1	0

Table 46. Frequencies of primary and secondary females in asynchronous polygynous pair bonds engaging in one or two nest attempts

1984-1987

	Primary female	Secondary female
One nest	2	4
Two nests	3	1

Males. Male reproductive success can be influenced both by the number of females with whom he mates and the tendency of his female to re-nest after a success or failure. Fledging success for males ranged from 0 to 9 in eight categories, with no males producing 1 or 6 young (Table 47). The number of young fledged per male was independent of the type of pair bond of the male (monogamous, serial monogamous, polygynous), both for all males (Kruskal-Wallis=.55, df=2, P=.759, Table 47) and for only males producing some young (Kruskal-Wallis=.05, df=2, P=.975, Table 47). The same findings resulted when males with

serial monogamous and polygynous pair bonds were combined into one category and compared with males with monogamous pair bonds both for all males (Mann-Whitney $U=490$, $df=1$, $P=.471$) and for just males producing some young (Mann-Whitney $U=205$, $df=1$, $P=.979$). Males with monogamous pair bonds were subdivided into those with females with one nest and those with females with multiple nest attempts, thus creating four types of pair bonds (Table 47), instead of three. The number of young fledged did not differ between the four types of pair bonds for all males (Kruskal-Wallis $=.403$, $df=3$, $P=.403$, Table 47) and for males producing some young only (Kruskal-Wallis $=.05$, $df=3$, $P=.997$, Table 47). The number of young was also not related to whether the male had one nest or multiple nests, regardless of the number of females (Mann-Whitney $U=582$, $df=1$, $P>.05$, Table 47).

There was a significant difference between years in male reproductive success (Kruskal-Wallis $=9.69$, $df=3$, $P=.021$). Therefore, the reproductive success of males by pair bond status was examined separately for each year. In no year was there a significant difference between reproductive success of males categorized as monogamous, serial monogamous or polygynous. Since serial monogamy and polygyny accomplish the same end for the male, these two were considered together. The tests were repeated with males classified as mating with a single female or with multiple females. Only in 1984, was there was a significant difference between the reproductive success of males mating with a single female and males mating with multiple females (Mann-Whitney $U=10$, $df=1$, $P=.025$, Table 48). This is also the year with the highest percentage of polygynously-bonded males and the

observed gametic contribution ratio which diverges the most from zero (Table 50). Polygynously-bonded males accounted for four of the five males that nested with multiple females in that year.

Multiple nesting attempts by the male may compensate for losses by predation. Considering all years together, males with multiple females were not significantly less likely to produce zero young than males with only one female ($G=.695$, $df=1$, $P>.05$, Table 47). When males with one nest per season were compared to males with multiple nests, regardless of the number of females, there was a non-significant trend for males with multiple nests to be less likely to produce zero young than those with only one nest ($G=3.579$, $df=1$, $P=.06$, Table 47). If males with multiple females were excluded from the analysis, the non-significant trend remained ($G=2.884$, $df=1$, $P=.09$, Table 47), indicating that multiple nest attempts by females of monogamously-bonded males accounted for some of this effect.

There was a significant relationship between the fledging success of males and the quality of the territory, even when males producing zero young were excluded from the analysis (Kruskal-Wallis= 6.50 , $df=2$, $P<.05$, Table 49). If only males producing some young and pairing with multiple females were considered, there was no longer a significant relationship between the number of young fledged and the quality of the habitat (Mann-Whitney $U=20$, $df=1$, $P=.413$, Table 49). If males producing some young and pairing with only one female were considered, the relationship between the number of young fledged and the quality of the territory just reached significance (Kruskal-Wallis= 5.93 , $df=2$, $P=.05$, Table 50). When monogamously-bonded males whose mates attempted one nest were considered alone, the number of young was independent of

the categories of habitat quality (Kruskal-Wallis=2.17, $df=1$, $P>.10$). The number of young produced by males who nested with a single female and produced some young in multiple nesting attempts was also independent of the quality of the habitat, but the results approached significance (Kruskal-Wallis=4.78, $df=2$, $P=.092$, Table 50). When these same males were considered but with the exclusion of territories with foraging indices less than 2, no trend remained (Mann-Whitney $U=41$, $df=1$, $P=.203$). A tentative conclusion from these results is that the significant relationship between young fledged per male and quality of the territory appears to result from a lower reproductive success of the males who are nesting with only one female on territories of the poorest quality.

Table 47. Frequencies of young fledged by males classified by pair bond status and the number of nests

1984-1987

Number of young fledged per male	Pair bond status (number of nests)			
	Monogamous (1)	Monogamous (> 1)	Serial monogamous (> 1)	Polygynous (> 1)
0	17	10	3	3
2	1	6	0	2
3	4	3	1	1
4	7	4	4	2
5	2	3	0	1
7	0	1	0	0
8	0	2	0	0
9	0	1	0	0

Table 48. Frequencies of young fledged by males with a single (S) or multiple (M) females, by year

Number of young fledged per male	1984		1985		1986		1987	
	S	M	S	M	S	M	S	M
0	7	1	4	0	10	3	6	2
2	2	0	1	0	2	1	2	1
3	2	0	2	0	1	1	2	1
4	1	3	4	1	2	2	4	0
5	0	1	3	0	0	0	2	0
7	0	0	0	1	0	0	1	0
8	0	0	0	0	0	0	2	0
9	0	0	1	0	0	0	0	0

Table 49. Frequencies of young fledged by males with a single (S) or multiple (M) females, by category of habitat quality

1984-1987

Number of young fledged per male	Foraging index (FI) of territory					
	FI ≤ 2		2 < FI ≤ 3		FI > 3	
	S	M	S	M	S	M
0	8	0	7	5	8	1
2	2	0	0	0	5	2
3	1	0	2	2	3	0
4	1	0	2	5	5	1
5	0	0	4	0	1	1
7	0	0	0	1	0	0
8	0	0	0	0	2	0
9	0	0	1	0	0	0

Table 50. Frequencies of young fledged by males with monogamous pair bonds with females producing single (1) or multiple (2) nests, grouped by habitat quality

1984-1987

Number of young fledged per male	Foraging index (FI) of territory					
	FI ≤ 2		2 < FI ≤ 3		FI > 3	
	1	2	1	2	1	2
0	6	2	4	3	3	5
2	0	2	0	0	1	4
3	0	1	1	1	2	1
4	1	0	0	2	3	2
5	0	0	2	2	0	1
8	0	0	0	0	0	2
9	0	0	0	1	0	0

Gametic contribution ratio

In order to describe the mating system as a whole, and incorporate the influence of the pair bond patterns of both males and females, an observed gametic contribution ratio (Gowaty 1981) was computed. A ratio of total males to total females attempting to contribute gametes to the reproductive effort was calculated for each year. This enabled me to take into account contributions due to serial monogamous as well as polygynous pair bonds and calculate an observed gametic contribution ratio. Extra pair fertilizations were not a part of these calculations. Since female savannah sparrows were observed rejecting the advances of males other than her mate, observational evidence argues against frequent occurrences of such fertilizations in this population. Nevertheless, a parentage study using genetic evidence such as those by Westneat (1987a) or Gowaty and Karlin (1984) would be necessary for certainty of this aspect and such procedures were beyond the scope of this present study. When this ratio was computed (Table 51), every year showed a ratio < 1 , indicating a polygynous system. In every year of the study, more females than males were attempting to contribute gametes in this population. When the years were ranked on the degree of polygyny based first on the percentage of polygynous males and secondly on the gametic contribution ratio, the rankings match with the exception of 1986 and 1987, which are reversed. This reversal of rankings between these two years can be accounted for by the unusually high (18.2% of nesting males) percentage of serially monogamous males in 1986. In that year, an unusually high number of females abandoned their nests and territories (Table 14), leaving room

for new females to move into the territorial system. The year 1986 was unusually cold and wet early in the nesting period and it is possible that some females were energetically unable to try for a re-nesting attempt after losing a nest. Polygynous pair bonds and male serial monogamous pair bonds may have the same effect on the observed gametic contribution ratio, even though they do not result from the same events in the social system.

I also wished to calculate a gametic contribution ratio which reflected the actual gametic contributions to the population and did so by restricting the calculation to only those individuals who produced some young in the year under consideration. When the tallies were adjusted by excluding those birds which produced zero young, the actual gametic contribution ratios diverged in some cases from the observed ratios (Table 52). In 1984 and 1987, the ratio was closer or equal to the value of 1 for monogamy. In 1985, there was little change in the ratio. Intriguingly, in 1986, the high loss of nests and subsequent territorial abandonment by the affected females actually produced a polyandrous gametic contribution ratio. Thus, factors other than observable pair bonds may have a decided influence on the actual proportions of the genders' contributions of gametes to the population. In 1986, the influence of weather on reproductive success seems to have overridden the effects of the observed pair bonds, resulting in a gametic contribution ratio that was the reverse of the expected.

Table 51. Observed gametic contribution ratios and percentages of polygynous pair bonds

1984-1987

Year	NUMBER OF BREEDERS		Ratio of Males/Females	Percentage of polygynous pair bonds	Percentage of serial monogamous pair bonds
	Males	Females			
1984	17	23	.74	23.5	5.9
1985	17	18	.94	5.9	5.9
1986	22	26	.85	9.1	18.2
1987	23	26	.88	13.0	4.4

Table 52. Actual gametic contribution ratios calculated using only individuals producing some young

1984-1987

Year	NUMBER OF BREEDERS		Ratio of Males/Females	Percentage of polygynous pair bonds	Percentage of serial monogamous pair bonds
	Males	Females			
1984	9	11	.81	23.5	5.9
1985	13	14	.92	5.9	5.9
1986	12	10	1.20	9.1	18.2
1987	17	17	1.00	13.0	4.4

These calculations exclude males and females who produced zero young in that year.

CHAPTER V

DISCUSSION

Both male and female savannah sparrows in this population exhibit territorial behavior. Both genders maintain a spatial priority of access to critical resources by social interaction (Kaufmann 1983), resulting in two territorial systems which may differ in purpose and perhaps in mechanism of establishment as well. Females, for example, differ from males in the focus of their aggression (other females), in their lack of song and in the amount of territorial overlap that is tolerated. None of these differences violate the essential components of a definition of territory. They may, however, indicate differences between the genders in the processes of territory selection and maintenance. An appreciation of differences and similarities between the territorial systems of the two genders is important for an understanding of the social system as a whole. Using the data from this study, I will examine each gender's territorial system both independently and as part of the interfacing social system. The ultimate goal of territoriality for both genders in this species is the acquisition of breeding opportunities. Therefore, I will begin by discussing in some detail the factors which have potential to affect reproductive success, particularly in relation to relevant data from my study. Final emphasis will be placed on an attempt to better understand the connection between the spacing systems of the two genders and the resulting mating system of the population.

Habitat quality and spacing of individuals

Previous work on territoriality has established an inverse relationship between food abundance and male territory size (Stenger 1958; Pitelka et al. 1959; Holmes 1970; Miller et al. 1970; Cody and Cody 1972a,b; Gill and Wolf 1975; Simon 1975; Salomonson and Balda 1977; Tjernberg 1985; Ridpath and Brooker 1987; and others). Davies and Lundberg (1984) demonstrated the same relationship for female territories in the dunnock (Prunella modularis) as did George (1987) for wintering female and male Townsend's solitaires (Myadestes townsendi). Myers et al. (1979) have delineated two mechanisms by which resources might determine territory size. First, an animal might directly sample the food abundance and adjust the size of its territory to include the necessary resources. Secondly, the territory size might be determined by the cost of competition with other individuals. Greater competition would occur for the higher quality sites. The cost of competition, in turn, is influenced further by the presence of other demands on an individual's time and energy which vary through time. Habitat quality itself may provide a third proximate determinant of territory size if the animal responds directly to a structural feature of the habitat which correlates with long-term expected food abundance (Hilden 1965; Seastedt and MacLean 1979; Franzblau and Collins 1980; Smith and Shugart 1987). Obviously, these mechanisms are not mutually exclusive and are, therefore, difficult to separate. Because of the lack of studies examining female territoriality, little effort has been made to look for possible similarities or differences in the proximate determination of territory sizes for each gender. There is no reason

to implicitly assume that the sexes would behave identically in this regard. In a system where the territory is held for both breeding and acquisition of food, understandings of the costs and benefits of territoriality are potentially complex and dynamic. The ultimate goal of the individual is one of increased reproductive success. The means of reaching this goal may differ between genders and may change as the breeding season progresses. Because of this, any attempt to understand the genesis and maintenance of a mating system must include an assessment of the factors which influence the spacing of individuals of both sexes. Based on the differing reproductive "strategies" that arise from the difference in gametic investment of males and females, Hixon (1987) predicted males to be area maximizers and females to be energy maximizers with respect to territorial behavior.

The significant inverse relationship between territory area and foraging index in the present study (Figure 2) strongly indicates that, in this case, the foraging index is a structural habitat feature which is directly related to a component of habitat quality for the bird. The higher density of foraging space is most likely to translate to higher efficiency in foraging and, thus, to a higher quality territory for the individual in terms of food acquisition. Both male and female territory sizes show the same inverse relationship to the foraging index. There appear to be differences, however, in the responses of the two genders to direct assessment of the resource base and to territorial intrusions. These are reflected in differences in the exclusivity of territorial borders for the two genders.

Male territorial establishment

Qualitative observations from this study and quantitative observations from others (Beaver unpub.; Reid 1987), have shown that upon arrival a male commences territorial displays and balances them with his need to feed. As mentioned in the section on behavior in the methods, the result of this conflict is feed-singing behavior that is most pronounced before a male acquires a female (Table 4). Feeding bouts are short, both within the context of feed-singing behavior as well as when they are interspersed between regular song bouts (Beaver unpub.). Thus, males do not devote substantial periods of time to feeding, as they might if they were endeavoring to sample the resources of the territory. Not only might this emphasis on singing be affected by the conflict early in the season between feeding and territorial and courtship displays such as song, it also may be that sampling early in the season does not give an accurate estimate of the prey abundance which occurs when the females arrive one to five weeks later. Males arriving in the first two weeks in April in southern Michigan experienced days of snow and sleet in every year. These conditions affect the immediate food resource in that they preclude the large scale emergence of insects from dormant stages.

This study documented three between season shifts (two contiguous with the old territory, one non-contiguous), of a male to a better quality site, indicating that males may possess an ability to assess habitat quality and may shift territories if a favorable vacancy occurs. Even without direct sampling of food abundance, males could use a structural feature, such as the one used to calculate the

foraging index, to assess the quality of the new territory. Shifts, however, could also be in response to the availability of females or a potential vacancy in the system, or to combinations of all of these factors. As reported, the beginning of the season in particular, males made minor shifts in their territorial borders in response to the movements and nest placement of the female they were courting. At this juncture, it is not possible to clearly determine the cause of these exceptions to or modifications of site fidelity.

Site fidelity is pronounced in this species, with evidence both from this study and previous studies. Returning to the same site usually appears to give the returning territory holder a dominance advantage, as yet unexplained in the literature, that enables the owner to hold a territory in spite of aggression from intruders or prior occupants. Such an advantage may outweigh any that could accrue from switching to a territory of higher caliber after arrival. In addition, in a system exhibiting site fidelity, few vacancies occur at the beginning of the season and even those vacant territories which do exist are already fairly well defined in size by the boundaries of returning males. The greater longevity of the males results in fewer vacant male territories at the beginning of the season than female territories. In a system with so few vacancies at the beginning of the season, there is little freedom for the incoming male to determine the initial size of his territory, as would be true in the absence of experienced neighbors. The phenomenon of site fidelity may thus restrict effects of age of the territory holder or effects of other factors on the size of the territory. Resource sampling may also be of more limited value to an individual if the area of the territory is

determined primarily by the vacancy that is present at the beginning of the season since there would be fewer options for directly matching the territory size with the abundance of resources.

Males also tolerate less overlap of borders than do females (Table 4). This may be in part because they are not confronted with the same time and energy conflicts as the nesting female and so can devote the majority of time to territorial displays. Alternately, it may be that the main impetus for territorial defense for the male is the acquisition of a female or females for mating (McLaren 1972).

Certainty of parentage on the part of the resident male necessitates the exclusion of any potential competitor for copulations. The best way to territorially guard against the risk of extra pair copulations is by complete spatial exclusion of all competitors.

When invading males were successful in settling, the resident male responded by decreasing the size of his territory rather than sharing overlapping space (Table 5). Indirectly, this reduction in size (also documented by Potter 1972) argues for territories whose sizes are set by the level of competition, not a direct assessment of food resources. A bird whose territory size is directly determined by a minimum amount resources critical for reproduction could be expected to attempt to maintain the size of its territory in the face of aggressive interactions. A bird whose territory size is directly determined by aggressive interactions with others of the same gender could be expected to decrease the size of the territory when the cost of aggressive interactions increases. A male who is already bonded to a female can shrink his territory yet still maintain his breeding access

to her, even if she continues to occupy a considerably larger territorial space than he does. Thus, decreasing the size of his territory after pair bonds are formed would not be apt to directly affect the reproductive success of the male.

Female territorial establishment

As described in the section on foraging and diet, upon arrival from migration, females fed assiduously and rebuffed all advances from males. They were involved in aggressive border disputes with other females, but did not have the potential for the same conflict in activities that the males faced with song and feeding. This period of concentrated feeding might serve several functions, which are not mutually exclusive. First, it might enable the female, before settling, to sample the resource base that she will need immediately for the production of eggs and ultimately for the nurturance of young. Sampling would have the potential to be beneficial for a female who is claiming a territory for the first time. The shorter lifespan of females translates to a greater turnover of territories between years than that for males, with more females initially settling on a new territory in the spring. Because of this, sampling may be potentially more beneficial to females than to males. Secondly, concentrated feeding may enable the female to procure the requisite resources for egg-laying. The minimum time of seven days before nesting for a newly arriving female indicates that a female may use this period in part to acquire the necessary reserves. Lastly, as this feeding period often involved the movement of the female through the territories of several males, this behavior may also enable her to assess the quality of males within a certain area that is restricted by the presence of other

territorial females. Reid (1987) suggested that the amount of time a male savannah sparrow is able to devote to song may serve as a cue to his vigor and thus influence the female savannah sparrow's choice of a mate. Even if this is so, such choices would be restricted by the aggressive costs inherent in the female territorial system (Brown and Downhower 1983). The two observations of females which began the pair bonding process with one male, but, before mating, moved and nested with a neighboring male support limited mate choice as another possible function of this period of concentrated feeding and movement throughout the territory.

In contrast to the males, female territories showed visible overlap, particularly in areas of higher habitat quality. Also, females were not observed to visibly change the size of their territories after initiating a nest, even if additional females settled in the area. The greater tolerance for territorial overlap among females and lesser degree of exclusivity, coupled with the lack of visible changes in the size of the territory, suggests that the size of the territory may be set directly by the resources, rather than directly by the interactions with neighboring females. Following this reasoning, the finding that female territories showed greater overlap in areas of higher habitat quality argues that there are more potential settlers competing for occupation of territories in these areas. Rather than shrink a territory below a certain minimum or try to maintain spatial exclusivity, females appear to tolerate increased overlap. The lesser degree of spatial exclusivity on the part of the female could result from two factors. In a resource rich area, the

abundance of resources could mitigate any losses which might accrue from two females sharing space, thus rendering spatial exclusivity relatively unimportant. Alternately, the female's ability to maintain spatial exclusivity could also be influenced by conflicts in time and energy arising from nesting demands. These conflicts will be discussed further in the section of time and energy constraints.

In areas of the lowest habitat quality, there is no overlap of female territorial boundaries. In spite of having nesting demands that are at least equal, if not greater, to those of females in the high quality sites, females in low quality areas seem to be able to maintain more exclusive borders. This is also the case even though the occupied space in low quality sites is larger than that occupied by females in high quality sites and would potentially require more effort to defend. This suggests a balance in these areas between the requisite territory size based on habitat quality and the number of aggressive interactions that the resident female experiences on the site. It suggests that there may be fewer potential settlers in these areas, thus making it easier for the female to maintain exclusive borders. This reasoning conflicts with the finding in this study of no habitat quality preference on the part of non-breeding females in the population. These floating females, however, were those that managed to stay on a territory and interact with the resident male for a long enough period to be identified and recorded by the observer. Thus, they do not represent a measure of all floating females in the system, but only of those who encountered a level of aggression that permitted at least temporary settlement. An extensive banding study of the floating population of this species could provide valuable additional

information on this aspect of intruder pressure and competition for space within the territorial system.

The food resource value of the territory may be more critical to the female than to the male because of differences between the genders in parental demands associated with nesting. Once a female has a nest, she is constrained to forage nearby, particularly during the incubation period when she is solely responsible for the nest. During incubation then, her interests would be best served by having good foraging in close proximity to the nest. This study could not encompass the focal nest, time-activity study which would provide these data for the savannah sparrow, but evidence from other open country, ground-nesting passerines indicate that such restricted female foraging does occur. Female seaside sparrows rarely forage away from the vicinity of their nests until they have young to feed (Post 1974). Females of other species such as Henslow's sparrow (Robins 1971) and bobolinks (Wiens 1969) have also been documented to forage closer to the nest when feeding young than the males.

If female savannah sparrows do forage close to the nest, as these examples from other species suggest, then one would expect the placement of the nest relative to food resources to be important. My data (Table 35) indicate that female savannah sparrows avoided placing their nests in areas of poor foraging. A preferential selection of nest sites could also result in heightened female-female competition for nest placement in areas of better foraging, particularly in areas where two females' territories overlap. This, in turn, could result in more incidences of female territorial aggression. Direct quantified support

for all these suppositions would require further studies which specifically compare male and female use of space and time, similar to Robins (1971). Even without such documentation, however, it appears that the importance of resources on the territory differs in principle between males and females, and may provide at least a partial explanation for the differences in exclusivity of borders of the genders.

Spatial interfacing of male and female territorial systems

Regardless of the ultimate causes of the differences in territorial exclusivity between genders, they have repercussions in how male and female territorial systems interface and, concomitantly, on the patterns of pair bonds. Equal spacing of males and females is expected to result in monogamous pair bonds. In the majority of cases, males were able to exclude competitors from an area sufficient in size to secure access to a single territorial female for breeding. Concurrently, females were able to prevent settlement and nesting by additional females within the same space. This equal dispersal of males and females relative to one another resulted in a majority of monogamous pairs in each season.

It is possible for the size of male territories to vary independent of the size of female territories, depending on the levels of aggression from neighboring males. If a male faces reduced aggression from neighboring males, then he can expand his territory and still maintain exclusive use of its space, possibly without incurring increased costs. If the expanded territory includes the territories of two females, a type I polygynous pair bond can occur. Three such bonds were recorded in this study. Similar situations have been reported in

some detail for the dunnoek (Davies 1985).

Increased aggression from neighboring males can also result in two males occupying the space that one female is maintaining territorially. The visible result is one unmated male and one mated male. This may be a temporary situation with the only visible effect being a delay in the acquisition of a female by one male. Or, such a situation may endure for the breeding season. In another year, a male occupying the same territory might secure a female with no noticeable delay. Thus, unmated males may occupy a space that will support a mated male in another year, an observation of this and other studies (Bedard and LaPointe 1984a).

A male may also be aggressively unable to secure a territory that is of acceptable quality to attract a female, but he can still hold a territory for some span of time in an area where no female is present. Such a situation could explain the occurrence of the non-breeding males (mentioned under the section on floaters) who held a territory for abbreviated periods of time and then joined the floating population. These unmated males (designated as bachelors in other studies) often abandoned their territory after a few weeks if no female appeared.

Two females may also occupy essentially the same space if neither one is able to aggressively exclude the other before nesting occurs. If one male defends this same space from other males, then he has the potential to become a polygynist. Observations of behavioral interactions of females involved in two polygynous pair bonds in this study indicate that polygynous pair bonds can form in this manner.

Finally, if two females increase the overlap of their borders in

high quality areas, and place their nests sufficiently close together, a male may be able to mate with two females without needing to expand the size of his territory. The data showing that the nearest neighbor of a female is more closely situated on territories of higher proportion of overlap, which is in turn related to the foraging index, indicate that this situation may be most likely in higher quality areas. The finding that the spacing of nests of nearest neighbor only showed this relationship during the second time period when most females were occupied with nest care indicates that spacing of females is perhaps being influenced by factors in addition to habitat quality. I will return to a discussion of these factors in the section on time and energy constraints.

Non-breeding individuals or floaters

The territoriality of both males and females in this population resulted in the presence of non-breeders or floaters of both genders. The first barrier to breeding in a site faithful, territorial population is the acquisition of a territory. The first priority of floaters is to find weak spots in the system that will allow them entry as territorial holders. As long as the habitat is suitable for breeding, the gradation of habitat quality may of be secondary importance to a floater, with the primary focus being on simply securing a position in the territorial system. After the initial establishment of territories, it was these floating individuals who were the potential competitors for territorial space through aggressive interactions. Floaters of both sexes, attempting settlement, were not observed to favor the higher quality territories when they actually attempted settlement. This provides indirect evidence that the most

important criteria used by a potential settler is not the gradation in the quality of the habitat. The most likely factor influencing settlement is the level of aggression encountered from the resident bird of the same sex. Outside support for this hypothesis comes from Arcese (1987) who focused on this question in a study of song sparrows and decided that the most important factor influencing intrusion was the quality of the male holding the territory.

The level of the resident's aggression, in turn, can be influenced by other demands on its energy and time as well as changes in hormone levels throughout the breeding season. Indirect evidence for a response of the male invaders to a decreased level of aggression by the resident male comes from the identical ranking of years by nest initiation date and date of invasion and the month or more that exists between the mean nest initiation date and the mean invasion date. Invaders were not successful in settling while the resident males still were unencumbered by nesting duties. Rather, they invaded when resident males were feeding young and fledglings. It appears that the invaders could be responding to the timing of the nesting cycle.

The success of this means of territory acquisition for male floaters was documented by the return and nesting of a percentage of the invaders in every year of the study (Table 12). In most cases, they returned to the territorial area that they had previously invaded, demonstrating some site fidelity. Bedard and LaPointe (1984b) report the same finding in their population in Quebec. A few floaters were also able to nest in the same year that they entered the system. In addition, the rapid replacement of birds which disappeared also

suggests that floaters may continually be present in the area, and continually assessing opportunities for territory acquisition (Smith 1978; Arcese 1987, 1989).

Data on female floaters are less extensive because of their more secretive behavior when entering the territorial system. The fact that all but one of the documented female floaters appeared when the resident female was occupied with a nest suggests that female floaters also may be responding in a similar way to fluctuating levels of aggression by the resident female. In a species such as the savannah sparrow, where females are initially more constrained physically by the demands of nest initiation, it is possible that there are gender-related differences in the fluctuation of territorial aggression throughout the season as well. I will return to this point in more detail in the section on time and energy constraints.

My data are not complete enough to make a complete assessment of the intruder pressure on holders of territories of varying quality, since only floaters who were successful in staying for a period of time were included in these analyses. It is possible that both the level of the resident bird's aggression and the quality of the territory are operating together. There may be more actual settlement attempts on higher quality territories, with successful settlement contingent on the level of aggression encountered by the floater. Any such assessment of intruder pressure requires the procurement of additional data on floaters, perhaps through a banding regimen continuous throughout the breeding season. Such a protocol should include an assessment of habitat quality as well as information on the resident birds' stages of the nesting cycle.

Factors influencing reproductive success

An individual is expected to evidence behaviors which result in its highest attainable reproductive success. The most accurate estimate of reproductive success involves a measure of the number of offspring which enter the breeding population. This number of recruits to the breeding population has been shown to be significantly correlated with the number of young reared to independence for a variety of species (Clutton-Brock 1988; Newton 1988). Since a territory is a prerequisite for reproduction for both male and female savannah sparrows, any factor which influences the number of offspring which secure a territory and breed can be considered a plausible component of reproductive success in this species.

It is possible that the quality of the territory may itself directly or indirectly influence the reproductive success of individuals through effects on clutch size, abilities of parents to engage in multiple nesting attempts, parental care demands, or effects on growth, survival and dominance ranks of the young. In addition, once a territory is acquired, the importance of its exclusive defense may differ both between genders and through time, depending on both the reproductive options of the two sexes and the seasonal time and energy constraints faced by individuals. These have the potential to have a temporal effect on the spacing systems of males and females as the season progresses.

Other possible avenues of reproductive productivity, in principle, do not require the possession of a territory, although territoriality may still have a decided influence on their occurrence and probability

of success. These avenues include extra pair fertilizations for the male and conspecific brood parasitism for the female.

Extra-pair copulations

Extra-pair copulations and sometimes, fertilizations have been documented in a variety of species of birds including the northern oriole (Flood 1985), great egret (Gladstone 1979), bobolink (Gavin and Bollinger 1985), rook (Roskaft 1983), brown-headed cowbird (Yokel 1986), white-fronted bee-eater (Emlen and Wrege 1986), and sand martin (Jones 1986). Females often resist copulations from males other than her pair-bonded mate, making cloacal contact difficult. Therefore, the outcome of many extra pair copulations is in doubt (Lumpkin 1981). Emlen and Wrege estimate that extra pair copulations have only a 5% probability of resulting in fertilization of a female during a given nesting attempt. Documentation of successful copulations depends on obtaining genetic evidence by using techniques such as electrophoresis. When Westneat (1987a,b) obtained both genetic and observational evidence from a population of indigo buntings, he found as many as 14% of the offspring were not from both of the putative parents. He found no evidence of egg dumping by females and suspected successful extra pair copulations as the cause, in spite of active female resistance. Genetic evidence indicated the neighboring territorial males as the most likely fathers. In the present study, savannah sparrow females were always observed to resist vigorously any copulation attempts by neighboring males, reducing the likelihood of successful fertilizations. No floating males were ever observed to attempt a copulation in the present study.

In addition, the vigilance and herding behavior that pair-bonded

males exhibited toward their females is most parsimoniously interpreted as mate guarding. Its occurrence was always enhanced by the presence of neighboring males who were intruding on the resident's territory and following the female. Territorial behavior on the part of the male may also decrease the incidence of stolen copulations, as the male maintains priority of access to the female as a critical resource by maintaining exclusivity of his borders. Both behaviors reduce the likelihood of successful extra-pair fertilizations.

Even if some pair bonded, territorial males are successful in their extra pair copulation attempts, the fact that they are most likely already to be territory holders means that their success would not affect the apparent gametic contribution ratio. They already would have been included in calculation as nesting males. The presence of successful extra pair copulations could, however, affect the actual gametic contribution ratio if it changed the proportion of males who eventually succeeded in raising some young.

Conspecific brood parasitism or egg dumping

Females must have a territory on which to place a nest. The only other option available to the female is conspecific brood parasitism or egg dumping. Most of the successful conspecific brood parasitizers to date have been discovered among colonial nesters or species where nest sites appear to be limiting, with a common example being cavity nesters. It has been documented for such species as the eastern bluebird (Gowaty and Wagner 1988), the common Moorhen (Gibbons 1986), American coot (Hill 1986), cliff swallow (Brown and Brown 1988), and a hummingbird, the hairy hermit (Snow 1973). A marked egg study is the

rigorous way to ascertain the presence of egg dumping in a population. In a species with a limited range of clutch sizes such as the savannah sparrow, one can also use the presence of inflated clutch sizes to look for conspecific brood parasitism. Weatherhead and Robertson (1978) reported one savannah sparrow nest with two five egg clutches. In the four years of the present study, however, no clutches of inflated size were found. This argues against egg dumping as an important reproductive strategy for this population of savannah sparrows. Given the rarity of the event (reported only by Weatherhead and Robertson) it also appears to be of rare occurrence in the species. In the savannah sparrow, female territorial behavior makes unmonitored intrusion by other females for any purpose difficult, particularly when the resident female is still not restricted to her nest by incubation. This further decreases the viability of egg dumping as a common reproductive strategy.

Clutch size

Clutch size was not found to be significantly related to the sequence of the nesting attempt or to habitat quality as assessed by the foraging index. Davies and Lundberg (1985) also found no effect of supplemental food on clutch size in the dunnock. In addition, there were no apparent observable effects of female age on clutch size. Variation in clutch sizes of an individual female within a season may be in response to an interaction of such factors as temporal and spatial fluctuations in both food supply and conspecific competition. I know of no study which attempts to look at clutch size at this level of individual specificity. Whereas variation in clutch size may contribute to the overall variation in reproductive success in this

species, it does not do so in a predictable way, given the current level of understanding.

Nest mortality

As the data indicate, predation of entire nests is the most significant source of mortality (four year average of 52.4% of all nests) and hence, reproductive variance among individuals. This level was reported by Ricklefs (1969) for a variety of avian species. Loss of nests due to desertion of eggs or young is the second most important source of mortality, occurring at levels more than twice as high as the average of six passerines reported by Ricklefs (1969). Eggs or young were sometimes killed by exposure to damp and cold, particularly if the female was for some reason unable to devote enough time to incubation or brooding, or if heavy rains resulted in nest flooding.

Incidences of nest and, in some cases, territory desertion occurring for no discernible cause may reflect the effects of female-female aggression. Three cases were observed in this study where two females were found settling synchronously on one territory. In all cases, as reported previously, one female always both abandoned her eggs and eventually left the territory without re-nesting. In two of these cases, female-female aggression was documented. Given the advantages of holding a territory and the advantages of re-nesting, one would not expect a female to leave without a reason. Aggression from the remaining female may be the deciding factor in some cases, determining whether or not a female can remain on the territory and re-nest, as appeared to be the situation with the female PUR/WT described earlier.

Multiple nesting attempts

Faced with unpredictable sources of mortality, the best option for both sexes would seem to be one of enhancing the opportunity for multiple nesting attempts. Multiple nesting attempts from a male perspective may involve serial nests with the same female or mating with multiple females. From a female perspective, multiple nesting always entails repeated production of clutches of eggs.

There was a significant difference between years in the number of females undertaking repeated nesting attempts. One likely source of variation between the years is the occurrence and timing of local weather events. Not only might weather directly influence the mortality of nests, weather which is physiologically stressful may thwart the ability of the female to make a repeated nesting attempt. In 1986, as I have presented in the section in the results on multiple nesting attempts, the inclement weather during the height of the breeding season may quite plausibly be linked with the high incidence of deserted nests due to both chilling and flooding as well as with the higher rate of territorial abandonment that year. This, in turn, was reflected in the highest percentage of serial monogamy in the four years.

Whereas some environmental factors may act as physiological stresses which contravene the re-nesting ability of the female, other environmental factors, such as the availability of food, may enhance her readiness to re-nest. Weather may play a role here, if certain patterns of temperature and rainfall greatly enhance the staple components of her diet and the diet of her young. These data on the interaction of weather and diet of the savannah sparrow, however, are

not available from the current study.

The availability of food may also be influenced by structural features of the habitat which enhance foraging, such as those measured for the calculation of the foraging index. When all females were considered together, there was no relationship between multiple nesting by females and the quality of the territory. Nevertheless, females on territories with higher foraging indices were more likely to re-nest following the failure of a nest than females on poorer quality territories. Perhaps a higher foraging index enables a female to forage more efficiently and become physiologically prepared for a second attempt, particularly following a failure. Better foraging opportunities may also compensate the female for the effects of any environmental stresses that coincide with nest failure, thus giving her an added advantage.

Given the limitations of a finite breeding season, early dates for arrival and nest initiation could potentially favorably influence the opportunity for multiple nesting attempts. An individual initiating nesting early in the season would usually have more opportunity to re-nest than an individual initiating a nest later. The timing of nest mortality for individual females might further affect the starting time of replacement nests and become a critical factor in a late arrival year. This contention that re-nesting attempts were affected by nest initiation dates was supported by the finding that the years that had the earliest arrival dates also had the highest percentage of re-nesting females. Although there were not significant differences in fledging success among years for females producing some young, the

trends were in the direction of a lower fledging success per female occurring in the late arrival year of 1984, and the highest fledging success per female occurring in 1985 and 1987, the years with the highest percentage of multiple-nesters and the earliest mean nest initiation dates (Figure 4 and Table 6).

An individual female may also be delayed in the timing of nest initiation by aggression from an already resident female. A delayed date for nest initiation might additionally contribute to a decreased probability of re-nesting for a late nesting female. Such aggressive interference with nesting was documented directly in the incident of female territorial competition between PUR/WT and GRN/ORG. Usually, however, the general difficulty of accurately assessing actual arrival dates of females coupled with the problems associated with documenting female aggression, make it extremely difficult to document directly the influence of female aggression on the timing of nest initiation of neighbors. Indirect evidence does exist. It is possible that female aggression may account for some of the variance in the time spans between arrival and nest initiations for individual females, producing cases such as the 19 and 25 day delays observed in 1985. Indirect evidence is also provided by the data that indicate that there is a relationship between the spacing of nearest neighbor's nests and the proportion of territorial overlap only in the second time period when most females were occupied with the demands of nest care. If the proportion of overlap alone were enough to explain nest spacing, then one would expect a significant relationship between the two variables in both time periods, since overlap was a one time measure made only at the beginning of the nesting cycle. One likely explanation for the

difference between these time periods, is that the resident female was able to initially delay the close nesting of neighboring females until the conflicts of nest care in the second time period made it impossible for her to completely prevent nesting by a neighboring female. I will consider this in more detail under time and energy constraints.

I have also observed areas on the study site where a male remained unmated until his neighbor's females had nests. When the neighboring females began nests, another female promptly settled in the vicinity and became the mate of the unmated male. Thus, there are tantalizing hints of the subtle influence of female aggression on the nesting dates of individuals, even among monogamously-paired birds. The limitations to direct documentation arise from the difficulty of recording female arrivals, identifying individual females before banding and sufficiently documenting female aggressive encounters, often subtly displayed.

Increased frequency of re-nesting could also be a result of increased predation on nests in the more densely populated areas. Nevertheless, nest mortality was found to be independent of the quality of the habitat. This argues against differential predation as an explanation for the higher incidence of females re-nesting following a failure on sites of higher foraging index.

There was a significant difference in the number of young produced per female when females were categorized by the number of nesting attempts and the fate of those attempts. No difference remained when all double brooding females were removed from consideration. There was a similar lack of significance when the data from 1987 were excluded,

thus excluding eight out of eleven double brooders. Thus, it appears that, in spite of their rarity, double brooding females in 1987 accounted for the some of the difference in reproductive success among females categorized by nest attempts and their fate.

In my study population, double brooding is not a common occurrence (Table 17). In most years, female savannah sparrows which are successful in raising the first brood do not re-nest (Table 17). Re-nesting females are usually trying to replace a lost nest. Dixon (1978) reported the same finding for a Kent Island, New Brunswick population of savannah sparrows which experienced a 50% rate of egg loss to predators. Nevertheless, in my study, the years with the highest percentages of females which engaged in multiple nesting attempts (Table 17) were not the same years that experienced the highest percentages of nest mortality (Table 14). Nor was there a significant difference between years in the numbers of successful and unsuccessful nests. This yearly variation in multiple nesting attempts, independent of nest mortality, once again suggests that other factors, which vary between years, affect the re-nesting ability of the female both following a failed nest and following a successful nest.

Although age appeared to play a role in double brooding, with one year old females less likely to re-nest following a successful nest than females older than one year, the distribution of ages did not differ among years. Thus, factors other than age must be invoked to explain the disparity in numbers of females who engaged in double broods among years.

The two years (1985 and 1987) with the earliest nest initiation dates were also the two years with the highest percentages of re-nesting

females and females with double broods (Table 17). It appears from these limited data that the initiation date and total span of the breeding season potentially may have an influence on the ability of females to re-nest, particularly following the time elapsed completing a successful nest. There are geographical differences in rates of double-brooding of savannah sparrow populations which lend some support to this idea. The highest rate of females engaging in multiple broods in the literature is reported from the "Ipswich" sparrow of Sable Island (Stobo and McLaren 1975); a subspecies with an extended nesting season and low rate of nest mortality. Re-nesting readiness in the Sable Island population is apparently further enhanced by the male taking over the major share of feeding of the older young and fledglings, allowing the female the opportunity to prepare for another brood.

Males with multiple nests (serial monogamous or polygynous pair bonds) only did better reproductively than males with single nests (monogamous pair bonds) in one year, 1984. This was the year with the highest percentage of polygynous pair bonds. It may be that the low percentages of polygynous or serial monogamous pair bonds and small sample sizes in this study, combined with a high rate of mortality for all nests makes it difficult to detect, statistically, a reproductive advantage to the male with two females. Males could also increase their reproductive success by mating with a single female who attempted more than one nest, yet in this study monogamously-bonded males with one nest and monogamously-bonded males with multiple nests did not differ in the number of young that they fledged.

In most years, single and multiple-nesting individuals of both sexes of this population, achieved equal reproductive success. Yet some degree of multiple nesting by females and some polygynous and serial monogamous pair bonds by the males occurred in every year, even those with no demonstrable advantage in number of young fledged by successful nesters. It is possible that the tendency to be a multiple nester serves to compensate for nest losses in a population which faces unpredictable, high predation rates and has evolved in part for this reason. There was a trend for males with multiple nests to be less apt to produce zero young than males with single nests. And there was a four year average of slightly more than two young per female produced in the population, sufficient to replace the parents and maintain the size of the population. In some years, or in some populations of savannah sparrows in which conditions are conducive to the production of multiple successful broods within a season, multiple nest attempts can result in significant reproductive advantage. Under those circumstances, it can lead to significant reproductive advantage for the multiple-nesting individual. In either the "break even" case or the "reproductive advantage" case, multiple-nesting by both sexes would be favored by selection for reproductive advantage.

Parental care and survival of the young

In an altricial species, the quality of parental care throughout the nesting cycle can be a vital component of reproductive success (Ricklefs 1984). Assessing the growth of nestlings and the extent of parental care efforts fell beyond the scope of this study. Therefore, I will rely on the literature as my main source of information on parental care. Williams (1987) reported that when both savannah

sparrow parents participated equally in feeding offspring, males had to augment their sustenance foraging by 75% and females by 87% to meet the food requirements of an average-sized brood of young. In the same study, feeding rates were higher for single-parent sparrows than for members of pairs. Weatherhead (1979a) experimentally widowed a set of females and found that the female made more foraging trips of shorter duration in an effort to compensate, but that even so, the young did not grow as rapidly as young being fed by two parents. He also found that the females' foraging became concentrated in the immediate vicinity of the nest. Martin (1974) reported that secondary females of polygynously pair-bonded bobolinks compensated for reduced male parental assistance by making more frequent, short feeding trips within 60 meters of the nest. Higher quality habitat near the nest could result in enhanced foraging, particularly for a secondary female whose foraging is restricted to the vicinity of the nests by the dictates of efficiency. The single parent disadvantage for a female could thus be mitigated. The value of bi-parental care might also vary yearly. Male parental care in snow buntings was particularly beneficial during a year of poor food availability when male-assisted nests produced twice as many young as nests under the care of the female alone (Lyon et al. 1987).

The significance of growth rate of young is equivocal. Alatalo and Lundberg (1986) reported that the smaller pied flycatcher fledglings, from secondary female nests of polygynously pair-bonded male pied flycatchers, experienced reduced parental care and suffered a lower survivorship than the larger fledglings from the nests of primary

females. Fledglings raised by single parent great tits experienced reduced growth and subsequent decreased reproductive success (Bjorklund and Westman 1986). Ross and McLaren (1981) failed to find a correlation between growth rate of nestling savannah sparrows and subsequent survival of the young. They also failed to find a relationship between survival of the young and several other factors related to parenting, including age or longevity of the parents, the brood size, or the habitat or time of the breeding season in which the nestlings were raised. They did not address the question of eventual territory acquisition and breeding.

The quality of parental care may also be influenced by the availability of food on the territory. In the present study, there was a trend for lower reproductive success among females producing some young on the territories of the very lowest caliber. No female with a single nest attempt produced any young on these territories. Females with multiple nests fledged smaller broods. These differences were not statistically significant perhaps due in part to small sample sizes. Or, it may be that the influence of foraging opportunities on the quality of parental care is not significant at a level of analysis which treats the season as a whole and uses fledging success as the measure of reproductive success. It is still possible that parental care may be more crucial to the young in bouts of inclement weather which may require extra brooding by the female to prevent the death of some of the young from exposure (particularly at vulnerable ages), or increased feeding effort in the event of food shortage. In these situations, bi-parental care might confer a decided advantage. Averaging all nests together may obscure subtle effects on both the

parents and the young which are difficult to measure but which contribute to the overall variation in the reproduction of a population.

Parental care and fecundity of the parent

Increased physical demands on a sole parent might result in fewer nesting attempts within the season and hence, a lower reproductive success, if the individual is not able to continue to defend a territory, replace a lost nest or attempt a double brood in a good year. Given the higher initial gametic investment of females, an increased stress might be expected to affect females more dramatically than males. If the limiting factor for re-nesting for the female is her ability to become physiologically prepared to lay a replacement clutch, then any stresses, such as additional parental duties, aggression from neighboring females or poor habitat quality, may negatively influence her ability to re-nest. These factors may also interact. Female great tits which attempted a double brood were documented to have experienced less weight loss during the first brood than did females with single nest attempts (DeLaet and Dhondt 1989). Indirect support from my study for the idea that male assistance may influence the ability of the female to engage in multiple nesting attempts comes from the finding that the older males were more apt to have females with multiple nests. This may be because the older males are better providers of parental care than younger, inexperienced males. Further support would require detailed time-activity data on male and female parental care efforts for individuals of varying ages.

One might also speculate that increased reproductive strain within

a season could result in lower probability of survival to another season, and thus affect lifetime reproductive success. This study did not directly examine the connection between parental investment and lifetime reproductive success. Because parental investment was not quantified and the study entailed relatively small sample sizes and high rates of between season adult mortality (Table 8), this question could not be addressed with data from this study. Other studies have attempted to address this factor and found conflicting results. For example, Newton (1988) found no relationship between female European sparrowhawk (Accipiter nisus) investment in terms of brood size and survival of the female to the ensuing year, nor did he find a negative effect on the next year's brood size. Conversely, Harvey et al. (1988) found that pied flycatchers which survived to the subsequent season had smaller clutch sizes in three comparisons and had fledged fewer young in two of the comparisons. Bryant (1979) found that the female sand martins with the highest annual reproductive success also experienced the greatest mortality. The implication is that individuals which endure lower reproductive stresses during the breeding season are more able to survive the ensuing stresses of the non-breeding season. In order for an individual to benefit by withholding reproductive effort in the immediate season, however, reproductive stress on an individual must be a larger contributing factor to between-season mortality than other factors. In the present study population, both breeding (Table 8) and non-breeding, territorial (Table 12) individuals experienced a high rate of mortality between seasons. Thus, it is most likely that other factors, in addition to reproductive stresses, play a large role in mortality. Faced with a low probability of surviving to the

subsequent season (.50 for males, .31 for females), the best option would seem to be one of breeding as soon and as frequently as possible rather than to withhold reproductive effort as a means of ensuring a longer life span. Given the high frequency of re-nesting attempts of females, the pervasive polygyny attempts by males, and the continual attempted settlement by non-breeders, this does seem to be the dominant mode of operation in this population. Data on lifetime reproductive success in a wide variety of species show that early lifetime and seasonal commencement of breeding and frequent breeding are the most productive strategies for all but exceptionally long-lived species (Ricklefs 1977; Clutton-Brock 1988).

Timing of breeding

The timing of breeding by an individual female has the possibility of affecting reproductive success in several ways. There is certainly a reproductive penalty for individuals who attempt breeding before they can secure adequate food resources for themselves or the young. But within the feasible breeding season, early breeders may enjoy several advantages. The trends linking mean dates of nest initiation with percentage of multiple nesting attempts documented by this study, suggest that early breeders may benefit in that they have more opportunity, in a time-limited breeding season, to engage in multiple nesting attempts. These multiple nesting attempts may either be for the production of replacement nests or double broods. When double broods are possible, this could result in a significant advantage over other individuals. For birds experiencing the loss of a first nest, multiple nesting can give them equality with individuals with

successful first nests only. Either way, given the high predation rate and relatively short breeding season in this population of savannah sparrows, earliness of breeding within a season has the potential to be an important component of individual reproductive success.

Timing of breeding may also influence the growth and survival of individual nestlings, particularly in situations of seasonal fluctuations in food abundance (Quinney et al. 1986; Bryant 1975). Fledglings which hatch early in the season may also gain experience in aggressive encounters which gives them a dominance advantage useful in survival (Kikkawa 1980) or in initially entering the territorial system (Arcese and Smith 1985; Matthysen 1987). In this population, an early fledging date may be an advantage to the juveniles who disperse to other breeding locations when they are first independent. Unbanded juveniles from other locations came into the study area at a time when the study population was occupied with re-nesting efforts. A late hatched bird would not have this opportunity. Eight of these juveniles eventually returned to territories, with the majority becoming breeders. Not only could these birds gain information about potential suitable breeding habitat both directly and through observations of resident birds, but also they may also gain experience in agonistic encounters which translates to better chances to acquire a territory, as suggested by Arcese and Smith (1985).

The timing of breeding in this population of savannah sparrows is most closely tied to the arrival dates from migration. Within this yearly time frame, individual females may be delayed from nesting by aggression from other females, as discussed in the section on multiple nesting attempts. Given the documented and potential reproductive

advantages to early breeding in the savannah sparrow, I would argue that the very pressure to begin breeding as soon as possible creates situations of competition for breeding opportunities in space and time and thus has important repercussions on the mating system of this species. Consideration of the temporal component, in particular, will follow.

Time and energy constraints

Maintaining a territory, maximizing chances for multiple nests, and investing in parental care appear to be the three primary avenues to reproductive success in a typical passerine such as the savannah sparrow. These activities sometimes result in conflicts in use of time and energy. The conflicts may be expected to differ for males and females, given their differing reproductive options, particularly as opportunities and demands change with the progression of the nesting cycle. With high nest mortality, these costs and benefits are in a constant state of flux for the population as re-nesting individuals continually return to the demands of earlier stages of the nesting cycle. This portion of the discussion will use behavioral data to indirectly examine time and energy constraints faced by males and females during the nesting cycle. It will also explore the effect this may have on territorial spacing of the two genders and thus on the types of pair bonds that are formed.

Territorial establishment

Initially, a male faces no obvious conflicts between establishing and maintaining a territory and securing breeding opportunities. He

need only feed enough to survive and to maintain his territory, without the added cost that the females face in the production of costly gametes. Reproductive success for the male, particularly at this stage, is limited by the copulations that he can secure. He is, therefore, occupied with the defense of the space occupied by a female or females in order to secure a mate or mates. Several of his activities such as song, territorial displays, mate guarding and male-male aggression may very likely serve the dual functions of territorial proclamation and attraction of a female, thus further mitigating potential conflict of activities. Overall, his investment in a territory is made even more valuable in terms of lifetime fitness by his potential to return and secure the same territory the following year.

A female is able, through aggression, to prevent the settlement of another female, while continuing to provision herself for egg laying. Doing so maintains priority of access to both the actual depletable resources on the territory, as well as to potential male parental care for the young. In this study, both have been shown to be potentially influential on the female's re-nesting abilities. The potential importance of male parental care to the female (Williams 1987) and the young (Weatherhead 1979a) has already been mentioned. The result, as mentioned earlier, is usually an equal spacing of territorial males and females that produces a mating system characterized by a predominance of monogamous pair bonds.

Nevertheless, early in the season, there is a potential conflict for the female between acquiring the requisite resources for egg

production (Welty 1975) and continuing to maintain territorial priority of access to food resources and male parental care. This conflict may be responsible in part for the greater tolerance of boundary overlap on the part of the female territory holders. It may also result in enhanced aggression in a case of two female claimants for one space. In such a situation, female territorial aggression has been observed to consist of physical contact fighting, including bloodied bills, and prolonged agonistic posturing. These are activities which appear to be very time and energy demanding as well as carry the risk of injury. The same sort of escalated aggression was not observed in this population for territorial males during the same portion of the breeding season. Such prolonged aggression at the onset of the nesting cycle has the potential to delay nesting by direct interference with nesting or by preventing a female from accumulating the food reserves which are necessary for nest initiation. This time and energy conflict is exacerbated if two females exert equal intensity in their claims on a territory. Presumably, if the contest continued long enough, one female would emerge as the victor. The issue that prevents the occasional definitive conclusion of the contest, however, may be a time constraint. Unable to continue to invest time and energy in trying to exclude a competitor and still acquire the potential advantages of early breeding, females may opt to begin nesting, producing situations of simultaneous settlement and synchronous nesting. The incident cited above involving the simultaneously settling females, PUR/WT and GRN/ORG, documents the adverse effects of female-female aggression may have on the actual successful simultaneous nesting of two females on one territory, whether this occurs directly, through continued

aggression on the part of the victor, or indirectly, through physiological stress. Given the lower frequency of synchronous nesting in type II bonds, such aggressive "tie" situations appear to be the exception rather than the rule. The resulting situation may be a polygynous pair bond which is temporary in nature, perhaps due in part to female-female aggression, yet contributes to the overall rate of polygyny in the population. The temporary nature of such bonds makes a detailed behavioral study of marked individuals a prerequisite for the accurate determination of percentage of polygynous pair bonds in a population.

Egg laying

With the pair bond formed, a male's aggression becomes more tightly focused around the female herself. He stays with her while she feeds throughout the territory. His borders may shift as he endeavors to incorporate the majority of her territory within his borders. He responds to intrusions by other males by either pursuing them until they leave the territory or by attempting to herd his female away from the intruder. The spatial emphasis is on maintaining priority of access to his female by excluding other males from her presence. In addition, he responds to intrusions by other females not with aggression but by attempting to court them and copulate with them.

Between laying bouts, females continue feeding with her mate in attendance. She is still free during feeding between laying bouts to aggress any other female who attempts settlement, and does so. She also responds with aggression to any intrusions by neighboring males. Her aggression toward intruders of both genders, excepting only her own

male, lends support to the hypothesis that the female is attempting to maintain direct priority of access to the food resources through territorial behavior and indirect access to her own male's potential parental care contribution.

Incubation

During incubation, the male has no parental care duties and minimal mate-guarding duties and thus is free to attract and attempt to mate with another female. The resurgence of singing associated with this stage of the nesting cycle, observed in this and other studies of savannah sparrows (LaPointe and Bedard 1984), as well as observed courtship attempts of available females indicate that he engages in this option. Male bananaquits, a resident tropical species with a long breeding season, also exhibit seasonally fluctuating levels of polygynous pair bonds, and actively court neighboring females during the incubation period of their first female (Wunderle 1984).

The female is potentially limited by her incubation duties in her ability to prevent settlement by other females through aggression. Williams (1987) estimates that the daily energy expenditure of an incubating female may not be significantly any lower than during other portions of the reproductive cycle. She must choose between the chance of monopolizing her mate's parental care contribution and the resources of the territory, or the maintenance of her current nest. Female pied flycatchers showed a marked decrease in the extent of their aggressive response to experimental female intruders after egg-laying (Breiehagen and Slagsvold 1988). In the present study, the number of recorded incidences of aggression between females was significantly less during the period of incubation and nestling care. The amount of time the

female spends first incubating and later, brooding and feeding young, can have direct and, in some cases immediate, repercussions on the health and survival of her offspring. Young may perish because of chilling, overheating or starvation if a female stays away from the nest for prolonged periods, particularly in periods of inclement weather. The extent to which her reproductive success may be affected by sharing her resources is less clear. Predictability may vary depending on the food abundance at the time of the intrusion. A female would be most likely to invest effort in the activity giving her most predictable results; in this case parental care of the young.

The conflict between parental care and territorial defense continues for the remainder of the breeding season, with the potential to influence the settlement and spacing of neighboring females. At this time, it is difficult both to measure subtle delays in nesting of individual females as well as ascertain their causes. Females may differ in their inherent ability to prepare for egg laying as well as in their times of arrival from migration. Both of these factors could contribute to differences in timing of nest initiation. In addition, I suggest that some of the variation in times of initial nesting of females may be due to fluctuations in female aggression as the resident female experiences temporal changes in the conflict between nest care and territorial defense. Such a delay in nesting might also account for males which only acquire a female after their neighbors have acquired females.

This study has taken a first step in documenting the presence of female territorial behavior. Variations in aggression of individual

males and females with respect to other demands on time and energy experienced by the individual, measured throughout the nesting cycle, should continue to be investigated in an experimental fashion. Prototypes for such a study are experiments involving model birds such as those of Weatherhead and Robertson (1980a), involving male savannah sparrows or Breiehagen and Slagsvold (1988), using pied flycatchers. Parental care demands may also be influenced by the vulnerability of the eggs or young according to the stage of development and influences of climatic factors. Therefore, in order to reap the maximum information from such a study, the procedure should include documentation of these sorts of factors in a fine-tuned approach. Williams (1987) advocates this sort of understanding of the influences of the microenvironment on the individual bird's allocation of energy to reproductive effort.

Lacking any direct assessment of temporal variation in female aggression and its influence on female spacing at the present time, the nearest neighbor nest spacing analyses provide a source of indirect evidence. The time periods are reflective of the activity of the majority of the females. It is during the second time period when most of the females are occupied with incubation or the care of young (Table 39), that the relationship emerges between the proportion of territorial overlap and the spacing of nearest neighbors (Figure 5). During this time of re-nesting efforts, females are nesting closer together on territories which exhibit greater overlap of boundaries. Since the proportion of overlap is related in turn to the foraging index, nest spacing can be seen as indirectly related to the higher foraging index through the placement of the female territories relative

to one another. If territory quality alone were influencing the nesting of females, one would expect to find the same relationship between the spacing of nests and proportion of overlap in both time periods. The expected relationship only emerges when the majority of the females are occupied with care of nests. This provides an indirect but fairly strong argument for the role of female aggression in the spacing of nests. It also provides evidence for the argument that the priorities of individuals may change as they experience temporal changes in the factors influencing reproductive success.

In turn, these changes in spacing of nesting females may have continuing effects on the formation of pair bonds throughout the season. A space previously held by two males and one female (one monogamous pair and one unmated male) has been observed to be transformed into a situation of two monogamous pairs when a second female nests after the first female is incubating a clutch. In two documented incidences in the present study, a second female settled in the same territory as an already mated male when his primary female was occupied with a nest, resulting in a type II polygynous pair bond. Wunderle (1984) reported increased levels in polygyny in bananaquits (Coereba flaveola) as the season progressed, but made no direct reference to the role of fluctuating female aggression, although he initially documented female territorial behavior. Dippers (Cinclus mexicanus) have been documented to be regularly polygynous, but with a high degree of asynchrony between the nests of the two females (Price and Bock 1973). Thus, male dippers who were originally monogamous, only became polygynous when their first female had nearly finished

raising her first brood. Derrickson (1989) reported a similar situation involving asynchronous nesting and polygyny in a study of northern mockingbirds (Mimus polyglottus). Most of the other examples of asynchronous nesting from Table 1 are from similar situations in polygynous pair bonds.

In the majority of the polygynous pair bonds in this study population, the females' nesting attempts are staggered in time (Figure 6). Such asynchrony in nesting in a polygynous pair bond could result from several causes. Some researchers have ascribed asynchronous nesting to the male's delay in attracting and inseminating a second female (Derrickson 1989). In such a case, the male is hypothesized to delay courtship of a second female in order to minimize aggression between the two females. Male savannah sparrow behavior refutes this explanation since a male in this species appears opportunistically to court any accessible female, regardless of the breeding stage of his primary female. Mate guarding and perch singing are mutually exclusive activities. Therefore, the increase in male perch song which often coincides with incubation by his first female is more likely to be the result of his having extra time to devote to song once he is freed from the constraints of mate guarding, rather than a result of intentional courtship delay. When his primary female leaves the eggs during egg-laying and incubation, the male ceases his song and joins her, most likely in an effort to mate guard once again. None of this suggests an inclination of the male to control the timing of the second female's clutch. Rather, he seems to try to both protect his investment in his first female while still trying to inseminate additional females.

A second possible cause of nesting asynchrony is an attempt on the

part of the second female to delay nesting (Blakley 1976; Weatherhead 1979a; Muldal et al. 1986). The proposed purpose of the delay on the part of the second female is for the secondary female to hatch young after the primary female, thus enabling the male to devote some parental care efforts to both nests. I found no evidence supporting voluntary delay of nesting on the part of the secondary female. To the contrary, the data document the continual presence of female floaters attempting settlement and the demonstrated advantages for early initiation of nesting, including the low probability of a female returning in the ensuing year. All of these make it seem unlikely that females are freely choosing to delay nesting. Also, given the high mortality of nests, the continued asynchrony of nests throughout the raising of young would be very unpredictable. A re-nesting attempt by the primary female could quickly eliminate any planned asynchrony and its advantages. Support for this latter argument comes from the high four year average (47%) of females engaged in re-nesting attempts.

A third explanation for asynchronous nesting is that the second female is prevented from settling and nesting until the first female faces conflicts between territorial defense and nest care. Good indirect evidence, again, comes from the data discussed above involving nest spacing and proportion of overlap in the two time periods. More direct evidence for this hypothesis awaits the type of time activity information which is currently only available for males.

Care of young

When dependent young are present, the male faces his first conflict between activities which can potentially increase his fitness. Feeding

young is an activity demanding in terms of both time and energy, as is territorial defense (Williams and Nagy 1985). A male must determine how much effort to devote to parental care, how much to territorial defense against male floaters which are attempting to settle, and how much toward the courtship of any females which might become available, including his own during a re-nesting attempt. Feeding the young may directly enhance the growth and survival of his progeny and make multiple nesting attempts by his female more likely (Westneat 1988). On the other hand, the acquisition of an additional female would give him insurance against the loss of his present nest as well as a chance for greatly enhanced success that season. If his current female is ready to make an additional nest attempt, the option giving the greatest probability of success is for the male to mate with his original female again and attempt a re-nest. Continued territorial defense against invading floaters could maintain his monopoly of his female in the event of the possibility of a re-nesting attempt. It might also allow him to secure a second female rather than lose her to an invader.

Not unexpectedly, male activities during this time period are varied. The indirect evidence below, however, provides the following possible outline of male priorities. Territorial defense appears to be the lowest in priority, followed by male parental care of young. The top priority appears to be the obtainment of multiple nest attempts either through re-nesting of his original female or through polygynous pair bonds. The choice between these latter options may depend upon the availability of additional females. This, in turn, may be influenced by the level of aggression exerted by the resident female,

which can be influenced by her parental care demands.

The fact that invaders do consistently acquire territories and sometimes females, often when males are occupied with young, suggests that males do favor parental care investment over territorial investment at this time period. Invaders initially face aggression from territorial males, but if they persist, they are eventually allowed to settle. As documented, the response of the resident males is to often reduce their territorial defense efforts by reducing the size of their territories in response to the invaders' aggression. Unlike the beginning of the season, territorial males with nests do not spend nearly unlimited time in territorial defense.

The genesis of the majority of polygynous pair bonds after the resident male's first nest was underway, indicates that males will opportunistically take advantage of a chance to mate with multiple females, even at a potential cost to their current nest and female. More subtly, even when polygynous bonds do not result, the presence of floating females may temporarily affect the extent of the male's involvement in parental care as he attempts courtship of any available female. Males in the present study were observed to temporarily cease their feeding of young when a courtship opportunity presented itself although these variations were not quantified. In addition, I observed males that were not feeding their young but rather were attempting copulations with their own females in preparation for a second nest even while that female was still engaged in feeding older nestlings or fledglings. Stobo and McLaren (1975) report the same finding for their highly polygynous population on Sable Island, Nova Scotia. Any study

attempting to quantify male parental investment should certainly take note of the temporal variation in each male's potential for polygynous matings. The presence of these male conflicts of interests makes his contribution of parental care a commodity which may be unpredictable for the female. Even if she is able to prevent pairing and nesting with her male by competing females, she cannot directly control the male's expenditure of parental effort in the face of the activities of neighboring females. These continual courtship attempts on the part of the male further suggest that the male places top priority on the attainment of multiple nests, even at the cost of providing male parental care to the young from his current nest.

Nevertheless, the territorial spacing of both genders usually limits the opportunities for multiple matings and polygynous pair bonds by the male. In the absence of alternative means of enhancing reproductive success, males do feed the young of their current nest. By this investment, they may not only enhance the growth of their young but also maximize their chances of having their female re-nest.

Females face the same conflicts in this time period as those encountered during incubation. Care of the young (feeding and brooding) is directly under the female's control and crucial to the success of the nest. Monopolization of male assistance is indirectly under the female's control, potentially unpredictable and not critical to the success of the nest, a hypothesis supported by the lack of differential reproductive success between primary and secondary females of polygynously-bonded males (Table 44). Prevention of predation, aside from enhanced crypticity of the nest, is also essentially beyond the control of the female and appears to be completely unpredictable.

It makes sense for the female to invest most heavily in the care of her current nest as her most critical strategy and that which gives the most predictable results.

The mating system of the savannah sparrow

Rationale for examining the assumptions of a model

Models which describe aspects of the natural world are formulated in an effort to focus the attention of the researcher on the major factors that are responsible for an observed pattern. The pattern in this case study is the mating system, comprised of patterns of individual pair bonds. With a graphical or mathematical approach, one can make and test predictions about the pattern. That is, the model can be verified or nullified by the careful collection and analysis of data and if verified, may have a predictive value as well. Thus, it is justifiably argued that models can result in an ecological and evolutionary understanding that is characterized by critical thinking at all stages of problem solving.

A model is built on a set of assumptions which can be viewed as its foundation. Predictions which follow from the model are only valid if the underlying assumptions are also, in so far as is possible, known to be valid. Increasingly, there is a call to test assumptions as hypotheses in their own right (Hixon 1987). This is particularly timely when data begin to be collected that call the validity of the assumptions into question.

The use of a model with unexamined, sometimes erroneous, assumptions may have far more subtle effects that go beyond the

invalidation of the predictions of the model. If data are collected to test the predictions of a model whose assumptions have not been clearly stated, the researcher runs the risk of unwittingly using the assumptions as an unexamined viewpoint through which all data are collected. One possible repercussion is that the researcher may completely miss collecting information that is crucial to a complete understanding of the system. This appears to have been the case repeatedly in avian mating system theory where female-female interactions are not part of the assumptions of prevailing explanatory models. Data collection has focused on male-male interactions and female choice of males and their territories. It has rarely included a consideration of female-female interactions as these are not incorporated in the assumptions or predictions of the model. This type of use of models may be partially responsible for the paucity of data on female-female interactions that exists even in some otherwise well-documented species which exhibit polygynous pair bonds.

A body of literature is thus built up which appears to offer support for the model by validating the predictions of the model. This support, however, remains suspect until the assumptions can also be examined and substantiated. If assumptions cannot yet be evaluated, Hixon (1987) discourages researchers from using the term "test" to describe an analysis of the predictions only.

It is with this rationale that I begin the portion of the discussion on the mating system of the savannah sparrow with an examination of the assumptions of the polygyny threshold model. I use data from the present study as well as from other studies of this species.

An examination of the assumptions and predictions of the polygyny threshold model

As described in the introduction, the polygyny threshold model, a restricted subset of the more inclusive resource distribution hypothesis, has been the model most frequently used in attempts to understand the incidence of polygyny in resource-based territorial passerines such as the savannah sparrow. Given the presence and possible relevance of male parental care in this species, referenced above, and the presence of a resource-based territorial system, the polygyny threshold model is an appropriate choice among current models at the outset. The examination of the assumptions and major predictions of the polygyny threshold model which follows uses data from my study on breeding statuses and habitat quality as estimated by the foraging index. The demonstrated significant inverse relationship between territory size and the foraging index and direct relationship between female border overlap and foraging index together provide a strong argument for the validity of using the foraging index as a indicator of habitat quality in the following discussion. In addition, indirect evidence supporting my use of the foraging index as an estimate of habitat quality comes from the females' preferential placement of nests in patches of presumed higher quality.

Assumptions. The polygyny threshold model assumes that: (1) habitat quality is the underlying and most important factor affecting female reproductive success; (2) that the female settlement pattern will match the rank order of territory quality and (3) that females will settle in an ideal free distribution, guided only by habitat quality. The model, as it applies to passerines, also assumes that "a

major factor affecting the differences in reproductive success of females will be the role of the male in the care of the offspring" (Orlans 1969).

This study has found females to be both territorial and site faithful. Territoriality implies a despotic settlement pattern rather than a free distribution, thus violating a fundamental assumption. To elaborate, female aggression has the potential to prevent females from choosing both where and when to settle. This study has documented numerous observations of female-female aggression when two females occupied the same space at the same time. The data on changes in nest spacing of nearest neighbors during a time when the neighbor was most likely to be occupied with nest care provide further indirect evidence of the importance of female aggression in the determination of female spacing. In addition, floating females did not appear to attempt settlement on higher quality territories in preference to lower quality territories. Rather, they appeared to temporarily settle on territories in an apparent opportunistic fashion, usually when the resident female had a nest. This may have been in response to decreasing levels of aggression by the resident female during this period. The data also directly refute the prediction of a settlement that matches the order of territories ranked by habitat quality. There was no tendency for early-arriving females to settle selectively on territories of higher quality. It is possible that the dominance advantage that seems to accrue to a returning site faithful individual of either gender outweighs any advantage that might be obtained by switching to a territory of higher quality in this species.

The value of male parental care to the females of this species, as

reported from other studies, is still equivocal. And, regardless of the quantified contribution of male parental care, behavioral observations from the period of nest care suggest that the male parental care may be an unreliable and unpredictable commodity for the female. A male always has the potential for a higher reproductive success by taking advantage of opportunities for obtaining multiple nests and may do so at the expense of his current nest. The female's best response to a potential loss or decrease in male parental assistance is the exclusion of other females from her territory. She cannot, however, control her male's behavior in response to opportunities from neighboring females. The unreliability of male parental care may reduce its value to the female relative to other factors that are more predictable components of the breeding situation.

Even without a current clear assessment of the value of male parental assistance to the female, it may be that other factors not considered by the model, such as potential interference with breeding by aggression by the resident female, have a more important influence on the reproductive success of an incoming female. In fact, it is possible that female aggression may have a larger negative effect than can be balanced by the factors of habitat quality combined with male parental assistance. Indirect evidence of the potential detrimental effect of female aggression comes from the relative rarity of synchronous nesting by two females of a polygynous male in this population, and the prevalence of asynchronous nesting in polygynous pair bonds of other species (Table 1). In addition, the three incidences of synchronous nesting by two females on one territory in

the present study all ended with one female deserting nest and territory. This suggests the possibility of the direct influence of female aggression on the reproductive success of at least one female in a space usually occupied by only one female. If female aggression is a more important factor influencing the reproductive success of a settling female than male parental care then one would not expect secondary females to settle on territories based on the compensatory effect of habitat quality. Rather, they should settle based foremost on the level of aggression encountered from the resident female. The change in nest spacing in the second time period when resident females were occupied with nest care offers further indirect support for this idea as does the lack of a habitat-related settlement pattern of floaters.

Predictions. In any model, the validity of predictions are dependent on the validity of the underlying assumptions. Most studies involving the polygyny threshold, however, have not directly stated or examined the assumptions. Instead, they have usually dealt with the following major predictions: (1) that the interaction of habitat quality and male parental care results in a reproductive success of secondary females on good quality territories which is equal or greater than that of monogamously-bonded females on low quality territories; (2) that because of the potential differences in reproductive success of monogamously-bonded and polygynously-bonded females which arise from differences in male assistance, there is a measurable threshold of habitat quality above which polygyny can be predicted to occur (polygyny threshold) where habitat quality is sufficient to compensate a secondary female for losses in male assistance and (3) that

monogamous pair bonds result when the variation in habitat quality is such that this threshold is not reached. Following is an examination of these major predictions relative to my data and their underlying assumptions.

The comparison of the reproductive successes of primary and secondary females implicitly assumes that no females are excluded from breeding by female territorial behavior. When some females are excluded from breeding by female territorial behavior, a floating female only needs to have a higher reproductive success than any females that are excluded from breeding in that season in order to make a breeding attempt worthwhile. As has been discussed above, breeding as early as possible in one's lifetime has been shown to be the preferred strategy for maximum lifetime reproductive success in a short-lived species such as the savannah sparrow. The presence of floaters attempting settlement throughout the breeding season in this population provides evidence against any intentional breeding delay in this species. Thus, if female floaters are present, polygyny can occur even if there is shown to be a disadvantage to the secondary female on a high quality territory relative to monogamous females on poor quality territories. Conversely, showing the predicted equal reproductive success described above cannot be considered a valid test of the model if the presence of female territoriality has invalidated the underlying assumption which led to that prediction. Female territoriality and female floaters were both clearly documented in this study. Increasingly, there are data supporting the existence of female territoriality in other passerines (Table 1), calling the validity of

the polygyny threshold model into question for other species as well.

If habitat variation is such that the polygyny threshold is reached, then the occurrence of polygyny above the threshold is expected to be directly correlated with the quality of the territory. Conversely, monogamy should prevail on all territories which fall below the polygyny threshold.

When the patterns of monogamous and polygynous pair bonds were examined, they did not completely follow the predicted pattern. There were actually more monogamous pair bonds on the territories of the highest habitat quality and more polygynous pair bonds on the territories in the middle category.

Nevertheless, a type of polygyny threshold seemed to exist in this study with no polygynous or serial monogamous pair bonds occurring on territories with a foraging index of less than 2. This lack of polygyny on territories with a foraging index less than two appeared to be the result of the placement of individual territories of males and females relative to neighboring territories of their respective genders. The largest territories of both genders occurred in the areas of lowest habitat quality. In addition, females in these areas did not overlap their boundaries, thus reducing the probability to the male of Type II polygynous pair bonds. Even if there were an opportunity for expansion for a male, the energetics of defending an even larger territory may preclude expansion and the subsequent formation of Type I polygynous pair bonds. A polygyny threshold could thus exist in the sense of the relative spacing of the two territorial systems, without having any reference to an explanation that invokes the compensatory effects of male parental care.

Under the polygyny threshold model, monogamy is predicted to result when habitat quality is not sufficient to compensate a female for loss in male assistance (Holmes 1984). Yet in this population, the same territory that sustained a polygynous pair bond one year, had a monogamous pair bond in another year. Neither the individual male nor the actual territory could be used as a predictor of polygyny in the ensuing year. Only two males were polygynists twice and they did so by forming Type I polygynous pair bonds, enclosing two female territories in their territory, not by attracting two females to one high quality territory.

The majority of the territories (Figure 2) in this population lay above the presumed polygyny threshold, yet monogamy still prevailed in the population in general and on high quality territories in particular. In explaining monogamy as a default condition, the polygyny threshold model provides no mechanism which can explain the predominance of monogamous bonds on territories which lie above an identified threshold of habitat quality. In an understanding which includes female territoriality, monogamy can be understood to predominate regardless of habitat quality, as the result of territorial aggression by the resident females. In such a system, the probability of polygyny increases as the cost of territorial defense rises for any individual female.

Yearly variation in the mating system of savannah sparrows

The settlement patterns and spacing of individuals of both genders in this population of savannah sparrows, while fundamentally tied into the variations in habitat quality, are also potentially influenced by

other factors, both singly and in interaction. The settlement and spacing of the genders relative to one another can, in turn, influence the patterns of pair bonds in any given year. Such additional influences include temporal fluctuations in male and female territorial aggression, the presence and possible variation in the demographics of a floating population of males and females, timing and other variation in nest mortality, and differences in the timing of the breeding season. In most situations in this population, the spacing of males relative to other males and females relative to other females resulted in monogamous pair bonds. Polygynous pair bonds, however, were documented in every year in varying percentages of the total number of pair bonds. A qualitative examination of factors which can potentially affect the incidence of polygynous pair bonds from year to year follows, in an effort to better understand the role of some of these factors in determining the mating patterns of the population.

In my study population, the potential for polygynous pair bonds is enhanced by the presence of a floating population of females. The proportion of floaters in a population is further influenced by the amount of usable habitat relative to the size of the adult breeding population (Faaborg 1988). The number of non-breeding birds may vary seasonally, although I have no data to address this demographic parameter. Because resident females may prevent settlement of additional females through aggression, however, the presence of floaters is not sufficient by itself to produce polygyny. It must be combined with a nest initiation period which is long enough (average of 67 days in this study) for late-settling females to procure a territory and nest when time constraints may cause a decrease in the aggression

of resident females and when there is still time to raise a brood. The nest initiation period, in turn, reflects the total time available for the raising of young to independence (average of 83 days in this study). Interestingly, even in a late arrival and nesting year, such as 1984, the nest initiation period was the same length as that of an early arrival year such as 1985 (Table 25). It appears as if the basic period of nest initiation at the population level might be genetically controlled rather than respond directly to factors such as yearly variations in weather and migration patterns. A more fruitful avenue of exploration of the nest initiation period might be an examination of differences between geographical populations of savannah sparrows.

The presence of male floaters, in contrast, can potentially decrease the frequency of polygynous pair bonds as late-settling males (invaders) enter the territorial system. In some cases (Table 12), these nesting invaders usurp late-settling females who might otherwise become second females of an already established male. Thus, instead of producing polygynous pair bonds, they create additional monogamous pair bonds in the population. If all monogamous bonds formed with invading male floaters had resulted instead in polygynous bonds with males who were already present, some appreciable differences in percentages of pair bonds would result. In 1984, monogamous pair bonds would decrease from 70.6% to 52.9% with a corresponding rise in polygynous pair bonds from 23.5% to 41.2%. In 1985, monogamous bonds would decrease from 88.2% to 82.4% with polygynous bonds doubling from 5.9% to 11.8% and in 1987, monogamous pair bonds would fall from 82.6% to 78.3% while polygynous bonds would rise from 13% to 17.4%. In the future, a more

complete understanding of the factors which may influence seasonal changes in the numbers and settlement of floaters of both genders has the potential to contribute much to the understanding of mating systems.

Nest mortality may also contribute to a lower incidence of polygynous pair bonds through two mechanisms. The first involves the probability of re-nesting by the female and thus affects the mating options faced by the male. The second involves the effect of nest loss on the aggressive behavior of the female.

In the first case, if a female has lost her nest and is capable of re-nesting, her male may do better to direct his attentions toward another successful mating with her, rather than attempt to attract an additional female for mating. The results of mating again with his original mate cannot help but be more predictable since she already has possession of a territory and he already has secured the pair bond with her. Also, the parental assistance by the male may enhance his first female's ability to re-nest. In this study, older males (who perhaps are better providers due to experience) were more likely to have a female with multiple nesting attempts. The yearly variance in the levels of multiple nesting and double brood attempts, however, indicate that other factors not under the control of the individual, such as temporal changes in weather and food abundance, may influence whether or not a female is able to initiate a re-nesting attempt. Thus, there is also an unpredictability for the male with regard to the probability of his female's re-nesting. An illustration of this occurred in 1986 when inclement weather apparently resulted in females being physiologically unable to re-nest. The result was a decrease of

polygynous pair bonds but an increase in serial monogamous bonds. The observed gametic contribution ratio was affected by serial monogamous pair bonds in the same direction as it would have been by polygynous pair bonds (Table 51). In contrast, the actual ratio was affected in the opposite direction by the high nest mortality and subsequent territorial desertion by females (Table 52).

In the second case, if a female suddenly lost her nest, she would be temporarily freed from the constraints of nest care. Consequently, she could devote more time and energy to the aggression of potential female settlers, thus preventing their nesting on her territory. A high level of nest mortality may thus act to decrease the possibility of the formation of polygynous pair bonds through the mechanism of female aggression.

In apparent refutation of these predictions, the variation in percentages of polygynous pair bonds in this population does not seem to be related to the yearly fluctuation in mortality rates. In contrast to the prediction, the year with the smallest percentage of polygynous pair bonds was also the year with the lowest nest mortality. Nonetheless, a statistical difference in nest mortality among years was not found in this population. Once again, it may be necessary either to find a population experiencing greater variability in nest mortality or compare geographically distinct populations which show a greater disparity in mortality rates in order to detect an effect of nest mortality on pair bond patterns.

Other factors which may have had an effect on the proportion of polygynous pair bonds were the synchrony of female and male arrivals

and the synchrony of female nesting. In 1985, there was only one recorded polygynous pair bond. As presented in the results, that year was also unique in the highly asynchronous arrival of some of the males and females on the breeding ground. In addition, the females arrived and nested dispersed through time, instead of in the temporal synchrony of other years, apparently as a result of conditions on migration. My results have shown the time necessary for a female to acquire the requisite resources for their first nests to be fairly standard from year to year, ranging only from 7 to 13 days across the four years in spite of differences in arrival times and weather patterns. Thus, an arrival spread out over more days would also mean that females would not be in as much competition for nesting in the same space at the same time. This lessened spatial and temporal competition could result in fewer polygynous pair bonds. In contrast, a highly synchronous arrival such as that of 1987 might have the opposite effect, increasing both female competition and the probability of polygynous pair bonds. Thus, the patterns of arrival of females from migration may have influenced the low rate of polygynous bonds present in 1985 as well as the higher level present in 1987.

In this Michigan population of savannah sparrows, it appears that the predominately monogamous mating system with a low, but regular incidence of polygynous pair bonds is the net result of an interplay of factors which affect spacing and nesting of individuals. The complexity of the interactions of these factors, as yet not completely resolved, means that the actual percentage of polygynous pair bonds in any one year or their specific spatial location cannot be predicted for this population at this time.

Geographical variations in savannah sparrow mating systems

Another way to examine the effect these variables have on the mating system of the species as a whole is by examining geographical populations of savannah sparrows which differ in combinations of these same variables as well as in proportions of polygynous pair bonds. Where applicable, the findings of each study will also be critically examined with respect to the interpretation presented by the authors as well as an interpretation which considers the effects of female territoriality.

Arctic Canada, 58.5 degrees N. Weatherhead (1979a) studied an overwhelmingly monogamous savannah sparrow population nesting near Churchill, Manitoba. At this latitude, the approximate span of nest initiation was only 23 days. Presumably, this reflects a limit on feasible nesting time imposed by weather, food, or perhaps migration demands associated with this high latitude. No females could be double-brooded, although they did re-nest if nest loss occurred early in the season (Weatherhead and Robertson 1980b). Approximately 30% of attempted nests were unsuccessful (Weatherhead 1979a). No data were presented on the proportion of females which re-nested after the loss of a nest.

Using arguments from the polygyny threshold model, Weatherhead (1979a) suggested that, in this population, females do not have time in the shortened breeding season to stagger their nests so as to acquire the necessary share of male parental care. Experimentally widowed females (mimicking secondary females) in the preferred habitat did significantly worse reproductively than females in the preferred habitat who had access to male parental care. He concludes that it is

the inability to secure male assistance by staggering the timing of the nest that precludes the occurrence of polygynous pair bonds, and thus supports the polygyny threshold model. Nevertheless, to adequately examine the predictions of the polygyny threshold model, he would also need to show that these experimentally widowed females did more poorly than assisted females on marginal habitat. This was not possible since no data were taken on reproductive success in the habitat he designated as marginal. In addition, he does not take into consideration the possible presence of floating females who need only do better than zero success in a year to make a nesting attempt worthwhile, even with the lower success resulting from a lack of male assistance (Wittenberger 1976; Vehrencamp and Bradbury 1984).

I suggest that it is indeed the brevity of the breeding season which results in a predominance of monogamous pair bonds, but that the polygyny threshold is not the mechanism. Instead, female territorial aggression could prevent settlement by non-breeding females until it is too late for the floaters to settle and successfully raise a brood within the remainder of the season. The moderate nest mortality would contribute toward the maintenance of unpredictable levels of female aggression as females were periodically liberated from nest care and free once again to repel potential female settlers. Together, these factors could account for the extreme rarity of polygynous pair bonds in a population with a very abbreviated nesting season.

Sable Island, Nova Scotia, 44 degrees N. Stobo and McLaren (1975) studied a population of the Ipswich sparrow, a recognized, morphologically distinct subspecies of the savannah sparrow which

breeds on a dune island, 150 km southeast of mainland Nova Scotia. These birds experienced long nest initiation periods with an average over three years of 75 days. This may be due in part, as the authors suggest, to the moderation of temperature extremes by the surrounding ocean. If there is a heritable component to the span of nest initiation, a prolonged time for nest initiation might be enhanced in this population by the lack of dispersal of young Ipswich sparrows. Welsh (1975) reported a considerably shorter span of approximately 67 days for a mainland population of savannah sparrows at a similar latitude, while Stobo and McLaren (1975) postulated a limited gene flow between the two populations. In addition, nest mortality rates on the island were low, ranging from 16% to 22% in the three years of the study. Almost all (96%) of the females were multiple nesters. With the extremely low predation rate, most females had two, three and sometimes four successful broods. Males assumed the major share of feeding of the young after fledging, thus enhancing the female's opportunity to re-nest (Ross 1980). This tactic would enhance the reproductive success of both sexes. The percentage of males engaging in polygynous pair bonds varied from a low of 12% to a high of 43%, with an average across the years of 26%. There was some suggestion that the year of low polygyny also experienced a lower density of females in general. Female aggression was directly documented in this population, including aggression between two females of a polygynously-bonded male. Of all the incidences of polygynous pair bonds, only 17% of them consisted of females nesting in synchrony. The remaining secondary females began a nest when the first female had eggs or young. As argued earlier, both female aggression and asynchronous nesting are

strong evidence for female territoriality.

Polygyny in this population was also interpreted relative to the predictions and assumptions of the polygyny threshold model. Although the secondary females were less successful reproductively than primary or monogamous females, the difference was not due to decreased fledging of nests due to lack of male parental assistance. Rather, it seemed to be due to having the opportunity for fewer additional nests, resulting from later settlement and nesting. On a per nest basis, there were no differences in reproductive success between the category of secondary females and the category including primary or monogamous females. This equal success matches the predictions of the model but for a reason not predicted by the model. Also in contrast to the model, polygynous pair bonds were not restricted to the habitat of apparent better quality. In one of the three years, there was a higher incidence of polygynous pair bonds occurring on the poor quality territories than on the good quality sites, again a phenomenon not accounted for by the model.

I suggest that the lengthened breeding season, extending into late summer and autumn, combined with an extremely low nest predation rate, results in circumstances conducive to high percentages of polygynous pair bonds. Territorial females are predictably occupied with nest duties and due to the conflict of interests between territorial defense and nest care, allow invasions by late-settling females. The resulting staggered nesting cycles of the two females not only permits the male to assist at both nests, but also to the male's advantage, frees him to court and mate with his primary female during her additional brood attempts. The extended nest initiation period may also increase the

probability that late-settling females will have the time to settle and complete a nest. This extended nest initiation period may be a result of moderated temperatures due to the geography of the habitat. It may also reflect the shorter migration distances to more northerly wintering sites than other savannah sparrow populations (Stobo and McLaren 1975). A population of savannah sparrows on Kent Island, New Brunswick at 44.5 degrees N, also exhibits the combination of low nest predation (5-15%) and high percentage (15 - 33%) of polygynous pair bonds (Wheelwright pers. comm.). Dixon (1978) also studied savannah sparrows on Kent Island ten years previous to Wheelwright. She reported a nest initiation period of only 44 days, considerably shorter than the period on Sable Island. This indicates that the extended breeding season alone may have less influence on the incidence of polygynous pair bonds than the low predation rates. Dixon also reported a much higher nest mortality rate of 50.5% during her study, primarily attributable to herring gulls and common crows. Unfortunately, for the purposes of this analysis, she did not report on the incidence of polygyny in the population during her study.

Isle Verte, Quebec, Canada, 48 degrees N. For four years, Bedard and LaPointe (1984a,b, 1985) studied a population of savannah sparrows nesting in a tidal marsh and abandoned field ecotone 225 km northeast of Quebec City. This population suffered high nest mortality (49.4% of first nests) due to predation. Nest mortality was further heightened by nest losses due to heavy rains and tidal flooding. The losses of 20% of all eggs and 38.8% of all nestlings were attributable to bad weather and flooding. These two factors resulted in a survival to fledging of an average of only 35% of the total eggs. In one year of

the study, when mortality from cold, rainy weather and tidal flooding combined with the high predation rate, only 15% of the eggs survived to fledging (LaPointe and Bedard 1986). No polygynous pair bonds were reported in this population. Males not only assisted in feeding the young, but also in brooding, the only population reporting a regular occurrence of this latter behavior. The mean length of the nest initiation period was 54 days. Approximately 34% of the females made more than one nesting attempt during this time. This is lower than the 47% four year average of multiple nesters in my southern Michigan population. Territorial males which failed to secure a female (designated as bachelors in this study) comprised from 20% to 35% of the total territory holders.

The researchers suggested that the high percentage of non-breeding territorial males was indicative of a shortage of females in the population (Bedard and LaPointe 1984a). They offered no possible explanation for this presumed imbalance. To the contrary, the lack of a statistical difference in return rates of adult territorial birds of the two sexes (Bedard and LaPointe 1984b) argues against a differential mortality unless it is restricted to a floating segment of the population. Female territoriality, on the other hand, makes it possible to account for the presence of non-breeding territorial males even if there is no shortage of females in the population. Territorial females, adjusting their territory size to reflect the resource abundance, may be able to prevent additional females from settling. Meanwhile, males may adjust the sizes of their territories to reflect the amount of competition from other males and crowd together in

territories that are smaller than the female territories. The result is a skewed sex ratio of territorial birds, but not of the population. In my study population, a three year average of 27% of the territorial males (including the late-settling males) remained unmated. If the late-settling males are not included in the averages from my population, 10% of the territorial males still fail to breed even in the documented presence of extra females. It is unclear from the Quebec study whether or not the late-settling males (invaders) were included as part of the estimate of unmated territorial males. The majority of such males in their study were yearlings, just like the invaders in my population. These birds may be acquiring territories for the following year, thus accounting for the fact that the territories possessed by an unmated male in one year are the territories possessed by breeders the next year. Further evidence that invaders may have been included in the tally of unmated males comes from the fact that territories were mapped and measured at the peak of the nesting season in the middle of June. Thus, there was time for invaders to have settled, before the territories were mapped, while the resident males were preoccupied with the care of nestlings.

The most striking difference of the habitat of this population, relative to the others that have been discussed, is the effects of tides on nest mortality and availability of suitable habitat. Fifty percent of all the territories were flooded at least once during the breeding season. Since tides occurred in pulses of 5-9 days, twice a month, for the duration of the nest initiation period (May 20 to July 17), some territories may have been flooded more than once. A minimum of three tides with flooding lasting a mean of 7 days would result in

the loss of 21 days of potential nest initiation for some areas of the habitat. If females are prevented from settling by such an environmental factor, in addition to the fluctuating levels of female aggression, the net result may well be that only a small proportion of total females can successfully attempt nesting in any one season. This combination of factors influencing the feasibility of female settlement could account for the low percentage of multiple-nesting females, the absence of polygynous pair bonds, the tendency of the males to invest time in brooding their current nest, and even the prevalence of unmated territorial males in the population.

CHAPTER VI

CONCLUSIONS

Toward a new model of mating systems in a territorial species

An existing model incorporating territoriality in both sexes

The presence of interacting territorial systems of both genders introduces a complexity that is only beginning to be addressed in models. Hixon (1987) has proposed a model which makes qualitative predictions for a species in which both sexes are territorial. He argued that fundamental reproductive options are likely to make the male an area maximizer and the female an energy maximizer. Territory area and competitor density are used as the two main variables in his model, with territorial defense and feeding as the two activities which must be balanced by the individual in a time and energy budget. Territory is implicitly defined using the male biased "exclusive use" criteria since all intruders are assumed to be effectively excluded. One main assumption, clearly stated, is that these models deal only with the period of initial territory establishment, before there are nesting and parental care requirements. The model does not include a change in demands on the individual or possible changes in spacing of individuals through time. He also assumes that individuals are free to expand or contract territories in response to variations in competitor density or food abundance. Neither of these main assumptions are met in the savannah sparrow territorial system, thus precluding the use of the model as it now stands for this species. Hixon is not unaware of the preliminary nature of this model. He repeatedly states that the

"detailed knowledge of the system" is required before specific quantitative predictions can be made and continually advocates the examination of assumptions of his and other models.

The advantage of Hixon's model is that it is one of the first to attempt an explanation of the mating system of the population as the result of the interface of a male territorial system and a female territorial system. Nevertheless, my study has indicated some basic modifications that would need to be incorporated into such a model if it were to apply to a passerine such as the savannah sparrow. Instead of considering the area of the territory alone as a factor, my data indicate that differences between the genders in exclusivity of borders may also be important in the way that these differences affect the placement of territories and nests relative to one another. Examining differences in territorial exclusivity is more probable when an inclusive definition of territory such as Kaufmann's (1983) is employed. In addition, the cost of competitor intrusions cannot be measured only relative to feeding time in a species with substantial parental care and a breeding season long enough to allow for late nesting. As indicated by the presence of asynchronous nesting by polygynously bonded females in many species, the formation of pair bonds is not an event that results only from the spacing of individuals at one point in time, before breeding commences. It is necessary to take under consideration additional factors which account for changes in costs of territorial defense over time as other time and energy demands, with the potential to influence reproductive success, are included. In the savannah sparrow, regardless of competitor density,

one could view the cost of territorial defense as rising whenever the territorial individual faces a conflict between territorial defense and other activities which have an effect on the individual's reproductive success. I agree with Hixon that more detailed information on the system is needed, particularly in the areas of time and energy budgets and intrusion pressure from floaters.

Some general principles of mating system theory

The following suggestions are drawn from the review of the literature which was a part of this study as well as from the actual data from the current study. I only summarize the basic principles here. The more detailed discussion and rationale exists as part of the chapter on background. Because these considerations have not been incorporated in the models to date, I think a summary is valuable.

Clear definitions of territoriality, and clear definitions of types of pair bonds and mating systems are essential to any new models dealing with mating systems of territorial species. This is not trivial. The definition which prevails in the literature may incorporate a bias which is detrimental at the outset to setting the assumptions of the model. In particular, an effort should be made to eliminate gender bias from the definitions that will provide the foundation for any hypotheses. For example, Kaufmann's (1983) definition of territoriality is eminently functional and does not make male behavioral traits an implicit part of the definition. For these reasons, I advocate its use over any other definitions currently employed in the literature.

It is best if definitions of mating systems do not include hidden explanatory mechanisms for special cases at the outset. It is true

that all polygyny is not alike in terms of how it results from the social structure. To avoid confusion and make it easier to construct hypotheses, however, the explanatory differences should be a part of the hypotheses, not the definition.

The variables influencing reproductive success and the actual reproductive success should be considered independently for each gender. One should avoid using one gender as the standard for the species. This consideration becomes particularly pertinent in cases of mixed mating systems where one type of pair bond is often in the majority. There is a tendency to focus on the gender who is most benefited by the dominant pair bond type and develop the model focusing on the behaviors of that gender. This approach has been evident in historical understandings of both polygyny and polyandry. It is more useful, I think, to view the resultant mating system of a species as the result of an interface of reproductive behaviors of both genders. Male and female reproductive options can then be examined independently with regard to temporal and spatial changes. Because pair bonds always involve physical access of the two genders to one another, as well as access to an acceptable breeding location, territoriality should always be considered as one of the potential variables influencing reproductive success. The territorial system, or lack of same, should be examined uniquely for each gender in order to produce a complete understanding of the social system which results from their interface.

It may not yet be possible to predict the mating patterns across most species or, in the case of the savannah sparrow, even across geographical races within a species. For almost species at this time

we do not have enough information to construct the models that can make finely-tuned predictions about individual mating patterns. What may better increase our understanding is a more complete examination of the assumptions of current models, resulting in the acquisition of data which can give a more thorough understanding of the factors influencing the reproductive success of both males and females of a species.

Summary and suggestions for further research

In the savannah sparrow, the sizes of territories have been demonstrated by this study to be related to a habitat feature that is very likely to be biologically correlated with the quality of the habitat. The spacing of females also reflects differences in habitat quality in the differences in border exclusivity that are correlated with habitat quality. Females appear to tolerate more border overlap than do males, particularly in areas of high habitat quality. Males, by contrast, attempt to maintain exclusive borders of the largest territory possible relative to the habitat quality. They appear to contract territorial borders in the face of increased intrusions, rather than increase border overlap. In the limited breeding season of this migratory, northern latitude passerine, early commencement of breeding conveys an advantage in the increased opportunity for re-nesting, following successes or, more commonly, following failures. This pressure to commence breeding translates into continual competition among males and competition among females for access to breeding territories. More information is needed on the demographics of the floaters of both sexes and intrusions by these individuals on

established territories.

Indirectly, the data indicate that the costs and benefits of territorial defense vary as the demands and opportunities associated with stages of the nesting cycle vary. For both genders, this results in an apparent decrease in aggression during the period of nest care and the opportunistic settlement by non-breeding adults on selected territories. Both polygynous pair bonds and additional monogamous pair bonds result, depending on the initial settlement patterns and genders of the additional birds. A fruitful avenue of further research would be the quantification of the demands of parental care for both males and females on territories varying in quality. Also, time-activity budgets for both genders across the breeding season, including the specific behavioral context described earlier in this paper, would also directly address the validity of the assumption of a time and energy conflict for the individual. Experimental elicitation of aggressive responses throughout the breeding cycle, again with the specificity described earlier, also has the potential to increase the understanding of individual variations in territorial defense and thus contribute to a further understanding of settlement patterns.

Habitat quality is not definitively linked to higher reproductive success in this study, although there are trends in the direction of higher success on higher quality territories, and a greater tendency for females to re-nest following a failure on higher quality territories. Small sample sizes, relative to a study focused at the population level, may preclude detection of significant differences in reproductive success at the level of fledged young. Even within the sample size limitations of a behavioral, observational study, further

work could be done on growth of young and parental feeding trip rates on territories which vary in quality in an effort to measure other variables related to food resources and reproductive success which may provide a more sensitive measure of differences.

The predominance of monogamous pair bonds in this population of savannah sparrows and others, as well as the relative rarity of polygynous pair bonds, results from the nearly equal spacing of males and females relative to each other throughout most of the breeding season. Territorial females are actively and successfully preventing settlement by secondary females in most cases and males are dividing the available space among themselves in a similar fashion. Polygynous pair bonds occur when the need to initiate a nest or later parental care demands prevent a resident female from totally excluding a potential settler from nesting near her. They may also occur when a male is able to expand his territory, either as a result of an increase in his own level of aggression or a decrease of the aggression of his neighbors, and secure the territories of two females. In this understanding, monogamy is an result of the active choices of males and females, not a default condition based only on habitat quality. Further predictability of patterns of pair bonds awaits a more detailed knowledge of the system particularly with regard to demographics of the floating population and to the time and energy constraints faced by territorial males and females.

LITERATURE CITED

- Alatalo, R.V. and A. Lundberg. 1984. Polyterritorial polygyny in the pied flycatcher Ficedula hypoleuca - evidence for the deception hypothesis. *Ann. Zool. Fennici* 21:217-228.
- Altmann, S.A., S.S. Wagner and S. Lenington. 1977. Two models for the evolution of polygyny. *Behav. Ecol. Sociobio.* 2:397-410.
- Anderson, M.G. 1985. Variations on monogamy in canvasbacks (Aythya valisineria). In: P.A. Gowaty and D. W. Mock (eds): *Avian Monogamy*. Washington, DC: American Ornithologists' Union, pp. 57-67.
- Andrew, R.J. 1956. Territorial behaviour of the yellowhammer Emberiza citrinella and corn bunting E. calandra. *Ibis* 98:502-505.
- Arcese, P. 1987. Age, intrusion pressure and defense against floaters by territorial male song sparrows. *Anim. Behav.* 35:773-784.
- Arcese, P. 1989. Territory acquisition and loss in male song sparrows. *Anim. Behav.* 37:45-55.
- Arcese, P. and J.N.M. Smith. 1985. Phenotypic correlates and ecological consequences of dominance in song sparrows. *J. Anim. Ecol.* 54:817-830.
- Archibald, H.L. 1975. Temporal patterns of spring space use by ruffed grouse. *J. Wildl. Manage.* 39:472-481.
- Armstrong, E.A. 1973. A study of bird song. New York: Dover.
- Baeyens, G. 1981a. Functional aspects of serial monogamy: the magpie bond in relation to its territorial system. *Ardea* 69:145-166.
- Baeyens, G. 1981b. The role of the sexes in territory defense in the magpie. *Ardea* 69:69-82.
- Bailey, T.N. 1974. Social organization in a bobcat population. *J. Wildl. Manage.* 38:435-446.
- Baird, J. 1968. Eastern Savannah Sparrow. In: O.L. Austin (ed): *Life histories of North American Cardinals, Grosbeaks, Buntings, Towhees, Finches, Sparrows and Allies* (Bent). Washington, D.C.: Smithsonian Institution Press, pp. 678-696.
- Barlett, J. 1988. Male mating success and paternal care in Nicrophorus vespilloides (Coleoptera: Silphidae). *Behav. Ecol. Sociobiol.* 23:297-303.

- Barlow, G.W. 1988. Monogamy in relation to resources. In: C.N. Slobodchikoff (ed): The Ecology of Social Behavior. San Diego: Academic Press, pp. 54-79.
- Beaver, D.L. 1988. The response of bird populations to three years of wastewater irrigation on oldfields in Michigan. Jack-Pine Warbler 66:87-103.
- Bedard, J. and G. LaPointe. 1984a. The savannah sparrow territorial system: can habitat features be related to breeding success? Can. J. of Zool. 62:1819-1828.
- Bedard, J. and G. LaPointe. 1984b. Banding returns, arrival times, and site fidelity in the savannah sparrow. Wilson Bull. 96:196-205.
- Bedard, J. and G. LaPointe. 1985. Influence of parental age and season on savannah sparrow reproductive success. Condor 87: 106-110.
- Bedard, J. and M. Meunier. 1983. Parental care in the savannah sparrow. Can. J. Zool. 61:2836-2843.
- Beehler, B.M. and M.S. Foster. 1988. Hotshots, hotspots, and female preference in the organization of lek mating systems. Am. Nat. 131:203-219.
- Beletsky, L.D. and G.H. Orians. 1987a. Territoriality among male red-winged blackbirds I. Site fidelity and movement patterns. Behav. Ecol. Sociobiol. 20:21-34.
- Beletsky, L.D. and G.H. Orians. 1987b. Territoriality among male red-winged blackbirds II. Removal experiments and site dominance. Behav. Ecol. Sociobiol. 20:339-349.
- Bell, B.D. 1967. Polygamy in the reed bunting. Brit. Birds 60:218-219.
- Bell, B.D. and R.J. Hornby. 1969. Polygamy and nest-sharing in the reed bunting. Ibis 111:402-405.
- Bergerud, A.T. and H.E. Butler. 1985. Aggressive and spacing behavior of female blue grouse. Auk 102:313-322.
- Bernstein, I.S. 1981. Dominance: the baby and the bathwater. Behav. Brain Sci. 4:419-457.
- Best, L.B. 1977. Territory quality and mating success in the field sparrow. Condor 79:192-204.
- Bibby, C.J. 1982. Polygyny and breeding ecology of the Cetti's warbler, Cettia cetti. Ibis 124:288-301.

- Birkhead, T.R., K. Clarkson and R. Zann. 1988. Extra-pair copulation and mate guarding in wild zebra finches Taeniopygia guttata. Anim. Behav. 36:1853-1855.
- Bjorklund, M. and B. Westman. 1986. Adaptive advantages of monogamy in the great tit (Parus major): an experimental test of the polygyny threshold model. Anim. Behav. 34:1436-1440.
- Blakley, N.R. 1976. Successive polygyny in upland nesting redwinged blackbirds. Condor 78:129-133.
- Blancher, P.J. and R.J. Robertson. 1985. Site consistency in kingbird breeding performance: implications for site fidelity. J. of Anim. Ecol. 54:1017-1027.
- Bollinger, E.K. and T.A. Gavin. 1989. The effects of site quality on breeding-site fidelity in bobolinks. Auk 106:584-594.
- Borgia, G., S.G. Pruett-Jones. and M.A. Pruett-Jones. 1985. The evolution of bower-building and the assessment of male quality. Z. Tierpsychol. 67:225-236.
- Bradbury, J.W. 1983. Leks and mate choice. In: P. Bateson (ed): Mate Choice. Cambridge: Cambridge Univ. Press, pp. 109-138.
- Brattstrom, B.H. 1974. The evolution of reptilian social behavior. Amer. Zool. 14:35-49.
- Breiehagen, T. and T. Slagsvold. 1988. Male polyterritoriality and female-female aggression in pied flycatchers Ficedula hypoleuca. Anim. Behav. 36:604-605.
- Brewer, R. and K.G. Harrison. 1975. The time of habitat selection by birds. Ibis 117:521-522.
- Brooke, M.L. 1979. Differences in the quality of territories held by wheatears (Oenanthe oenanthe). J. Anim. Ecol. 48:21-32.
- Brown, C.R. and M.B. Brown. 1988. Genetic evidence of multiple parentage in broods of cliff swallows. Behav. Ecol. Sociobiol. 23:379-387.
- Brown, J.L. 1964. The evolution of diversity in avian territorial systems. Wilson Bull. 76:160-169.
- Brown, J.L. 1969. Territorial behavior and population regulation in birds. Wilson Bull. 81:293-329.
- Brown, J.L. and G.H. Orians. 1970. Spacing patterns in mobile animals. Ann. Rev. Ecol. Systematics 1: 239-262.

- Brown, L. and J.F. Downhower. 1983. Constraints on female choice in the mottled sculpin. In: S.K. Wasser (ed): Social behavior of female vertebrates. New York: Academic Press, pp. 39-54.
- Bryant, D.M. 1975. Breeding biology of house martins in relation to aerial insect abundance. *Ibis* 117:180-216.
- Bryant, D.M. 1979. Reproductive costs in the house martin Delichon urbica. *J. Anim. Ecol.* 48:655-675.
- Bull, C.M. 1988. Mate fidelity in an Australian lizard Trachydosaurus rugosus. *Behav. Ecol. Sociobiol.* 23:45-49.
- Carlsson, B.G., B. Hornfeldt and O. Lofgren. 1987. Bigyny in Tengmalm's Owl Aegolius funereus: effect of mating strategy on breeding success. *Ornis Scandinavica* 18:237-243.
- Catchpole, C.K. 1971. Polygamy in reed warblers. *Brit. Birds* 64:232-233.
- Catchpole, C.K. 1972. A comparative study of territory in the reed warbler (Acrocephalus scirpaceus) and sedge warbler (A. schoenobaenus). *J. of Zool.* 166:213-231.
- Catterall, C.P., W.S. Wyatt and L.J. Henderson. 1982. Food resources, territory density and reproductive success of an island silvereye population Zosterops lateralis. *Ibis* 124:405-421.
- Clutton-Brock, T.H. 1988. Reproductive success: Studies of individual variation in contrasting breeding systems. Chicago: University of Chicago Press, pp. 538.
- Clutton-Brock, T.H., D. Green, M. Hiraiwa-Hasegawa and S.D. Albon. 1988. Passing the buck: resource defense, lek breeding and mate choice in fallow deer. *Behav. Ecol. Sociobiol.* 23:281-296.
- Cody, M.L. and C.B.J. Cody. 1972a. Territory size, clutch size, and food in populations of wrens. *Condor* 74:473-477.
- Cody, M.L. and C.B.J. Cody. 1972b. Areal versus lineal territories in the wren, Troglodytes troglodytes. *Condor* 74:477-478.
- Crawford, R.D. 1977. Breeding biology of year-old and older female red-winged and yellow-headed blackbirds. *Wilson Bull.* 89:73-80.
- Curry, R.L. 1988. Group structure, within-group conflict and reproductive tactics in cooperatively breeding Galapagos mockingbirds, Nesomimus parvulus. *Anim. Behav.* 36:1708-1728.
- Davies, N.B. 1985. Cooperation and conflict among dunnocks, Prunella modularis, in a variable mating system. *Anim. Behav.* 33:628-648.

- Davies, N.B. and A. Lundberg. 1984. Food distribution and a variable mating system in the dunnock, Prunella modularis. J. Anim. Ecol. 53:895-912.
- Davies, N.B. and A. Lundberg. 1985. The influence of food on time budgets and timing of breeding of the Dunnock Prunella modularis. Ibis 127:100-110.
- DeLaet, J.F. and A.A. Dhondt. 1989. Weight loss of the female during the first brood as a factor influencing second brood initiation in Great Tits Parus major and Blue Tits P. caeruleus. Ibis 131:281-289.
- Derrickson, K.C. 1989. Bigamy in northern mockingbirds: circumventing female-female aggression. Condor 91:728-732.
- deVries, T. 1975. The breeding biology of the Galapagos hawk. Le Gerfaut 65:29-57.
- Dewar, J. 1920. The law of territory. Brit. Birds 14:89-90.
- Dhondt, A.A. 1987. Reproduction and survival of polygynous and monogamous Blue Tit Parus caeruleus. Ibis 129:327-334.
- Dickinson, T.E. and M.R. Lein. 1987. Territory dynamics and patterns of female recruitment in Red-winged Blackbirds (Agelaius phoeniceus). Can. J. Zool. 65:465-471.
- Dixon, C. 1978. Breeding biology of the savannah sparrow on Kent Island. Auk 95:235-246.
- Dixon, K.L. 1988. Reversal of dominance in a pair of song sparrows. J. Field Ornithol. 58:4-5.
- Dolbeer, R.A. 1976. Reproductive rate and temporal spacing of nesting of red-winged blackbirds in upland habitat. Auk 93:343-355.
- Dow, D.D. 1979. Agonistic and spacing behaviour of the noisy miner Manorina melanocephala, a communally breeding honeyeater. Ibis 121:423-436.
- Downhower, J.F. and K.B. Armitage. 1971. The yellow-bellied marmot and the evolution of polygamy. Am. Nat. 105:355-370.
- Drum, M. 1939. Territorial studies on the eastern goldfinch. Wilson Bull. 51:69-77.
- Duffy, A.M. 1982. Response of brown-headed cowbirds to simulated conspecific intruders. Anim. Behav. 30:1043-1052.
- Dulude, A.-M, G. Baron and R. McNeil. 1987. Role of male and female ring-billed gulls in the care of young and territorial defense. Can. J. Zool. 65:1535-1540.

- Dunbar, R.I.M. and E.P. Dunbar. 1977. Dominance and reproductive success among female gelada baboons. *Nature* 266:351-352.
- Dunn, P.O. and S.J. Hannon. 1989. Evidence for obligate male parental care in black-billed magpies. *Auk* 106:635-644.
- Dyrce, A. 1986. Factors affecting facultative polygyny and breeding results in the great reed warbler. *J. Orn.* 127:447-461.
- Dyrce, A. 1989. Polygyny in the aquatic warbler Acrocephalus paludicola. *Ibis* 131: 298-300.
- Eckert, C.G. and P.J. Weatherhead. 1987. Ideal dominance distributions: a test using red-winged blackbirds (Agelaius phoeniceus). *Behav. Ecol. Sociobiol.* 20:43-52.
- Eliason, B.C. 1986. Female site fidelity and polygyny in the blackpoll warbler (Dendroica striata). *Auk* 103:782-790.
- Emlen, S.T. and L.W. Oring. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science* 197:215-223.
- Emlen, S.T. and P.H. Wrege. 1986. Forced copulations and intra-specific parasitism: two costs of social living in the white-fronted bee-eater. *Ethology* 71:2-29.
- Faaborg, J. 1988. *Ornithology: an ecological approach*. Englewood Cliffs, NJ: Prentice Hall.
- Faaborg, J. and C.B. Patterson. 1981. The characteristics and occurrence of cooperative polyandry. *Ibis* 123:477-484.
- Ficken, M.S. 1962. Agonistic behavior and territory in the American redstart. *Auk* 79:607-632.
- Fitch, M.A. and G.W. Shugart. 1984. Requirements for a mixed reproductive strategy in avian species. *Am. Nat.* 124:116-126.
- Flood, N.J. 1985. Incidences of polygyny and extrapair copulation in the northern oriole. *Auk* 102:410-413.
- Fox, S.F., E. Rose. and R. Myers. 1981. Dominance and the acquisition of superior home ranges in the lizard Uta stansburiana. *Ecology* 62:888-893.
- Franzblau, M.A. and J.P. Collins. 1980. Test of a hypothesis of territory regulation in an insectivorous bird by experimentally increasing prey abundance. *Oecologia* 46:164-170.
- Frederick, P. 1987. Responses of male white ibises to their mate's extra-pair copulations. *Behav. Ecol. Sociobiol.* 21:223-228.

- Freed, L.A. 1986. Territory takeover and sexually selected infanticide in tropical house wrens. *Behav. Ecol. Sociobiol.* 19:197-206.
- Fuller, T.K. 1978. Variable home-range sizes of female gray foxes. *J. Mamm.* 59:446-449.
- Galbraith, D.A., M.W. Chandler and R.J. Brooks. 1987. The fine structure of home ranges of male Chelydra serpentina: are snapping turtles territorial? *Can. J. Zool.* 65:2623-2629.
- Garson, P.J. 1980. Male behaviour and female choice: mate selection in the wren? *Anim. Behav.* 28:491-502.
- Gauthier, G. 1987. The adaptive significance of territorial behaviour in breeding buffleheads: a test of three hypotheses. *Anim. Behav.* 35:348-360.
- Gauthier, G. and J.N.M. Smith. 1987. Territorial behaviour, nest-site availability, and breeding density in buffleheads. *J. Anim. Ecol.* 56:171-184.
- Gauthreaux, S.A. 1978. The ecological significance of behavioral dominance. In: P.P.G. Bateson and P. H. Klopfer (eds): *Perspectives in Ethology*. New York: Plenum Press, pp. 17-54.
- Gavin, T.A. and E.K. Bollinger. 1985. Multiple paternity in a territorial passerine: the bobolink. *Auk* 102:550-555.
- George, T.L. 1987. Behavior of territorial male and female Townsend's solitaires (Myadestes townsendi) in winter. *Am. Mid. Nat.* 118:121-127.
- Gibbons, D.W. 1986. Brood parasitism and cooperative nesting in the moorhen, Gallinula chloropus. *Behav. Ecol. Sociobiol.* 19:221-232.
- Gill, F.B. and L.L. Wolf. 1975. Economics of feeding territoriality in the golden-winged sunbird. *Ecology* 56:333-345.
- Gipps, J.H.W., M.P. Flynn, J. Gurnell and T.D. Healing. 1985. The spring decline in populations of the bank vole, Clethrionomys glareolus, and the role of female density. *J. Anim. Ecol.* 54:351-358.
- Gladstone, D.E. 1979. Promiscuity in monogamous colonial birds. *Am. Nat.* 114:545-557.
- Gosling, L.M. 1987. Scent marking in an antelope territory. *Anim. Behav.* 35:620-622.
- Gowaty, P.A. 1980. The origin of mating system variability and behavioral and demographic correlates of the mating system in eastern bluebirds (Sialia sialis). Unpubl. Ph.D. diss. Clemson University.

- Gowaty, P.A. 1981. An extension of the Orians-Verner-Willson model to account for mating systems besides polygyny. *Am. Nat.* 118:851-859.
- Gowaty, P.A. and A.A. Karlin. 1984. Multiple maternity and paternity in single broods of apparently monogamous eastern bluebirds (*Sialia sialis*). *Behav. Ecol. Sociobiol.* 15:91-95.
- Gowaty, P.A. and S.J. Wagner. 1988. Breeding season aggression of female and male eastern bluebirds (*Sialia sialis*) to models of potential conspecific and interspecific egg dumpers. *Ethology* 78: 238-250.
- Graul, W.D. 1974. Adaptive aspects of the mountain plover social system. *Living Bird* 12:69-74.
- Haland, A. 1983. Home range use and spacing in Mallard *Anas platyrhynchos* broods. *Ornis Scand.* 14:24-35.
- Hannon, S.J. 1984. Factors limiting polygyny in the willow ptarmigan. *Anim. Behav.* 32:153-161.
- Hannon, S.J. and F.C. Zwickel. 1979. Probable non-breeders among female blue grouse. *Condor* 81:78-82.
- Hannon, S.J. and J.N.M. Smith. 1984. Factors influencing age-related reproductive success in the willow ptarmigan. *Auk* 101:848-854.
- Hannon, S.J., L.G. Sopuck and F.C. Zwickel. 1982. Spring movements of female blue grouse: evidence for socially induced delayed breeding in yearlings. *Auk* 99:687-694.
- Harris, M.P. 1970. Territory limiting the size of the breeding population of the oystercatcher (*Haematopus ostralegus*)- a removal experiment. *J. Anim. Ecol.* 39:707-713.
- Harvey, P.H., M.J. Stenning and B. Campbell. 1985. Individual variation in seasonal breeding success of pied flycatchers. *J. Anim. Ecol.* 54: 391-398.
- Harvey, P.H., M.J. Stenning and B. Campbell. 1988. Factors influencing reproductive success in the pied flycatcher. In: T.H. Clutton-Brock (ed): *Reproductive Success: Studies of individual variation in contrasting breeding systems*. Chicago: University of Chicago Press, pp. 189-200.
- Hays, H. 1973. Polyandry in the spotted sandpiper. *Living Bird* 11:43-57.
- Hensley, M.M. and J.B. Cope. 1951. Further data on removal and repopulation of the breeding birds in a spruce-fir forest community. *Auk* 68:483-493.

- Herzog, P.W. and D.A. Boag. 1977. Seasonal changes in aggressive behavior of female spruce grouse. *Can. J. of Zool.* 55:1734-1739.
- Hilden, O. 1965. Habitat selection in birds. *Ann. Zool. Fenn.* 2:53-75.
- Hilden, O. 1975. Breeding system of Temminck's Stint Calidris temminckii. *Ornis Fennica* 52:117-144.
- Hill, G.E. 1986. Severe aggression between female black-headed grosbeaks. *Wilson Bull.* 93:486-488.
- Hinde, R.A. 1956. The biological significance of territories of birds. *Ibis* 98:340-369.
- Hixon, M. 1987. Territory area as a determinant of mating systems. *Amer. Zool.* 27:229-247.
- Hobson, K.A. and S.G. Sealy. 1989. Female-female aggression in polygynously nesting yellow warblers. *Wilson Bull.* 10:84-86.
- Holcomb, L.C. 1974. The question of possible surplus females in breeding red-winged blackbirds. *Wilson Bull.* 86:177-179.
- Holmes, R.T. 1970. Differences in population density, territoriality, and food supply of dunlin on arctic and subarctic tundra. In: A. Watson (ed): *Animal populations in relation to food resources*. Oxford: Blackwell Scientific Publication, pp. 303-320.
- Holmes, R.T. 1971. Density, habitat and the mating system of the western sandpiper (Calidris mauri). *Oecologia* 7:191-208.
- Holmes, W.G. 1984. The ecological basis of monogamy in Alaskan hoary marmots. In: J.O. Murie and G. R. Michener (eds): *The biology of ground-dwelling squirrels*. Lincoln, NE: Univ. of Nebraska, p. 459.
- Horne, E.A. and R.G. Jaeger. 1988. Territorial pheromones of female red-backed salamanders. *Ethology* 78:143-152.
- Howard, E. 1920. *Territory in bird life*. London: John Murray, pp. 224.
- Howard, R.D. 1978. The evolution of mating strategies in bullfrogs, Rana catesbeiana. *Evolution* 32:850-871.
- Hrdy, S.B. and G.C. Williams. 1983. Behavioral biology and the double standard. In: S.K. Wasser (ed): *Social Behavior of Female Vertebrates*. New York: Academic Press, pp. 3-17.
- Huey, R.B., E.R. Pianka and T.W. Schoener. 1983. *Lizard Ecology - studies of a model organism*. Cambridge, Mass.: Harvard University Press, pp. 501.

- Hunter, L.A. 1987. Acquisition of territories by floaters in cooperatively breeding purple gallinules. *Anim. Behav.* 35:402-410.
- Hurly, T.A. and R.J. Robertson. 1984. Aggressive and territorial behavior in female red-winged blackbirds. *Can. J. Zool.* 62:148-153.
- Hurley, T.A. and R.J. Robertson. 1985. Do female red-winged blackbirds limit harem size? I. A removal experiment. *Auk* 102:205-209.
- Jaeger, R.G. and W.F. Gergits. 1979. Intra- and interspecific communication in salamanders through chemical signals on the substrate. *Anim. Behav.* 27: 150-156.
- Jaeger, R.G., J.M. Goy, M. Tarver and C.E. Marquez. 1986. Salamander territoriality: pheromonal markers as advertisement by males. *Anim. Behav.* 34:860-864.
- Jaeger, R.G., D. Kalvarsky and N. Shimizu. 1982. Territorial behavior of the red-backed salamander: expulsion of intruders. *Anim. Behav.* 30:490-496.
- Jarman, P.J. 1974. The social organization of antelope in relation to their ecology. *Anim. Behav.* 48:215-265.
- Jenni, D.A. and G. Collier. 1972. Polyandry in the American jacana (Jacana spinosa). *Auk* 89:743-765.
- Johnson, C.N. 1986. Philopatry, reproductive success of females, and maternal investment in the red-necked wallaby. *Behav. Ecol. Sociobiol.* 19:143-150.
- Johnson, E.D.H. 1961. The pair relationship and polygyny in the Stonechat. *Brit. Birds* 54:213-225.
- Jones, G. 1986. Sexual chases in sand martins (Riparia riparia): cues for males to increase their reproductive success. *Behav. Ecol. Sociobiol.* 19:179-185.
- Jonsson, P.E. 1987. Sexual size dimorphism and disassortative mating in the Dunlin Calidris alpina schinzii in southern Sweden. *Ornis Scand.* 18:257-264.
- Joste, N., J.D. Ligon and P.B. Stacey. 1985. Shared paternity in the acorn woodpecker (Melanerpes formicivorus). *Behav. Ecol. Sociobiol.* 17:39-41.
- Kaufmann, J.H. 1983. On the definitions and functions of dominance and territoriality. *Biol. Rev.* 58:1-20.

- Kawata, M. 1987. Pregnancy failure and suppression by female-female interactions in enclosed populations of the red-backed vole, Clethrionomys rufocanus bedfordiae. Behav. Ecol. Sociobiol. 20: 89-97.
- Kellner, C.J. and G. Ritchison. 1988. Possible functions of singing by female Acadian flycatchers (Empidonax virescens). J. Field Ornithol. 58:55-59.
- Kenyon, R.F. 1972. Polygyny among superb lyrebirds in Sherbrooke Forest Park, Kallista, Victoria. Emu 72:70-76.
- Kikkawa, J. 1980. Winter survival in relation to dominance classes among silvereyes Zosterops lateralis chlorocephala of Heron Island, Great Barrier Reef. Ibis 122:437-446.
- Kleiman, D.G. 1977. Monogamy in mammals. Quart. Rev. Biol. 52:39-69.
- Kleiman, D.G. and J.F. Eisenberg. 1973. Comparisons of canid and felid social systems from an evolutionary perspective. Anim. Behav. 21: 637-659.
- Kleiman, D.G. and J.R. Malcolm. 1981. The evolution of male parental investment in mammals. In: D.J. Gubernick and P. H. Klopfer (eds): Parental Care in Mammals. New York: Plenum Press, pp. 347-387.
- Knapton, R.W. and J.R. Krebs. 1974. Settlement patterns, territory size, and breeding density in the song sparrow (Melospiza melodia). Can. J. Zool. 52:1413-1420.
- Krebs, J.R. 1982. Territorial defense in the great tit (Parus major): Do residents always win? Behav. Ecol. Sociobiol. 11:185-194.
- Krebs, J.R., M. Avery and R.J. Cowie. 1981. Effect of removal of mate on the singing behaviour of great tits. Anim. Behav. 29:635-637.
- Lack, D. 1935. Territory and polygamy in a Bishop-bird, Euplectes hordeacea hordeacea. Ibis 5:817-836.
- Lack, D. 1944. Early references to territory in bird life. Condor 46: 108-111.
- Lack, D. 1968. Ecological adaptations for breeding in birds. London: Methuen & Co, Ltd.
- LaPointe, G. and J. Bedard. 1984. Seasonal and individual variability of behavior rates in male savannah sparrows. Biol. Behav. 9:343-356.
- LaPointe, G. and J. Bedard. 1986. Savannah sparrow, Passerculus sandwichensis, reproductive success. Can. Field Nat. 100:264-267.

- LaPrade, H.R. and H.B. Graves. 1982. Polygyny and female-female aggression in red-winged blackbirds (Agelaius phoeniceus). *Am. Nat.* 120:135-138.
- Lawn, M.R. 1982. Pairing systems and site tenacity of the willow warbler Phylloscopus trochilus in southern England. *Ornis Scand.* 13:193-199.
- LeBoeuf, B.J. 1974. Male-male competition and reproductive success in elephant seals. *Amer. Zool.* 14:163-176.
- Lenington, S. 1980. Female choice and polygyny in red-winged blackbirds. *Anim. Behav.* 28:347-361.
- Leonard, M.L. and J. Picman. 1987a. Nesting mortality and habitat selection by marsh wrens. *Auk* 104:491-495.
- Leonard, M.L. and J. Picman. 1987b. Female settlement in marsh wrens: is it affected by other females? *Behav. Ecol. Sociobiol.* 21:135-140.
- Lightbody, J.P. and P.J. Weatherhead. 1987. Interactions among females in polygynous yellow-headed blackbirds. *Behav. Ecol. Sociobiol.* 21:23-30.
- Lumpkin, S. 1981. Avoidance of cuckoldry in birds: the role of the female. *Anim. Behav.* 29:303-305.
- Lyon, B.E, R.D. Montgomerie and L.D. Hamilton. 1987. Male parental care and monogamy in snow buntings. *Behav. Ecol. Sociobiol.* 20: 377-382.
- MacDonald, D.W. 1983. The ecology of carnivore social behaviour. *Nature* 301:379-384.
- Manuwal, D.A. 1974. Effects of territoriality on breeding in a population of Cassin's auklet. *Ecology* 55:1399-1406.
- Manzur, M.I. and E.R. Fuentes. 1979. Polygyny and agonistic behavior in the tree-dwelling lizard Liolaemus tenuis (Iguanidae). *Behav. Ecol. Sociobiol.* 6:23-28.
- Marler, P. 1971. On aggression in birds. In: *Topics in the study of life: the bio source book*. New York: Harper and Row, pp. 343-350.
- Martin, S.G. 1974. Adaptations for polygynous breeding in the bobolink, Dolichonyx oryzivorus. *Am. Zool.* 14:109-119.
- Marzluff, J.M. and R.P. Balda. 1988. The advantages of, and constraints forcing, mate fidelity in Pinyon Jays. *Auk* 105:286-295.

- Matthysen, E. 1986. Some observations on sex-specific territoriality in the nuthatch. *Ardea* 74: 177-183.
- Matthysen, E. 1987. Territory establishment of juvenile nuthatches after fledging. *Ardea* 75:53-57.
- Maxson, S.J. 1978. Spring home range and habitat use by female ruffed grouse. *J. Wildl. Manage.* 42:61-71.
- Mayfield, H. 1960. The Kirtland's warbler. *Bull. Cranbrook Inst. Sci.*, pp. 1-242.
- McLaren, I. 1972. Polygyny as the adaptive function of breeding territory in birds. *Transactions of the Connecticut Academy of Arts and Sciences* 44:191-210.
- McLean, I.G. 1984. Spacing behavior and aggression in female ground squirrels. In: J.O. Murie and G. R. Michener (eds): *The biology of ground-dwelling squirrels*. Lincoln, NE: Univ. of Nebraska, p. 459.
- Meunier, M. and J. Bedard. 1984. Nestling foods of the savannah sparrow. *Can. J. Zool.* 62:23-27.
- Middleton, A.L.A. 1988. Polyandry in the mating system of the American Goldfinch. *Can. J. Zool.* 66:296-299.
- Mikkonen, A.V. 1985. Establishment of breeding territory by the chaffinch, *Fringilla coelebs*, and the brambling, *F. montifringilla*, in northern Finland. *Ann. Zool. Fennici* 22:137-156.
- Miller, G.R., A. Watson and D. Jenkins. 1970. Responses of red grouse populations to experimental improvement of their food. In: A. Watson (ed): *Animal populations in relation to their food resources*. Oxford: Blackwell Scientific Publication, pp. 323-335.
- Mitani, J.C. 1987. Territoriality and monogamy among agile gibbons (*Hylobates agilis*). *Behav. Ecol. Sociobiol.* 20:265-269.
- Mock, D.W. 1985. An introduction to the neglected mating system. In: P.A. Gowaty and D. W. Mock (eds): *Avian Monogamy*. Washington, DC: American Ornithologists' Union, pp. 1-10.
- Morse, D.H. 1976. Hostile encounters among spruce-woods warblers (*Dendroica: Parulidae*). *Anim. Behav.* 24:764-771.
- Morton, E.S., J.F. Lynch, K. Young and P. Mehlhop. 1987. Do male hooded warblers exclude females from non-breeding territories in tropical forest? *Auk* 104:133-135.

- Muldal, A.M, J.D. Moffatt and R.J. Robertson. 1986. Parental care of nestlings by male red-winged blackbirds. *Behav. Ecol. Sociobiol.* 19:105-114.
- Murray, B.G., Jr. 1985. The influence of demography on the evolution of monogamy. In: P.A. Gowaty and D. W. Mock (eds): *Avian Monogamy*. Washington,DC: American Ornithologists' Union, pp. 100-107.
- Myers, J.P, P.G. Connors and F.A. Pitelka. 1979. Territory size in wintering sanderlings: the effects of prey abundance and intruder density. *Auk* 96:551-561.
- Newton, I. 1988. Age and reproduction in the sparrowhawk. In: T.H. Clutton-Brock (ed): *Reproductive success: Studies of individual variation in contrasting breeding systems*. Chicago: University of Chicago Press, pp. 201-219.
- Newton, I, M. Marquiss, D.N. Weir and D. Moss. 1977. Spacing of sparrowhawk nesting territories. *J. Anim. Ecol.* 46:425-441.
- Nice, M.M. 1937. Studies in the life history of the song sparrow I. *Transactions of the Linnaean Society of New York* 4:1-247.
- Nice, M.M. 1943. Studies in the life history of the song sparrow II. *Transactions of the Linnaean Society of New York* 6.
- Nilsson, L. 1983. Laying of replacement clutches in the willow warbler Phylloscopus trochilus in Lapland, Sweden. *Ornis Scand.* 14:48-50.
- Noble, G.K. 1939. The role of dominance in the social life of birds. *Auk* 56:263-273.
- Nolan, V., Jr. 1978. The ecology and behavior of the prairie warbler Dendroica discolor. Ornithological monograph 26, Am. Ornithologists Union, pp. 595.
- Odum, E.P. 1945. The concept of the biome as applied to the distribution of North American birds. *Wilson Bull.* 57:191.
- Odum, E.P. and E.J. Kuenzler. 1955. Measurement of territory and home range size in birds. *Auk* 72:128-137.
- Orians, G.H. 1969. On the evolution of mating systems in birds and mammals. *Am. Nat.* 103:589-603.
- Oring, L.W. 1982. Avian Mating Systems. In: D.S. Farner, J. R. King and K.C. Parkes (eds): *Avian Biology*. New York: Academic Press, pp. 1-92.
- Oring, L.W. and M.L. Knudson. 1973. Monogamy and polyandry in the spotted sandpiper. *Living Bird* 11:59-73.

- Osborne, D.R. 1982. Replacement nesting and polyandry in the wattled jacana. *Wilson Bull.* 94:206-208.
- Payne, R.B. 1983. Bird songs, sexual selection, and female mating strategies. In: S.K. Wasser (ed): *Social behavior of female vertebrates*. New York: Academic Press, pp. 55-90.
- Picman, J. 1977. Intraspecific nest destruction in the long-billed marsh wren, Telmatodytes palustris palustris. *Can. J. Zool.* 55:1997-2003.
- Picman, J. 1987. Territory establishment, size, and tenacity by male red-winged blackbirds. *Auk* 104:405-412.
- Picozzi, N. 1984a. Sex ratio, survival and territorial behaviour of polygynous hen harriers Circus c. cyaneus. *Ibis* 126:356-365.
- Picozzi, N. 1984b. Breeding biology of polygynous hen harriers Circus c. cyaneus in Orkney. *Ornis Scand.* 15:1-10.
- Pierotti, R. 1981. Male and female parental roles in the western gull under different environmental conditions. *Auk* 98:532-542.
- Pitelka, F.A. 1959. Numbers, breeding schedule and territoriality in pectoral sandpipers of northern Alaska. *Condor* 61:233-263.
- Pleszczynska, W. 1978. Microgeographic prediction of polygyny in the lark bunting. *Science* 201:935-936.
- Pleszczynska, W. and R.I.C. Hansell. 1980. Polygyny and decision theory: testing of a model in lark buntings (Calamospiza melanocorys). *Am. Nat.* 116:821-830.
- Post, W. 1974. Functional analysis of space-related behavior in the seaside sparrow. *Ecology* 55:564-575.
- Post, W. and J.S. Greenlaw. 1975. Seaside sparrow displays: their function in social organization and habitat. *Auk* 92:461-492.
- Post, W. and J.S. Greenlaw. 1982. Comparative costs of promiscuity and monogamy: a test of reproductive effort theory. *Behav. Ecol. Sociobiol.* 10:101-107.
- Potter, P. 1972. Territorial behavior in savannah sparrows in southeastern Michigan. *Wilson Bull.* 84:48-59.
- Powell, R.A. 1979. Mustelid spacing patterns: variations on a theme by *Mustela*. *Z. Tierpsychol.* 50:153-165.
- Prescott, D.R.C. 1986. Polygyny in the Willow Flycatcher. *Condor* 88:385-386.

- Price, F.E. and C.E. Bock. 1973. Polygyny in the dipper. *Condor* 75: 457-459.
- Pruett-Jones, S.G. and M.A. Pruet-Jones. 1988. A promiscuous mating system in the Blue Bird of Paradise Paradisaea rudolphi. *Ibis* 130: 373-377.
- Quay, T.L. 1958. The foods and feeding habits of the savannah sparrow in winter. *Elisha Mitchell Scientific Society* 74:1-6.
- Quinney, T.E, D.J.T. Hussell and C.D. Ankney. 1986. Sources of variation in growth of tree swallows. *Auk* 103:389-400.
- Radabaugh, B.E. 1972. Polygamy in the Kirtland's Warbler. *Jack-Pine Warbler* 50:48-52.
- Ralls, K. 1977. Sexual dimorphism in mammals: avian models and unanswered questions. *Am. Nat.* 111:917-938.
- Ramsay, M.A. and I. Stirling. 1986. On the mating system of polar bears. *Can. J. Zool.* 64:2142-2151.
- Reid, M.L. and S.G. Sealy. 1986. Behavior of a polygynous yearling yellow warbler. *Wilson Bull.* 98:315-317.
- Reid, M.L. 1987. Costliness and reliability in the singing vigor of Ipswich sparrows. *Anim. Behav.* 35:1735-1743.
- Ricklefs, R.E. 1969. An analysis of nesting mortality in birds. Washington, D.C.: Smithsonian Institution Press, pp. 48.
- Ricklefs, R.E. 1977. On the evolution of reproductive strategies in birds: reproductive effort. *Am. Nat.* 111:453-478.
- Ricklefs, R.E. 1984. The optimization of growth rate in altricial birds. *Ecology* 65:1602-1616.
- Ridpath, M.G. and M.G. Brooker. 1987. Sites and spacing of nests as determinants of wedge-tailed eagle breeding in arid western Australia. *Emu* 87:143-149.
- Robins, J.D. 1971. Differential niche utilization in a grassland sparrow. *Ecology* 52:1065-1070.
- Roell, A. 1979. Bigamy in jackdaws. *Ardea* 67:123-129.
- Roskaff, E. 1983. Male promiscuity and female adultery by the Rook Corvus frugilegus. *Ornis Scan.* 14:175-179.
- Ross, H.A. 1980. The reproductive rates of yearling and older Ipswich sparrows, Passerculus sandwichensis princeps. *Can. J. of Zool.* 58: 1557-1563.

- Ross, H.A. and I.A. McLaren. 1981. Lack of differential survival among young Ipswich sparrows. *Auk* 98:495-502.
- Saether, B-E. and T. Fonstad. 1981. A removal experiment showing unmated females in a breeding population of chaffinches. *Anim. Behav.* 29:637-639.
- Salomonson, M.G. and R.P. Balda. 1977. Winter territoriality of Townsend's Solitaires (Myadestes townsendi) in a pinon-juniper-ponderosa ecotone. *Condor* 79:148-161.
- Savard, J-P.L. 1982. Intra and interspecific competition between Barrow's goldeneye (Bucephala islandica) and bufflehead (Bucephala albeola). *Can. J. Zool.* 60:3439-3446.
- Schoener, T.W. 1971. Theory of feeding strategies. *Ann. Rev. Ecol. Syst.* 2:369-404.
- Schoener, T.W. 1983. Simple models of optimal feeding-territory size: a reconciliation. *Am. Nat.* 121:608-629.
- Searcy, W.A. 1986. Are female red-winged blackbirds territorial? *Anim. Behav.* 34:1381-1391.
- Seastedt, T.R. and S.F. MacLean. 1979. Territory size and composition in relation to resource abundance in lapland longspurs breeding in arctic Alaska. *Auk* 96:131-142.
- Seastedt, T.R. and S.F. MacLean. 1980. Polygyny and nest spacing in lapland longspurs: a hypothesis. *Anim. Behav.* 28:313-314.
- Sedgwick, J.A. and F.L. Knopf. 1989. Regionwide polygyny in willow flycatchers. *Condor* 91:473-475.
- Selander, R.K. 1972. Sexual selection and dimorphism in birds. In: B. Campbell (ed): *Sexual selection and the Descent of Man, 1871-1971*. Chicago: Aldine Pub. Co., pp. 180-230.
- Simon, C.A. 1975. The influence of food abundance on territory size in the iguanid lizard Sceloporus jarrovi. *Ecology* 56:993-998.
- Slagsvold, T, J.T. Lifjeld, G. Stenmark and T. Breiehagen. 1988. On the cost of searching for a mate in female pied flycatchers Ficedula hypoleuca. *Anim. Behav.* 36:433-442.
- Smith, J.L.D, C. McDougal and D. Miquelle. 1989. Scent marking in free-ranging tigers, Panthera tigris. *Anim. Behav.* 37:1-10.
- Smith, J.N.M. 1988. Determinants of lifetime reproductive success in the song sparrow. In: T.H. Clutton-Brock (ed): *Reproductive Success*. Chicago: Univ. of Chicago Press, pp. 154-172.

- Smith, S.M. 1978. The "underworld" in a territorial sparrow: adaptive strategy for floaters. *Am. Nat.* 112:571-582.
- Smith, T.M. and H.H. Shugart. 1987. Territory size variation in the ovenbird: the role of habitat structure. *Ecology* 68:695-704.
- Snow, B.K. 1973. Social organization of the hairy hermit Glaucis hirsuta. *Ardea* 61:94-105.
- Snow, B.K. 1974. Lek behaviour and breeding of Guy's hermit hummingbird Phaethornis guy. *Ibis* 116:278-297.
- Sokal, R.R. and F.J. Rohlf. 1981. *Biometry*. New York: W.H. Freeman and Co.
- Sonerud, G.A., J.O. Nybo, P.E. Fjeld and C. Knoff. 1987. A case of bigyny in the Hawk Owl Surnia ulula: spacing of nests and allocation of male feeding effort. *Ornis Fenn.* 64:144-148.
- Spence, J.R. and R.S. Wilcox. 1986. The mating system of two hybridizing species of water striders (Gerridae). *Behav. Ecol. Sociobiol.* 19:87-95.
- Stamps, J.A. 1983. Sexual selection, sexual dimorphism and territoriality. In: R.B. Huey, E. R. Pianka and T. W. Schoener (eds): *Lizard Ecology - studies of a model organism*. Cambridge, Mass.: Harvard University Press, pp. 169-204.
- Stamps, J.A. 1988. Conspecific attraction and aggregation in territorial species. *Am. Nat.* 131:329-347.
- Stamps, J.A. and M. Buechner. 1985. The territorial defense hypothesis and the ecology of insular vertebrates. *Quart. Rev. Biol.* 60:155-181.
- Stenger, J. 1958. Food habits and available food of ovenbirds in relation to territory size. *Auk* 75:335-346.
- Stenger, J. and J.B. Falls. 1959. The utilized territory of the ovenbird. *Wilson Bull.* 71:125-140.
- Stewart, R.E. and J.W. Aldrich. 1951. Removal and repopulation of breeding birds in a spruce-fir forest community. *Auk* 68:471-482.
- Stobo, W.T. and I.A. McLaren. 1975. *The Ipswich Sparrow*. Halifax, Nova Scotia: Nova Scotian Institute of Science, pp. 102.
- Stutchbury, B.J. and R.J. Robertson. 1985. Floating population of female tree swallows. *Auk* 102:651-654.
- Stutchbury, B.J. and R.J. Robertson. 1987. Behavioral tactics of subadult female floaters in the tree swallow. *Behav. Ecol. Sociobiol.* 20: 413-419.

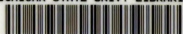
- Teather, K.L. and R.J. Robertson. 1985. Female spacing patterns in brown-headed cowbirds. *Can. J. Zool.* 63:218-222.
- Temrin, H. and S. Jakobsson. 1988. Female reproductive success and nest predation in polyterritorial wood warblers (Phylloscopus sibilatrix). *Behav. Ecol. Sociobiol.* 23:225-231.
- Thompson, W.L. 1960. Agonistic behavior in the house finch Part II: Factors in aggressiveness and sociality. *Condor* 62:378-402.
- Thornhill, R. and J. Alcock. 1983. *The Evolution of Insect Mating Systems*. Cambridge, MA: Harvard University Press, pp. 547.
- Tinbergen, N. 1936. The function of sexual fighting in birds; and the problem of the origin of "territory". *Bird-Banding* 7:1-8.
- Tinbergen, N. 1939. The behavior of the snow bunting in spring. *Transactions of the Linnaean Society of New York* 5:91.
- Tjernberg, M. 1985. Spacing of golden eagle Aquila chrysaetos nests in relation to nest site and food availability. *Ibis* 127:250-255.
- Toft, G.O. 1984. Conflict of interests between the sexes, and possible mate fidelity in polygynously mated Lapwings Vanellus vanellus. *Ornis Fenn.* 61:124.
- Trivers, R.L. 1972. Parental investment and sexual selection. In: B. Campbell (ed): *Sexual selection and the descent of man, 1871-1971*. Chicago: Aldine Publishing Co., pp. 136-179.
- Ueda, K. 1986. A polygamous social system of the fan-tailed warbler Cisticola juncidis. *Ethology* 73:43-55.
- Vehrencamp, S.L. and J.W. Bradbury. 1984. Mating systems and ecology. In: J.R. Krebs and N. B. Davies (eds): *Behavioural Ecology: An evolutionary approach*. Sunderland, MA: Sinauer, pp. 251-278.
- Verner, J. 1964. Evolution of polygamy in the long-billed marsh wren. *Evolution* 18:252-261.
- Verner, J. 1977. On the adaptive significance of territoriality. *Am. Nat.* 111:769-775.
- Verner, J. and M.F. Willson. 1966. The influence of habitats on mating systems of North American passerine birds. *Ecology* 47:143-147.
- Waage, J.K. 1987. Choice and utilization of oviposition sites by female Calopteryx maculata (Odonata: Calopterygidae). *Behav. Ecol. Sociobiol.* 20:439-446.
- Walkinshaw, L.H. 1966. Summer biology of Traill's Flycatcher. *Wilson Bull.* 78:31-46.

- Warriner, J.S, J.C. Warriner, G.W. Page and L.E. Stenzel. 1986. Mating system and reproductive success of a small population of polygamous snowy plovers. *Wilson Bull.* 98:15-37.
- Waser, P.M. and R.H. Wiley. 1979. Mechanisms and Evolution of Spacing in Animals. In: P. Marler and J. G. Vandenberg (eds): *Handbook of Behavioral Neurobiology: Social Behavior and Communication*. New York: Plenum Press, pp. 159-223.
- Wasser, S.K. and M.L. Waterhouse. 1983. The establishment and maintenance of sex biases. In: S.K. Wasser (ed): *Social Behavior of Female Vertebrates*. New York: Academic Press, pp. 19-35.
- Wasserman, F.E. 1977. Mate attraction function of song in the white-throated sparrow. *Condor* 79:125-127.
- Weatherhead, P.J. 1979a. Ecological correlates of monogamy in tundra-breeding savannah sparrows. *Auk* 96:391-401.
- Weatherhead, P.J. 1979b. Do savannah sparrows commit the Concorde Fallacy? *Behav. Ecol. Sociobiol.* 5:373-381.
- Weatherhead, P.J. and R.J. Robertson. 1978. Intraspecific nest parasitism in the savannah sparrow. *Auk* 95:744-745.
- Weatherhead, P.J. and R.J. Robertson. 1980a. Altruism in savannah sparrows? *Behav. Ecol. Sociobiol.* 6:185-186.
- Weatherhead, P.J. and R.J. Robertson. 1980b. Sexual recognition and anticuckoldry behaviour in savannah sparrows. *Can. J. Zool.* 58: 991-996.
- Webster's New Collegiate Dictionary. 1977. Springfield, MA., G. and C. Merriam Company.
- Weeden, J.S. 1965. Territorial behavior of the tree sparrow. *Condor* 67:193-209.
- Wegge, P. and J. Rolstad. 1986. Size and spacing of capercaillie leks in relation to social behavior and habitat. *Behav. Ecol. Sociobiol.* 19:401-408.
- Welsh, D.A. 1975. Savannah sparrow breeding and territoriality on a Nova Scotia dune beach. *Auk* 92:235-251.
- Welter, W.A. 1935. The natural history of the long-billed marsh wren. *Wilson Bull.* 47:3-34.
- Welty, J.C. 1975. *The Life of Birds*. Philadelphia: W. B. Saunders Co. pp. 623

- Westneat, D.F. 1987. Extra-pair copulations in a predominately monogamous bird: observations of behaviour. *Anim. Behav.* 35:865-876.
- Westneat, D.F. 1987. Extra-pair fertilizations in a predominately monogamous bird: genetic evidence. *Anim. Behav.* 35:877-886.
- Westneat, D. 1988. The relationships among polygyny, male parental care, and female breeding success in the indigo bunting. *Auk* 105: 372-374.
- Wickler, W. and U. Seibt. 1981. Monogamy in crustacea and man. *Z. Tierpsychol.* 57:215-234.
- Wickler, W. and U. Seibt. 1983. Monogamy: an ambiguous concept. In: P. Bateson (ed): *Mate Choice*. Cambridge: Cambridge Univ. Press, pp. 33-50.
- Wiens, J.A. 1969. An approach to the study of ecological relationships among grassland birds. *Ornithological monograph* 8: American Ornithologists' Union, pp. 93.
- Wiens, J.A. 1973. Interterritorial habitat variations in grasshopper and savannah sparrows. *Ecology* 54:878-884.
- Wiley, R.H. 1974. Evolution of social organization and life-history patterns among grouse. *Quart. Review Biol.* 49:201-227.
- Williams, G.C. 1966. Natural selection, the costs of reproduction and a refinement of Lack's principle. *Am. Nat.* 100:687-692.
- Williams, J. 1987. Field metabolism and food consumption of savannah sparrows during the breeding season. *Auk* 104:277-289.
- Williams, J.B. and K.A. Nagy. 1985. Daily energy expenditure by female savannah sparrows feeding nestlings. *Auk* 102:187-190.
- Williams, L. 1952. Breeding behavior of the Brewer Blackbird. *Condor* 54:3-47.
- Willson, M.F. 1966. Polygamy among swamp sparrows. *Auk* 83:666.
- Wilson, E.O. 1975. *Sociobiology: The new synthesis*. Cambridge, Mass.: Harvard University Press, pp. 697.
- Wittenberger, J.F. 1976. The ecological factors selecting for polygyny in altricial birds. *Am. Nat.* 110:779-799.
- Wittenberger, J.F. 1979. The evolution of mating systems in birds and mammals. In: P. Marler and J. G. Vandenberg (eds): *Handbook of behavioral neurobiology*, vol 3, social behavior and communication. New York: Plenum Press.

- Wittenberger, J.F. and R.L. Tilson. 1980. The evolution of monogamy: hypotheses and evidence. *Ann. Rev. Ecol. Syst.* 11:197-232.
- Wolf, L.L. 1969. Female territoriality in a tropical hummingbird. *Auk* 86:490-504.
- Wolfson, A. 1952. The cloacal protuberance - a means for determining breeding condition in live male passerines. *Bird-Banding* 23:159-165.
- Wootton, J.T, E.K. Bollinger and C.J. Hibbard. 1986. Mating systems in homogeneous habitats: the effects of female uncertainty, knowledge costs, and random settlement. *Am. Nat.* 128:499-512.
- Wrangham, R.W. 1980. Female choice of least costly males; a possible factor in the evolution of leks. *Z. Tierpsychol.* 54:357-367.
- Wrangham, R.W. and D.I. Rubenstein. 1986. Social evolution in birds and mammals. In: D.I. Rubenstein and R. W. Wrangham (eds): *Ecological aspects of social evolution*. Princeton: Princeton University Press, pp. 452-470.
- Wunderle, J.M. 1984. Mate switching and a seasonal increase in polygyny in the bananaquit. *Behaviour* 88:123-144.
- Yasukawa, K. and W.A. Searcy. 1982. Aggression in female red-winged blackbirds: a strategy to ensure male parental investment. *Behav. Ecol. Sociobiol.* 11:13-17.
- Yeaton, R.I. 1972. Social behavior and social organization in Richardson's ground squirrel (Spermophilus richardsonii) in Saskatchewan. *J. Mamm.* 53:139-147.
- Yokel, D.A. 1986. Monogamy and brood parasitism: an unlikely pair. *Anim. Behav.* 34:1348-1358.
- Young, C.M. 1970. Territoriality in the common shelduck Tadorna tadorna. *Ibis* 112:330-335.
- Young, H. 1951. Territorial behavior in the eastern robin. *Proc. Linnaean Society New York* 62:1-37.
- Zach, R. and B.G. Falls. 1975. Response of the ovenbird (Aves: Parulidae) to an outbreak of the spruce budworm. *Can. J. Zool.* 53: 1669-1672.
- Zar, J.H. 1984. *Biostatistical Analysis*. Englewood Cliffs, NJ: Prentice-Hall, Inc.
- Zimmerman, J.L. 1966. Polygyny in the dickcissel. *Auk* 83:534-546.

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