SOME ASPECTS OF DOMINANCE BEHAVIOR IN THE SONG SPARROW,

(<u>MELOSPIZA MELODIA</u>)

by

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ABSTRACT

I studied the effect of behavioral dominance on survival and recruitment in the song sparrow (Melospiza melodia). The aims of this study were: 1) to determine if superior dominance status allows high survival and priority of access to breeding territory; 2) to measure the influence of phenotypic characters on dominance status; 3) to test the hypothesis that familiarity with a site is a prerequisite to achieving dominant status.

Dominance was estimated by observing the agonistic encounters of young sparrows at feeders, and this estimate was correlated with the subsequent survival and settlement of yearlings. Correlations were also sought between dominance and several characteristics of individuals. To study site attachment, I temporarily confined 24 early-hatched birds in two groups. This allowed them experience in agonistic encounters, but prevented them from gaining site attachments until all young birds had become independent. The dominance of these captive birds was estimated after their release and compared to that of control birds.

In both sexes, higher proportions of dominants survived and settled than subordinates in each year of study. Only age and sex were consistently correlated with dominance; young hatched early were dominant to those hatched later, and males were more dominant than females. Overall, age accounted for 59% of the

variation in dominance. Captive males and females were as dominant as control young of equal age, and were dominant to birds hatched later.

These results support the hypotheses that dominant status in song sparrows allows high survival and priority of access to a breeding territory. Natural selection should favor parents that raise many early offspring. Familiarity with a local area was not a prerequisite to achieving dominant status. The assumption that large size is advantageous in agonistic encounters was not supported by this study, and a review of the literature suggests that many studies that support this assumption are based on inadequate analyses.

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$SIGNOFF

GENERAL INTRODUCTION

Dominance behavior is prevalent among social vertebrates as diverse as fish and primates, and high dominance status often affects an individual's access to resources crucial to survival and reproduction (Wilson 1975). However, little is known about the qualities of individuals that determine dominance status (Wilson 1975). This is because researchers have generally concentrated their effort on only a small portion of the life history of a species, and have had little information about the prior histories or the fates of the study subjects.

The ideal species for a study of behavioral dominance is one that can be marked for individual identification, is easily observed, and is relatively short-lived. Song sparrows (Melospiza melodia) are such a species, and the population on Mandarte Island, B.C., Canada, is resident, and individuals can be color-marked as nestlings soon after they hatch. Yearling song sparrows roam in lose flocks before settling on territories in late fall or early spring, and some aspects dominance behavior have been investigated within these flocks (Knapton 1973, Smith et al. 1980). Thus, the Mandarte song sparrow population provided me with an excellent opportunity to investigate dominance behavior in detail.

This thesis contains two chapters and an appendix. In the first chapter, I explore the advantages of dominant status among

yearlings, and assess the influence of several factors on dominance such as age, sex, morphology, site familiarity, and nestling size and condition.

Chapter Two deals with one often-stated determinant of dominance, body size. The theory of sexual selection assumes that large size is advantageous in agonistic encounters to explain sexual size dimorphism in vertebrates (Selander 1972, Payne 1984). I review the evidence with regard to this assumption from bird studies, and provide explicit tests with data from the song sparrow. In the Appendix, I describe a method to analyze win/loss data using standard statistical procedures that is more accurate than methods previously used by behavioral ecologists.

CHAPTER ONE: CORRELATES AND CONSEQUENCES OF BEHAVIORAL DOMINANCE IN WILD SONG SPARROWS

INTRODUCTION

Characters that lead to high survival and reproductive success are favored by natural selection. Dominant status is typically associated with superior survival and reproductive success among polygynous vertebrates (LeBoeuf and Peterson 1969, Wiley 1973, Hrdy 1977, Clutton-Brock et al. 1982), and similar correlations have been documented for monogamous birds (Fretwell 1969, Knapton and Krebs 1974, Smith 1978, Kikkawa 1981). Since dominant status confers such advantages, an understanding of the determinants of dominance should provide insight into the operation of natural selection on individuals.

Dominance behavior can clearly influence the reproductive success of individuals yet, few studies have investigated the causes and consequences of dominant and subordinate status in detail within one species. This is because it is difficult to follow large numbers of animals from birth to successful recruitment. Studies of dominance in birds have been largely restricted to winter flocks which contained individuals of mixed sex and age (e.g. Sabine 1959, Fretwell 1969, Glase 1973, Ketterson 1979) or to the laboratory (e.g. Collias 1943, Baker and Fox 1978, Searcy 1979a). In only one bird study have the prior histories and the fates of the individuals involved been

known (Kikkawa 1981). As a result, there is a suprising lack of understanding of the determinants of dominance status in wild birds.

The song sparrow population on Mandarte Island, B.C., Canada, offers an unusual opportunity to study dominance behavior. Song sparrows there are resident, and the population has been completely color-marked since 1975. Nearly all young that recruit to the population are hatched on the island and have been previously banded as nestlings (Smith 1981). Thus, detailed observations on large numbers of birds of known parentage can be made. I studied dominance behavior among yearling song sparrows from 1982 to 1984 to assess the effect of dominance on survival and settlement. I also explored two classes of factors that might influence dominance. The first class involved aspects of the individual itself, such as sex, size, and age. The second class involved aspects of natal care and the natal environment, such as parental age, brood size, order within the brood, number of nestmates of the same sex, and nestling size and condition. In general, I expected dominance to depend upon sex (e.g. Glase 1973), and to increase with size (e.g. Searcy 1979a) and age (e.g. Smith et al. 1980). If the condition of nestlings influences dominance, older parents might raise more dominant offspring because they are better at raising young (Smith 1981). Similarly, dominance might decrease with increasing brood size if larger broods are more difficult to provision, or dominance might increase with increasing brood

size if early experience with nestmates positively affects dominance. I tested whether dominance was positively related to the number of nestmates, as found by Boag and Alway (1980). I also examined several other factors that I thought might affect dominance. In particular, I present the results of an experiment designed to determine if prior residence in an area might affect yearling dominance. In this experiment, 24 birds were temporarily removed from the population to prevent them from acquiring site attachments or establishing relations with free-living neighbors.

METHODS

Study Area and Study Population

Mandarte Island is a small (6 ha.), cigar-shaped island dominated by shrubs and grasses. It lies in the Haro Strait approximately 20 km. N.N.E. of Victoria, B.C., Canada. A detailed description of the habitat characteristics of the island, and the population biology of the song sparrows resident there, is given by Tompa (1964). More recent accounts of the nesting phenology, heredity, and mating system of the sparrows can be found in Smith (1981), Smith and Dhondt (1980), and Smith et al. (1982), who also provide details of the general methods employed on the island since 1974. In brief, on Mandarte Island song sparrows typically live from one to four years, and are resident and monogamous. Males and females cooperate to raise

from one to four broods per year, but two is the modal number. The sexes are slightly dimorphic in size, with males being larger, and both sexes mature at one year of age.

I studied the population from the spring of 1982, when 25 females bred on the island, through the springs of 1983 and 1984, when 53 and 55 females bred. During this period, all successful nests were found by observing females from a ladder or natural vantage point while they were nest-building, or when they returned to the nest after feeding themselves. Nestlings were fitted with a numbered aluminum United States Fish and Wildlife Service band, and from one to four colored plastic bands, at five or six days of age in most cases. This allowed me to follow individuals from their departure from the nest to their death, or until they dispersed from the island.

Morphology

I took three measurements from each nestling: weight to the nearest 0.5 gm; tarsus length to the nearest 0.1 mm, from the posterior end of the tibiotarsus to the anterior end of the lowest undivided scute; and length of the flattened wing to the nearest 0.5 mm. Age was known from the date of hatching, or was estimated by comparison with nestlings of known age. As an index of condition, I used the cube root of nestling weight divided by nestling tarsus length. Dividing weight by a skeletal measure corrected for body size and gave a measure of

the 'fatness' of individuals (Slagsvold 1982, Boersma and Ryder 1984). I identified the number of young reaching independence by close observation of parents feeding fledged young, and by subsequent sightings or captures of young off their natal territories. I sexed juveniles using a discriminant function which combined wing and tarsus length with body weight to successfully classify 114 of 116 (98.3 %) birds of known sex. The sex of these birds was known from their singing behavior, or by observing mated pairs. In order to pool data from nestlings of different age, birds of different sex, and birds born in different years, I standardized variables using (x-xbar)/s.d.

I captured over 85 percent of independent young produced each year using mist-nets. Upon capture, birds were weighed and measured as described above. Weights were corrected to 1200 h following Dhondt and Smith (1980). Only measurements from birds over 55 days of age were used to estimate size; by this time young have essentially completed growth (Smith and Zach 1979). Most birds were captured more than once. I therefore averaged measurements from successive captures of the same individual.

Estimating Dominance

Dominance was estimated by observing aggressive interactions at feeders provisioned with millet, and calculating the proportion of total interactions won by each individual (Fretwell 1969, Baker and Fox 1978, Ketterson 1979, Kikkawa

1981, Watt et al. 1984). This method gives a continuous measure of dominance that gives similar but less ambiguous results than hierarchical ranking (Baker and Fox 1978). All observations were recorded between 15 July and 15 September of each year at one of four feeders placed in areas where juveniles were concentrated. The winner and loser of agonistic encounters were recorded only when the outcome was certain, and when interactions were the result of a clear initiation (gape, wings lowered, or head forward posture; see Kikkawa 1961, and Knapton 1973, p.76-77). In this way, I tried to minimize observer subjectivity. In 1982 and 1983, respectively, 1,808 and 3,670 agonistic encounters were recorded among free-living birds. In 1983, 642 encounters were also recorded among temporary captives.

The accuracy of this dominance estimate depends upon the number of observations gathered per bird (Appendix). Therefore, when calculating single correlation statistics each value in an X,Y pair was corrected for its mean value, and then multiplied by the number of observations that the dominance estimate was based upon. This weighting scheme is explained in detail in the Appendix. The angular transformation was not applied to the proportions of wins because they were approximately normally distributed. I used unweighted scores in all other statistical analyses, and only used those birds with over five observations. While there is reason to believe that a non-interacting class contains a large proportion of subordinates (Kikkawa 1981), I

did not find a significant correlation between the number of encounters per individual and that bird's dominance ($r=0.146$, $n=175$, $p>0.05$). Fourteen percent (30 of 205) of yearlings of known sex were observed in fewer than five interactions, and these birds were excluded from most of the following analyses. In no case did this exclusion significantly alter the results of this study. In analyses of frequency data, dominants are defined as those birds winning greater or equal to the median proportion of total encounters for their sex, and subordinates are those winning fewer encounters. An exception to this scheme is table 2, where birds are divided by the median score for the population as a whole. I used G-tests of independence, goodness of fit, and heterogeneity (Sokal and Rolhf 1969) to test for significant associations between dominance class and various attributes of individuals. Product-moment correlations (Sokal and Rolhf 1969) were used to test for significant relationships between continuous characters. All significance levels reported in this thesis are two-tailed.

Temporary Removal Experiment

Between 6 and 18 June 1983, I removed 28 juveniles from the population, when approximately one half of the juvenile population had reached independence. Each bird was placed in one of two aviaries measuring 2m x 3m x 2.3m in height. Four birds died within 36 hours of capture, presumably because they would not feed in captivity. All other birds maintained their

weight well on a diet of live mealworms (Tenebrio sp.), millet, and a mixture of crushed dog meal, chopped boiled egg, wheat germ, cod liver oil, crushed oyster shell, and vitamin supplement. I provided water for drinking and bathing. One cage housed 10 females, and the second housed 12 males and 2 females. Dominance relations were allowed to equilibrate for one week after the last bird was added, before observations began. Dominance among caged birds was scored as described for free-living birds. The birds were released on 22 July 1983, when nearly all birds hatched that year had reached independence.

RESULTS

Dominance, Survival, and Settlement

In 1982, 107 birds survived to independence, and in 1983, 128 birds did so. Thirty of these birds were not captured or sexed. Of these thirty, only three visited feeders regularly, and the remainder were seen only once or had disappeared from the island by early August. I therefore based my analyses upon the 205 birds of known sex.

If dominant status is advantageous to individuals, two likely benefits are increased survival and access to territory. I considered birds to have 'survived' if they remained on Mandarte Island on 30 April of the year following birth.

'Settlers' are those birds known to have defended territories for at least one month on or before 30 April. Some birds may have dispersed to survive or settle in other populations. Therefore, my estimates of survival and settlement are conservative. Two classes of male survivors existed on 30 April of each year; floaters (after S.M. Smith 1978) and settlers. No female floaters were known to exist beyond 15 April in either year of study. Therefore, survival and settlement are equal for females. I used these definitions to test for relationships between dominance, settlement, and survival.

Table 1 contains the numbers of individuals of different sex and social status that survived as floaters or settlers, or had disappeared from Mandarte Island on 30 April of 1983 and 1984. Dominant males and dominant females survived and settled at significantly higher rates than subordinates of their respective sex in each year of the study. Thirty non-interacting birds survived (53.3%) and settled (36.7%) in proportions similar to subordinates (53.9% and 37.1%, respectively).

The proportion of birds that survived in each year was dependent upon the sex considered. Female survival was significantly higher from 1982-1983 than from 1983-1984 ($G=3.95$, d.f.$=1$, $p<0.05$). Male survival, however, was equal between years ($G=0.025$, d.f.$=1$, NS). This was because significantly more males survived as floaters from 1983-1984 than from 1982-

1983 (G=7.53, d.f.=1, p<0.01), whereas females that failed to settle in 1984 did not survive as floaters. In 1983, males and females survived equally well (G=0.55, d.f.=1, NS), but males survived significantly better than females in 1984 (G=7.91, d.f.=1, p<0.005).

The proportion of males and females that settled in each year was similar (1983, G=0.60, d.f.=1, NS; 1984, G=0.96, d.f.=1, NS). But overall, settlement was significantly higher in 1983 than in 1984 (G=6.63, d.f.=1, p<0.025). This was true for each sex (males, G=5.46, d.f.=1, p<0.025; females, G=3.95, d.f.=1, p<0.05). Therefore, while the number of birds that survived and that settled in each year was different, dominance consistently predicted the likelihood of individual survival and settlement in each year and within each sex. These results strongly suggest that dominance is a key determinant of which individuals of each sex survive and settle on Mandarte Island.

Effects of Sex, Size, and Age on Dominance

Among birds, dominance status has often been related to characteristics of individuals such as sex, size, and age. In general, males dominate females, and dominance increases with size and age, though exceptions exist for each of these relationships (Chapter Two). In this section, I consider the effect of these three characteristics on the dominance of yearling song sparrows.

Table 1. The number of settlers, floaters, and birds absent from Mandarte Is. on April 30 of the year following hatch. Birds are divided by year, sex, and social status. Gsur denotes the G-statistic that results from comparing the status of all survivors to those absent, and Gset results from a comparison of settlers to all others. In each case d.f.=1 and significance is indicated by: p<0.05* p<0.01**, p<0.001***.

Year	Group	Class/Sex	N	Settled	Floater	Absent	
1983	male	dominant	20	16	3	1	Gsur=7.31**
		subordinate	20	10	2	8	Gset=3.89*
		total	40	26	5	9	
1983	female	dominant	19	16	0	3	Gsur=4.33*
		subordinate	19	10	0	9	Gset=4.33*
		total	38	26	0	12	
1983	total	dominant	39	32	3	4	Gsur=11.36***
		subordinate	39	20	2	17	Gset=8.36**
		total	78	52	5	21	
1984	male	dominant	30	18	8	4	Gsur=6.65**
		subordinate	31	7	13	11	Gset=8.84**
		total	61	25	21	15	
1984	female	dominant	17	11	0	6	Gsur=3.86*
		subordinate	19	6	0	13	Gset=3.86*
		total	36	37	0	19	
1984	total	dominant	47	29	8	10	Gsur=7.64**
		subordinate	50	13	13	24	Gset=12.66***
		total	97	42	21	34	

I found that dominance depended upon sex. In each year, about twice as many males were dominant, as compared to females (Table 2). In 1982, 38 females won, on average, 42.7 percent of their encounters, while 40 males won 57.5 percent of their encounters. In 1983, these figures were 41.4 percent for 36 females and 58.7 percent for 61 males. These data support the conclusions of others on song sparrows (Knapton 1976, Smith et al. 1981).

Table 2. The number of dominant and subordinate birds of each sex in each year of study. Significance levels are: p<0.025*, p<0.005**, p<0.001***.

Year	Sex	N	Dominant	Subordinate	G-statistic
1982	male	40	25	15	
	female	38	13	25	6.21*
1983	male	61	38	23	
	female	36	11	25	9.16**
Total	male	101	63	38	
	female	74	24	50	15.44***

The theory of sexual selection assumes that large size is advantageous in aggressive competition to explain sexual size dimorphism in vertebrates (Darwin 1907, Selander 1972). I therefore expected to find positive correlations between dominance and the three morphological measures I recorded. Surprisingly, I instead found significant negative correlations

between tarsus length and dominance within males and females in both years. Table 3 also shows that weight was positively related to dominance among females in 1982, and that wing length was positively related to dominance among females in 1983, but that no other correlation differed significantly from zero. However, morphology sometimes varied significantly with hatch date (Table 4), and, as I show below, dominance also depends upon hatch date. I therefore calculated partial correlation coefficients for the effects of morphological characters on dominance, while controlling for the effects of hatch date on morphology. Table 5 shows that dominance was independent of the morphological characters that I measured when the effect of hatch date on those characters was controlled statistically. Similarly, among captive birds none of these three measures was significantly correlated with dominance. These results offer no support for the assumption that large size is advantageous in agonistic encounters at feeders. Furthermore, they suggest that intrasexual competition can not explain sexual size dimorphism in this species.

Several studies of birds have found that adults dominate juveniles (e.g. Rohwer et al. 1981, Smith et al. 1981), but the effect of age within a year-class has gone largely uninvestigated (but see Kikkawa 1981). I used hatch date as the independent variable to assess the effect of age on dominance. The hatching period of young surviving to independence extended from 24 April to 4 July in 1982, and from 1 April to 8 July in

Table 3. Correlation coeficients for the relationship between three measures of size and dominance. Significance levels are: p<0.05*, p<0.01**, p<0.001***.

Year	Sex	N	Weight	Wing Length	Tarsus Length
1982	male	36	0.280	0.285	−0.337*
	female	36	0.462**	−0.044	−0.467**
1983	male	55	−0.173	0.255	−0.365**
	female	33	−0.295	0.469**	−0.683***

Table 4. Correlation Coefficients for the relationship between three measures of size and hatch date. Significance levels are: p<0.05*, p<0.01**.

Year	Sex	N	Weight	Wing length	Tarsus length
	male	36	−0.387*	−0.163	−0.309
1982					
	female	36	−0.457**	−0.088	0.054
	male	55	0.041	0.323*	−0.063
1983					
	female	33	−0.075	0.259	−0.286

Table 5. Correlation coefficients for the relationship
between three measures of size and dominance, controlling
for the effects of hatch date on morphology. No correlation
is significantly different from zero.

Year	Sex	N	Weight	Wing Length	Tarsus Length
	male	36	−0.039	−0.130	−0.058
1982					
	female	36	−0.082	−0.145	−0.086
	male	55	0.202	0.181	0.118
1983					
	female	33	0.118	−0.014	−0.115

1983. Thus, 70 and 98 days separated the earliest and latest hatched young in 1982 and 1983 respectively. Table 6 shows that for both sexes, and in each year, dominance was strongly and negatively correlated with hatch date. Overall, hatch date accounted for 59% of the variation in dominance scores. Hatch date was even significantly related to dominance among captive birds (r=-.45, N=24, p=.026), where just 24 days separated the oldest bird from the youngest.

Table 6. Correlation coefficients and coefficients of determination (r-squared) for the relationship between hatch date and dominance. All r-values are significanlty different from zero (p<0.001).

Year	Sex	N	Correlation	r-squared
1982	male	40	-0.825	0.680
	female	38	-0.560	0.314
1983	male	61	-0.760	0.578
	female	36	-0.906	0.820
Total	male	101	-0.755	0.570
	female	74	-0.781	0.610
	total	175	-0.768	0.590

Together, these results confirm that sex is a key determinant of dominance within yearlings, but offer no support for the idea that morphology affects dominance. However, without detailed information on the effect of hatch date on different morphological characters, I might have concluded that dominance was positively, negatively, or not at all affected by size, depending upon the measure used. This finding underscores

the importance of knowledge of the prior histories of individuals. Age was a powerful predictor of dominance, even among captives separated by little more than three weeks. Hypotheses which could explain this relationship are discussed below (see Effect of Captivity on Dominance).

Effects of Natal Care and Natal Environment on Dominance

Dominance is sometimes affected by factors extrinsic to the individual (e.g. Boag and Alway 1980, Safriel 1981, Hrdy 1977). In this section, I consider the effects of several factors that could influence dominance. These factors include parental age, brood size, order within the brood, the number of nestmates of the same sex, and nestling size and condition.

Table 7. The number of dominant and subordinate young produced by pairs of different age. Data from both years of study are combined.

Class	N	Pair	Type	
		Yearling	Mixed	Adult
Dominant	88	22	30	36
Subordinate	87	20	29	38

To explore the effect of a parent's age and breeding experience on the dominance of young, I classified pairs into three groups based upon their previous experience at raising

young: inexperienced pairs (first year birds), mixed pairs (one adult, one first year), and experienced (both adults). Table 7 shows that there was no tendency for more or less experienced pairs to have different proportions of dominant and subordinate young.

No study has investigated the effects of brood size on dominance, but there are reasons to expect that it might have some influence (see Introduction). Table 8 shows the numbers of dominant and subordinate young reared in broods of one to four at the time of banding during 1982 and 1983. In each year, broods of three produced more dominant young than others, but this difference was significant only for both years combined (Table 8). Broods of one, two, and four produced similar proportions of dominant and subordinate young (G=0.14, d.f.=2, NS), but combined they produced fewer dominants than expected compared to a 50:50 ratio (G=4.10, d.f.=1, p<.05). Broods of three produced significantly more dominants than expected (G=4.44, d.f.=1, p<.05). Thus, there was no clear trend across brood sizes. This result might be expected if broods of three were more common early in the season, as early-hatched young were more dominant than those hatched later (table 6). To explore this possibility, I classed all birds as 'early' or 'late' based upon the median hatch date for each year, and compared the frequency of early and late young from broods of three to those of all other broods combined. As expected, more early-hatched young came from broods of three than from broods

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Table 8. The number of dominant and subordinate birds from broods of different size. Broods of one and two were pooled to calculate the G-statistic for 1982 and 1983.

Year	Class	N	Brood Size				G-statistic
			One	Two	Three	Four	
1982	Dominant	39	3	2	23	11	4.31, d.f.=2
	Subordinate	39	0	6	14	19	NS
1983	Dominant	49	1	10	30	8	4.55, d.f.=2
	Subordinate	48	5	13	19	11	NS
Total	Dominant	88	4	12	52	19	8.64, d.f.=3
	Subordinate	87	5	19	33	10	p<0.05

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of one, two, and four (G=7.05, d.f.=1, p<0.01). This suggests that brood size influenced dominance through the intervening variable of age.

Safriel (1981) found that age determined dominance within broods of oysterchatchers (Heamatopus ostralegus). Dominance within a brood might therefore affect dominance after independence. I investigated this possibility indirectly by exploring the effect of an individual's relative size within a brood on its eventual dominance status, assuming that relative size is a measure of dominance within broods because it reflects the age of young. Eggs usually hatch asynchronously in the nests of song sparrows, particularly in four-egg clutches, where the oldest young are typically one day older than the youngest (unpubl. Observations). The resulting difference in the size

of young can be pronounced (up to 20% by weight). Table 9 lists

Table 9. The number of dominant and subordinate young from
different sized broods in relation to their relative size
within the brood. Data from both years of study are
combined.

Brood Size	Class	N	Order	Within	Brood	
			First	Second	Third	Fourth
One	Dominant	4	4	–	–	–
	Subordinate	5	5	–	–	–
Two	Dominant	12	9	3	–	–
	Subordinate	19	12	7	–	–
Three	Dominant	53	19	13	21	–
	Subordinate	33	11	15	7	–
Four	Dominant	19	5	9	4	1
	Subordinate	30	10	5	6	9
Total	Dominant	88	37	25	25	1
	Subordinate	87	38	27	13	9

the number of dominant and subordinate young from broods of one

to four in relation to their relative size in the nest at

banding.   Surprisingly, I found no interaction between relative

nestling size and later dominance class; once independent, the

smallest young in nests were as likely to become dominant as the

largest.   Indeed, of the 64 largest young from broods of two,

three, and four, 32 became dominant while 32 became subordinate.

Similarly, of the 49 smallest young in broods, 25 and 24 became

dominant and subordinate.   These results do not support the idea

that dominance within a brood affects the dominance of

independent birds.

Boag and Alway (1980) found that dominance could be increased in two species of Galliformes by experimentally increasing the number of nestmates of the same sex that an individual was raised with. To explore this possibility in song sparrows, the sex of all young in a nest needed to be known. In many cases I did not have this information because some nestlings either failed to reach independence, or were not captured thereafter. I therefore pooled all available broods from 1982 and 1983 where the sexes of young were fully known to increase my samples. Table 10 shows that females without sisters became dominant more often than those with one, or especially two sisters. However, males without brothers were dominant as often as those raised with one or two brothers.

Table 10. The number of nestmates of the same sex in relation to dominance status. Data from both years of study are combined.

Sex	Status	N	Nestmates of Same Sex			G-statistic
			zero	one	two	
male	dominant	45	21	17	7	3.04,d.f.=2
	subordinate	27	8	16	3	NS
female	dominant	32	15	16	1	6.29,d.f.=2
	subordinate	32	9	16	7	p<0.05

These results are inconsistent with those found by Boag and Alway (1980).

I used partial correlation analysis to investigate the effects of nestling weight, tarsus and wing length, condition,

and hatching date on dominance. Only nestlings five or six days of age were used because samples of others were small. I pooled data for five and six-day-olds after standardizing for their differences in size. Table 11 shows that in both 1982 and 1983

Table 11. Correlation coeficients for three measures of nestling size and nestling condition in relation to hatch date. Significance levels are: $p < 0.05*$, $p < 0.01**$, $p < 0.001***$.

Year	N	Weight	Wing length	Tarsus Length	Condition
1982	76	0.434***	0.540***	0.377***	-0.234*
1983	175	0.358***	0.206**	0.244**	0.035

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nestling size increased significantly as the season progressed. However, condition declined significantly with advancing date in 1982, and was constant throughout 1983. Using data from 66 birds banded as five or six-day-olds and later scored for dominance, I found no significant correlations between dominance and nestling morphology after controlling for the effect of hatch date (weight, $r = -0.074$; wing, $r = -0.012$; tarsus, $r = -0.084$; condition, $r = 0.062$; $n = 66$ in all cases). Thus, while nestling morphology varied significantly throughout the 1982 and 1983 breeding seasons, these differences did not influence dominance.

In this section, I considered the effects of several factors on the dominance status of yearling song sparrows. The previous breeding experience of parents was not associated with the eventual status of young. Nestling size relative to other

nestmates, or to those hatched at other times in the year, also did not predict dominance status. Although condition declined with hatch date in 1983, it was not related to dominance among independent yearlings. Brood size was associated with dominance, but only through the effect of age. The dominance of females was negatively related to the number of sisters they were raised with, but there was no parallel trend among males. Overall, the factors considered here had only minor effects on dominance compared to the strong effects of sex and age considered earlier.

Effect of Captivity on Dominance

The dominance of yearling song sparrows was closely correlated with date of hatch (Table 6). Two hypotheses might explain that result. First, dominance may develop with increasing experience in agonistic encounters. Individuals with more experience could be more skilled in fighting and assessing the ability of others. Second, dominance may be a function of an individual's familiarity with a given site (Brian 1949, Brown 1963).

I tested the second hypothesis by temporarily holding 24 birds that hatched in the first half of the 1983 breeding period, until essentially all young hatched that year had reached independence. By this time, most of the early-hatched birds had restricted distributions, and some males sang sub-song

within these local areas. Temporary captives were held in groups as described above (see Methods). Therefore, while captives were as old and experienced in agonistic ecounters as early-hatched free birds, they could not have become familiar with particular sites or have established relations with free-living birds. Three groups were thus created: early-hatched controls, early-hatched captives, and late-hatched controls. If site dominance explains the negative correlation between age and dominance, I would expect captives to resemble late-hatched controls in dominance more closely than they resemble early-hatched controls. To test this prediction, I compared the dominance of captives, estimated after release, to that of a group of control birds, chosen such that the mean hatch date of each group was approximately equal. Males and females were compared to controls separately to account for differences in dominance due to sex.

Contrary to the prediction of the site dominance hypothesis, the mean dominance of captive males (0.697, N=12) was very similar to that of the earliest hatched free males (0.724, N=19, p>0.5, Mann-Whitney U-test). Captive females were also not significantly different from the earliest hatched free females (0.512 vs. 0.451, means for 11 captive and 9 free females respectively; p>0.2, Mann-Whitney U-test). However, male and female captives were significantly more dominant than late-hatched free birds (p<0.01, Mann-Whitney U-tests). Furthermore, male and female captives survived at rates similar

to those of free birds (Table 12). A larger proportion of captive males and females settled than free birds, but this result only approaches significance when the data for both sexes are combined (G=3.63, d.f.=1, p>0.05). Familiarity with a particular site was therefore not essential to dominant status for either males or females. These results are consistent with the hypothesis that dominance develops with experience in aggressive encounters independently of the location of the individual. However, dominance could develop independently of experience of any kind. I am currently conducting an experiment to determine whether experience in agonistic encounters is necessary to achieve dominant status.

Table 12. The numbers of settlers, floaters, and birds absent from Mandarte Is. on 30 April 1984. Captive and free birds are divided by year, sex, and social status.

Group	Class/Sex	N	Settled	Floater	Absent
	male	55	18	20	17
Control	female	33	14	0	19
	pooled	88	32	20	36
	male	12	7	4	1
Captive	female	12	7	0	7
	pooled	24	14	4	6

DISCUSSION

Physical attributes, amount of experience, and motivational state probably all contribute to success or failure in agonistic encounters (Parker 1974, Brown 1975). When these factors are relatively stable through time and variable among individuals, some individuals will consistently win more encounters than others. Dominant status will be especially advantageous when it results in priority of access to resources crucial to survival and reproduction, and when it does, the determinants of dominance will be subject to selection. In the following discussion, I consider my method of estimating dominance, the determinants of dominance identified by this study, and some evolutionary consequences of dominance behavior.

Measures of Dominance

In this study, dominance was estimated by observing agonistic encounters at feeders, but some birds did not visit feeders. These few non-interactors survived and settled in proportions similar to subordinates (see Results). Kikkawa (1981) also believed that non-interacting silvereyes were usually subordinate.

Dominance is typically defined by an individual's ability to gain access to resources, although dominance orders sometimes vary with the resource contested (Richards 1974, Syme 1974). My

measure of dominance estimated the priority of access to a food resource (millet). I also determined which individuals gained access to territory and which did not. This constitutes a second measure of dominance. I showed above that for males and females in each year of this study, these two measures of dominance were significantly correlated. This result supports the earlier findings of Glase (1973) for black-capped chickadees (<u>Parus</u> <u>atricapillus</u>) , of Knapton (1976) for song sparrows, and of Smith (1978) for rufous-collared sparrows (<u>Zonotrichia</u> <u>capensis</u>). These studies, however, involved many fewer individuals. Not only did dominance estimated at feeders successfully predict survival and settlement in this study, but it also predicted which males survived as non-territorial floaters in 1984. There were few floaters in 1983 (Table 1). These results confirm that an empirical measure of success at feeders is a valuable tool for assessing the success of individuals within natural populations.

Consequences of Dominance

Previous studies have shown that dominant birds enjoy high survival rates compared to subordinates (Fretwell 1968, Glase 1973, Kikkawa 1981), though pronounced advantages were only observed by Baker et al. (1981) when food was scarce. My results support this general view, but they also present an intriguing inconsistency. Males tended to dominate females in this study (Table 2), and I therefore expected males to survive

better than females. This expectation was supported in 1983-4, but males and females survived equally well in 1982-3 (see Results).

One explanation for this could be that males only experience a significant survival advantage over females when survival is generally low, since survival in 1983-4 was significantly lower than in 1984-3. However, when survival was equally high for each sex in 1982-3, dominants still survived significantly better than did subordinates within each sex (see Results). Thus, this explanation was not completely supported.

An additional explanation could be that competition is more intense within each sex than between the sexes. For example, survival, as measured here, might result from a) life or death, or b) dispersal or non-dispersal. Dispersers could be those birds which are not successful in competition for territory (Gauthreaux 1978). Competition for territory should be stronger within each sex than between them. Thus, even when survival was relatively high, dominance could still have affected the number of birds that remained on the island through dispersal.

Together, these explanations suggest that dominance influences dispersal within each sex in years even when survival is high, but that survival must be relatively low before significant between sex effects are observed. Further study is needed to test these explanations more thoroughly. The

important point here is that, while dominance successfully predicted which birds survived in each year and sex, the more dominant sex (males) only survived better when recruitment was low.

The relationship found between dominance and settlement was similar to the relationship between dominance and survival. These results support earlier work based on many fewer individuals (Odum 1942, Glase 1973, Smith 1976, 1978, Knapton 1976).

The Determinants of Dominance

I now consider the attributes of individuals that were associated with dominance. Sex is the most frequently observed determinant of dominance (Brown 1975, Wilson 1975). Among birds, males typically dominate females, though exceptions exist (Chapter Two). The results of this study further support this general pattern. An additional point is that overall, males survived significantly better than females (G=6.14, d.f.=1, p<0.01). This result may explain the consistent skew in favor of males in the adult sex-ratio in this population (Smith et al. 1982).

Body size is generally thought to strongly influence dominance status (e.g. Searcy 1979a,b,d, Dawkins and Krebs 1978, Payne 1984). However, few authors consider the problems

of interpretation that arise because of the close correlations between size, sex, and age that are present in many species (Chapter Two). Most studies of intraspecific dominance in birds that have controlled for these factors have found no relationship between dominance and morphology (Chapter Two). This study provides another example of a species in which morphology does not have a strong influence on dominance. I used three measures of size, and I also knew the influence of hatch date on morphology and on dominance. Without this information, I might have concluded that dominance was positively, negatively, or not at all related to 'body size', depending upon the measure chosen. No other study of dominance in birds has studied the effect of morphology on dominance in such detail. For this reason, the results of previous studies that have not considered relationships between age and size, and between age and dominance, should be carefully re-examined. Many authors assume that large size is advantageous in agonistic encounters over mates and resources to explain sexual size dimorphism (e.g. Selander 1972, Searcy and Yasukawa 1983, Payne 1984). The results of this study offer no support for this assumption in a monogamous species. Similar studies should be carried out in polygamous species to test this assumption further. The relationship between size and dominance is given a more extensive consideration in Chapter Two.

Dominance was strongly related to the age of yearlings for males and females in each year of this study. Overall, age

accounted for a striking 59% of the variation in dominance scores, and was the only significant predictor of dominance among captive sparrows, where only 24 days separated the oldest bird from the youngest. This is the most fascinating finding of this study. Among silvereyes, Kikkawa (1981) found a weak but not significant tendency for older yearlings to dominate younger ones. However, Kikkawa's result has recently been confirmed after weighting dominance estimates by their errors (see Appendix; Kikkawa, personal communication). Glase (1973) used skull ossification to age yearling chickadees, and found a trend for earlier-hatched young to dominate those hatched later. Among great tits, late-hatched young disperse further (Dhondt and Huble 1968, Dhondt 1979), and survive less well (Perrins 1963, Dhondt 1979) than those hatched earlier. These observations support Dhondt and Huble's (1968) hypothesis that age-related dominance is a driving force behind dispersal and survival among great tits. I suggest that these authors observed a widespread phenomenon among yearling birds that engage in frequent agonistic encounters, and that age-related dominance may be an important mechanism underlying juvenile dispersal in many territorial birds.

I considered two hypotheses that could explain the correlation between age and dominance. The experience hypothesis, proposed here, asserts that individuals acquire their fighting skills through participation in aggressive encounters, and that the level of these skills is the main

determinant of dominance. The site dominance hypothesis (e.g. Brown 1969) states that familiarity with an area increases the likelihood of winning encounters because local birds are more acquainted with strategic perches, cover, and food resources than are intruders. As an additional mechanism, Krebs (1983) proposed that territory owners often win encounters because they are more likely to escalate fights than are intruders. Owners might do this because they have invested energy establishing territorial boundaries with neighbors, and thus have more to lose than do intruders. I tested the site dominance hypothesis by experimentally preventing older yearlings from gaining familiarity with particular sites or potential neighbors, while allowing them to gain experience in aggressive interactions. I released the captives when the youngest yearlings had become independent. Captives and late-hatched birds therefore had equal opportunity to develop site familiarity and relations with neigbors. The results of this experiment firmly rejected site familiarity as a prerequisite of dominant status among yearling song sparrows. Both male and female captives were as dominant at feeders after release as comparably-aged birds, and both groups of captives were significantly more dominant than birds hatched later. These results are consistent with the experience hypothesis. However, they are also consistent with hypotheses that explain dominance independently of experience of any particular kind. A test of the experience hypothesis is underway.

Of the several factors considered under the title 'Effects of Natal Care and Natal Environment', two were associated with dominant status: the number of nestmates of the same sex, and brood size. Brood size was a significant predictor of dominance, but this was explained by the relationship between hatch date and dominance. Broods of three were more common earlier in the season, and thus produced more of the older yearlings. Boag and Alway (1980) found that among two species of Galliformes, dominance was positively correlated with the number of nestmates of the same sex in the natal brood. I found the opposite to be true in females, and found no effect in males. However, the differences in the dominance of females with varying numbers of sisters are small. Song sparrow young are altricial, but Galliformes have precocial young. Further data are needed to see if these different results are general for birds with altricial and precocial young.

Parental age had no effect on the proportion of dominants produced. Similarly, neither the relative size of a young within a brood, nor the absolute size or condition of nestlings, was significantly associated with dominance after independence. Contrary to the pattern for two other small passerines (Perrins 1963, Howard 1980), the size of nestlings at a given age increased with hatch date in both years of this study.

Perrins (1969) suggested that late-hatched great tits suffered high mortality after fledging, because they fledged in

poorer condition than young hatched earlier. Late-hatched song sparrows suffered poor survival compared to those hatched earlier in both years of this study, but they fledged in poorer condition in only one year. Garnett (1981) found that tarsus length in wild juvenile great tits was negatively related to date of hatch. He therefore proposed that the relationship observed by Perrins (1969) in the great tit, was due to a dominance advantage gained by larger, early-hatched birds. To test this idea, he studied dominance among nine captive juvenile great tits and found that in the first week of study, age was significantly related to dominance. In the second week tarsus length was correlated with dominance, but age was not. Unfortunately, he did not account for his previous observation that hatch date and tarsus length were negatively related. Nevertheless, he suggested that size was the most important determinant of dominance, and that age influenced dominance only in the early development of young.

My results show that the striking effect of age on dominance in the song sparrow persists well beyond the period postulated by Garnett (1981) for the great tit, and that correlations between morphology and dominance may weaken when the relationships between date of hatch, morphology, and dominance are taken into account. I suggest that the relationship between hatch date and juvenile survival in the great tit (Perrins 1969, Dhondt 1979), is at least partly due to an effect of hatch date on dominance similar to the one observed

in this study. In summary, the characteristics of individuals identified by this study that exhibited strong correlations with dominance were sex and hatch date. No other characteristic investigated was found to be strongly related to the dominance of yearling song sparrows.

Dominance and Natural Selection

Dominant status was clearly advantageous to yearling song sparrows during the period of this study. The determinants of dominance identified by this study suggest that selection for dominant young will exert pressure on females to lay early in the season. Females that lay early may also raise more broods than those laying later (Smith 1981). Also, parents that raise many males may produce more recruits than those raising many females, since males tended to survive better than females.

However, selection for dominant young will be opposed by countervailing selection pressures. For example, young hatched early are smaller at a given age than those hatched later (Table 11), they remain longer in the nest before fledging, and they are also more likely to die of exposure from unfavorable early season weather (Unpublished data). Furthermore, experimental evidence suggests that it is difficult for females to lay early (Smith et al. 1980), and these effects may balance those of low dominance among their offspring.

The present analyses only allow speculation about how these opposing selection pressures have affected the evolution of nesting phenology in the Mandarte song sparrow population, and further study is needed to determine their relative contributions. However, if we are interested in an individual yearling, which controls neither its hatch date or its sex, my findings suggest that dominance status is largely the result of chance. Most pairs in this study nested more than once per year, and they were therefore committed to raise both early and late-hatched young.

Dominance has been shown to be heritable in several species of Galliformes (Craig et al. 1965, Boag and Alway 1981, Boag 1982, Moss et al. 1982). However, among the song sparrows studied here, P. Bets (personal communication) found no evidence for heritability of dominance. Together, the above considerations suggest that selection for hatch date, and thus the dominance status of yearlings, will result from a suite of balancing selection pressures. The dominance status achieved by a yearling sparrow probably depends largely on events beyond its control. Given this conclusion, it would be interesting to know if individuals adopt different behavioral stratagies depending upon their status.

In conclusion, dominant status as measured at feeders was a good predictor of survival and settlement among yearling song sparrows. This pattern was observed in two consecutive years,

even though population parameters differed markedly between years. Of the several phenotypic characteristics investigated, only sex and age exercised strong effects on dominance. Twice as many males were dominant as were females, and age accounted for over 59% of the total variation in dominance among individuals summed over both years. Site familiarity was not a prerequisite to achieving dominant status, and my results were consistent with the hypothesis that the amount of experience that an individual has had in agonistic encounters is a key determinant of dominance. The dominance of yearling song sparrows is probably ultimately determined through the interaction of the selection pressures that affect laying date.

CHAPTER TWO: DOMINANCE, BODY SIZE, AND HABITAT DISTRIBUTION

INTRODUCTION

Darwin (1907, p.59) believed that sexual size dimorphism in birds "is the result of the advantage gained by larger and stronger males over their rivals during many generations", and this view persists (e.g. Searcy and Yasukawa 1983, Payne 1984). Even the smallest advantage to large individuals could act as a selective mechanism in competition for mates or resources, but some authors assume that the effect of size on dominance is large, and rely on it to explain ecological processes such as the winter and breeding season distributions of birds (Fretwell 1969, 1972, Gauthreaux 1978, Dhondt et al. 1979, Ketterson 1979, Lundberg et al. 1981, Ulfstrand et al. 1981). In support of this assumption, several studies have claimed that body size is a key determinant of intraspecific dominance in birds (Fretwell 1968, Baker and Fox 1978, Ketterson 1979, Searcy 1979a, Garnett 1981).

Though less often cited, many studies of birds fail to support the idea that large size is an advantage in agonistic encounters (Murchison et al. 1935, Shoemaker 1939, Collias 1943, Tordoff 1954, Moore 1972, Glase 1973, Knapton 1973, Rohwer 1975, Schneider 1979, Kikkawa 1981, Price 1984, Watt et al. 1984, D.A. Boag pers. com., this study), or in obtaining mates (Lill 1974, Searcy 1979b, Stiles and Wolf 1979), breeding

territories (Knapton 1973, Yasukawa 1979, Hannon and Roland 1984, J.N.M. Smith and D. Schluter in prep.), or breeding positions within cooperative groups (Brown et al. 1982). There are also exceptions of a different kind. For example, among wintering sparrows, smaller adult females often dominate larger juvenile males (Knapton 1973, Schneider 1979, Parsons and Baptista 1980, Rohwer et al. 1981). F.R. Gelbach (personal communication) found that territorial male screech owls (Otus asio) were significantly smaller than males without territories. Similarly, Jehl (1970) observed in two species of monogamous sandpipers, that small males were the first to attract mates. These findings all contradict the assumption that large individuals have an advantage in contests for resources, and they suggest that size does not determine dominance.

Why, then, is this assumption so popular ? One reason is that sexual selection, which assumes an advantage of large size in intrasexual competition (Darwin 1907), has so often provided an explanation for size differences between males and females (e.g. LeBoeuf and Peterson 1969, Hrdy 1977, Clutton-Brock et al. 1982, Payne 1984). In addition, this assumption has much intuitive appeal, and this may also explain its uncritical acceptance.

In this paper, I offer an assessment of the assumption that large size is advantageous in agonistic ecounters, and is thereby a key determinant of intraspecific dominance in birds.

The first section examines some measures of body size, and illustrates, with examples from the literature, how their use may be confounded by a dependence upon sex and age, or an independence from the mass of individuals. In the second section, I present data from a study of dominance among wild song sparrows (Melospiza melodia), and determine the slope of the relationship between the difference in the size of contestants and the probability of winning an agonistic encounter. Then, using a simple model, I estimate the slope of this relationship necessary to account for differences in the size of individuals between habitats observed by Lundberg et al. (1981) and Ulfstrand et al. (1981).

MEASURES OF SIZE AND DETERMINANTS OF DOMINANCE

Problems in measuring body size

Body size is a familiar term, but there is no consensus on how to measure it (see review by Clark 1979). Clark (1979) defined body size as the mass of the individual, and I follow this definition here. Amadon (1943) recommended that the cube root of live weight be used as the standard for interspecific comparisons of body size. However, using weights for studies of dominance within species creates two problems. Most obvious, dominance is typically determined by observing agonistic encounters at a food resource; individuals which are consistently successful are dominant to those that are less

successful (e.g. Brown 1963, Searcy 1979a). We might therefore expect dominants to outweigh subordinates. Weight could also affect dominance; heavier birds might have an advantage, or light, hungry birds might fight harder than satiated ones. The result is that correlations between live weight and dominance can be variously interpreted. A second problem is that weights change daily and seasonally, especially in small birds (Clark 1979). As a result, researchers have sought indices of body size that are less variable and are not affected by dominance.

Wing length, and to a lesser extent tarsus, bill, and keel length, have become popular indices of body size (e.g. Slagsvold 1982, Hannon and Roland 1984, Payne 1984). However, linear dimensions often fail to correlate well with either fat-free weight or live weight (e.g. Power 1969, Bailey 1979, Halse and Skead 1983). Among male juncos (Junco hyemalis) , Helms et al. (1967) found that wing length did not predict fat-free dry weight. The correlation was weak for resident females, and was significant only for migrant females. They concluded that "extreme care must be used by authors using wing length as an indicator of mass" (p.571, 1967).

Many authors report allometric relationships between wing length and body weight among populations distributed along latitudinal clines (e.g. Power 1969, James 1970 and references therein). Searcy (1979d) and Yasukawa (1979) reasoned that a positive relationship between mean wing length and mean body

weight between populations of red-winged blackbirds (Agelaius phoenicius) (Power 1969), justified their assumptions that the relationship also held within populations. In fact, Power (1969) found that within 10 male and 7 female populations of red-wings, there were 7 negative and 10 positive correlations between wing length and the cube root of body weight, just one being statistically significant.

Using wing length as an index of body size is further complicated by the fact that it increases with age (Table 13), and is subject to seasonal variation due to wear (e.g. Brown et al. 1983). In contrast, tarsus length and bill dimensions do not appear to change with age, at least in some passerines (P.T. Boag 1983 and references therein, Alatalo et al. 1984), and tarsus length does not vary due to wear. The value of these or other characters as indices of body size will depend upon their ability to predict weight and other linear dimensions accurately. When linear dimensions are not strongly correlated, they may indicate shape more than size.

P.T. Boag (1983) used principal component analysis to identify variables that described overall increases in the size of Galapagos finches (Geospiza spp.) better than weight or linear dimensions alone. This is a promising technique to estimate the body size of birds when individual morphological characters are not closely correlated.

Table 13. Some species in which wing length increases with age.

Study   Species

Mueller et al. 1976   Accipiter gentillis
Mueller et al. 1979   Accipiter striatus
Mueller et al. 1981   Accipiter cooperii
Newton et al. 1983   Accipiter nisus
L. Rotterman and C. Monet   Agelaius phoenicius
personal communication
Gatti 1983   Anas platyrhynchos
Slagsvold 1980   Corvus corone cornix
A. Lundberg pers. comm.   Ficedula hypoleuca
Blake 1962, Ketterson 1979   Junco hyemalis
Moore 1972   Junco phaeonotus
Wishart 1981   Mareca americana
J.N.M. Smith in prep.   Melospiza melodia
Ulfstrand et al. 1981   Parus major
Selander and Johnston 1967   Passer domesticus
Greenberg et al. 1972   Phasianus colchicus
N.B. Davies pers. comm.   Prunella modularis
Searcy 1979c   Xanthocephalus xanthocephalus
Rohwer et al. 1981   Zonotrichia querula
Kikkawa 1981   Zosterops lateralis

Sex, Age, and Size

Most populations include individuals of different sex and age. The majority of bird species exhibit sexual size dimorphism (Amadon 1959), and males are usually the larger sex. In turn, dominance depends upon sex, and males typically dominate females (Shoemaker 1939, Collias 1943, Brian 1949, Collias and Taber 1951, Tordoff 1954, Marler 1955, Hinde 1956, Kikkawa 1961, Dixon 1965, Glase 1973, Knapton and Krebs 1974, Smith 1976, 1984, Baker and Fox 1978, Schneider 1979, Rohwer et al. 1981, Smith et al. 1981, Brawn and Sampson 1983, Peters and Grubb 1983 and references therein, Watt et al. 1984, but

see Thompson 1960 and Coutee 1967). Wing length, a popular index of body size, increases with age in many species (Table 13; but see Ewald and Rohwer 1980), and age is a primary determinant of dominance (Brown 1963, Moore 1972, Knapton 1973, 1976, Smith 1978, 1984, Searcy 1979a, Schneider 1979, Ewald and Rohwer 1980, Rohwer et al. 1981, Kikkawa 1981, Smith et al. 1980, De Vos 1983, Watt et al. 1984, Chapter One). We should therefore expect positive correlations between wing length and dominance when the effects of sex or age are not controlled for.

Two main points were made in this section. First, body size must be determined accurately. If a single morphological character predicts dominance, but is not correlated with other measures of size, it is incorrect to argue that 'body size' determines dominance. A focus on body size should not obscure the importance of single characters either. Morphological characters may have different heritabilities, or may be subject to different selection pressures (P.T. Boag 1983). Their different effects on dominance should be as interesting as any shared effect. Second, characters that influence dominance, and covary with body size, must be identified and controlled for if we wish to test the hypothesis that size determines dominance. Both age and sex may affect size, but may independently influence dominance. These considerations provide the backround for a review of studies that have shown positive correlations between size and dominance in birds.

Examples From the Literature

The following examples illustrate the problems mentioned above. Each study claims to have found positive correlations between 'body size' and dominance. Fretwell (1969) found that wing length could predict dominance in the junco, and this result is repeatedly cited as evidence that body size is a key determinant of dominance (e.g. Fretwell 1972, Wilson 1975, Ketterson 1979, Morse 1980). However, Fretwell included birds of both sex in his analysis, and in juncos, males are larger than females (Balph 1975) and dominant to them with few exceptions (Moore 1972, Baker and Fox 1978, Balph 1975, Ketterson 1979). I partitioned his data (figure 7, p.17, 1969) into dominant and subordinate individuals (greater or less than 50% wins) of each sex using the criteria given in Balph (1975) for sexing juncos by wing length. Because the sexes overlap in wing length (77-79mm), 19 birds could not be reliably sexed, and I excluded these birds from my analysis. Table 14 shows that dominance was dependent upon sex, and this result is independent of the sexing criteria; the data may be divided equally among the sexes over the zone of overlap without altering the result. In addition, there was no correlation between wing length and dominance within males or females (r=-.02, n=15, NS and r=-.18, n=6, NS, respectively). This shows that Fretwell's finding resulted from comparing males with females. Furthermore, wing length does not reliably predict the fat-free dry weight of juncos (Helms et al. 1967), and increases with age (Table 14).

Table 14. The effect of sex in Fretwell's figure 7
(see text). It is likely that dominance depends
on sex (Fisher's Exact Probability Test, two-tailed
p=.011, n=21).

	Male	Female
Dominant	13	1
Subordinate	2	5

Other studies suffer similar problems. Baker and Fox (1978) found no relationship between dominance and wing length among juncos in the field, but did find a positive correlation among captive birds. Discounting the field result, they conclude that "to predict dominance the single best source of information is wing length" (p.708, 1978). While this may be true, their procedure suffers from the same setbacks as Fretwell's. Ketterson (1979) recognized the problem of sex and age differences in size and dominance among juncos. She found a positive effect of wing length on dominance even when corrected for sex and age. These studies show that wing length can predict dominance in juncos. However, because wing length in juncos is correlated with age and sex, and is not correlated with fat-free dry weight, speculation about the influence of body size on dominance is risky at best. In the yellow-eyed junco (<u>Junco phaeonotus</u>), Moore (1972) found no correlation

between wing length, or tail length, and dominance among males or females in either of two years.

Searcy (1979a) controlled for sex differences in size and dominance among captive red-winged blackbirds by studying only males. He further identified birds as either yearlings or adults (over one year). Wing length was positively correlated with dominance among adults, but not among juveniles. There are two problems with the interpretation of these results. First, wing length in male red-wings increases significantly, each year, up to six years of age (L. Rotterman and C. Monet personal communication). However, the age of the adults in Searcy's study and the effect of age past one year on dominance are unknown (Searcy personal communication). Maturation is delayed in red-wings, thus the effect of age past one year may be large. Second, wing length varies independently of body weight in red-wings (Power 1969), and may not indicate body size. Garnett (1981) studied dominance among captive great tits, and his conclusions, which depended on which week's data were considered, were discussed in Chapter One.

To summarize this section, sex and age are key determinants of intraspecific dominance in birds, and these variables are often tightly linked to body size. Authors have in general not accounted for these confounding factors when choosing indices of body size. Each study that has claimed support for the hypothesis that body size determines dominance in birds suffers

drawbacks which seriously limit its interpretation. We clearly to need account for these factors when studying the influence of morphology on intraspecific dominance in birds.

HABITAT DISTRIBUTION AND DOMINANCE IN THE SONG SPARROW

In this section, I present data from a study of dominance among wild song sparrows to determine the relationship between three morphological measures and the probability of winning an agonistic encounter. Lundberg et al. (1981) and Ulfstrand et al. (1981) observed that male pied flycatchers and great tits, respectively, were larger in high quality breeding habitat than in lower quality areas. They attributed their observations to the effect of size related dominance in competition for breeding territory. I used a simple model to estimate the slope of the relationship between the difference in contestant size and the probability of winning an encounter that would be necessary to account for the differences that they observed. By comparing the empirically derived slopes for song sparrows to those required to segregate birds into separate habitats on the basis of size, I provide a test of the hypothesis that size-related dominance is a mechanism behind habitat segregation in birds.

The Advantage of Size in Wild Song Sparrows

In Chapter One, I discussed the determinants of dominance in the song sparrow. In this section, I re-examine the data on

the morphology of interacting sparrows to determine how the difference in the size of interactors affected the outcome of individual ecounters. I previously showed that larger and smaller birds in each sex won approximately the same proportion of encounters, but this analysis did not consider the relative size of competitors. The main purpose of this analysis was to provide a comparison for the results from a model presented below. The general methods employed here follow those described in Chapter One.

For this analysis, I only included encounters between birds of the same sex in order to control for differences in size and in dominance between males and females (Chapter One), and only yearlings were considered to prevent the introduction of any bias in favor of larger, more dominant adults (Knapton 1976, Smith et al. 1981). The total sample was further reduced because many encounters included birds for which I had incomplete morphological information.

Wing and tarsus length and body weight are independent measures of size in yearling song sparrows (wing vs. weight, $r=.116$, NS; wing vs. tarsus, $r=.048$, NS; tarsus vs. weight, $r=.293$, $p<0.01$; $N=116$). I used each of them to derive the relationship between the difference in contestant size and the probability of winning an agonistic encounter.

I estimated the slope of each relationship using a least-

squares multiple regression model (Sokal and Rohlf 1969). A value of one or zero was assigned to the outcome of encounters (y-coordinate) and I used the size difference of contestants as the x-coordinate. I also included the difference in the age of contestants as an x-variable, because I have previously shown that age is a powerful correlate of dominance, and is in turn significantly correlated with some morphological characters (Chapter One). By this method, each encounter is counted twice; as a win and as a loss. For tests of significance the degrees of freedom are therefore equal to half the sample size.

Results

Table 15 gives the partial regression statistics for each character within each sex for both years. As expected from a similar analysis presented in Chapter One, the effect of the different morphological characters was not the same between the sexes or the years of study. In 1982, only age played a significant role in the outcome of encounters among males, and the trend for all morphological measures was negative. For females in 1982, both hatch date and tarsus length were highly significantly related with the probability of winning encounters. However, tarsus length had a negative effect on winning encounters, rather than a positive effect as would be predicted given the assumption that large size is advantageous in agonistic encounters. However in 1983, wing length was significantly positively related to winning in males, and

contrary to results for 1982, no morphological variable exhibited negative effects. Hatch date was highly significantly related to winning. For females in 1983, only hatch date was significantly related to the probability of winning encounters.

Overall, for both males and females in each year, hatch date was by far the most powerful predictor of the outcome of encounters. These results demonstrate two important points: 1) morphology can be positively or negatively correlated with the probability of winning agonistic encounters; 2) correlations between morphology and winning encounters may be significantly different between years and between males and females.

The significance levels of these regressions rest on the assumption that interactions represent independent observations. I used each interaction because the outcome of encounters between two birds was not always the same. I therefore had no objective way by which to exclude individual interactions. The significance levels should therefore be viewed with some caution.

I also determined the relative importance of size and sex to the outcome of encounters between males and females by comparing the size of winners and losers when differences in age were ten days or less. Males and females overlap very little in wing length, so there were no cases where females were larger than males and nearly equal to them in age. Males and females

Table 15. Results of multiple regression of three morphological characters and hatch date on the probability of winning agonistic encounters. Degrees of freedom and standard errors are adjusted to one half the sample size (see text). Significance levels are: $p<0.01$**, $p<0.001$***.

Year	Sex/variable		Partial Regression Coefficient	S.E.
1982	male	n=760		
	weight		-0.017	0.022
	wing		-0.005	0.021
	tarsus		0.043	0.062
	hatch date		-0.014***	0.002
1982	female	n=490		
	weight		-0.015	0.026
	wing		-0.015	0.026
	tarsus		-0.137**	0.062
	hatch date		-0.007***	0.002
1983	male	n=1930		
	weight		0.014	0.014
	wing		0.030**	0.011
	tarsus		0.017	0.025
	hatch date		-0.008***	0.0006
1983	female	n=314		
	weight		0.047	0.041
	wing		0.023	0.043
	tarsus		-0.072	0.079
	hatch date		-0.006***	0.002

often overlap in tarsus, however, and I therefore asked the question of how often females defeated males when they were of similar age. For both year's data combined, females won 132 of 880 encounters when smaller than the male contestant, 2 of 14 when equal in size, and 11 of 63 when larger than the male. Thus, the frequency with which females defeated males was independent of size as measured by tarsus length (G=0.89, d.f.=2, NS). Similar results were obtained using weight.

Dominance and Habitat Distribution

Lundberg et al. (1981) and Ulfstrand et al. (1981) observed that male pied flycatchers and great tits, respectively, were larger in high quality plots of deciduous forest than in lower quality pine forest plots. They interpreted these differences as the result of a dominance advantage to large males in agonistic encounters over territory. Pied flycatchers and great tits are similar to song sparrows in mass and linear dimensions, and all three species share some important aspects of their natural history. In each species, males compete for territories, and song sparrows and great tits form dominance hierarchies in the non-breeding season (Knapton and Krebs 1974, Brian 1949, Hinde 1952). We might therefore expect these species to be similar in the effect of morphology on dominance. A simple linear model may be used to determine how large the advantage of size must be to account for the size differences observed in pied flycatchers and great tits between habitats.

The model assumes a large population of size N, in which the outcome of randomly occurring agonistic encounters depends upon the size of contestants. The winners of encounters go to habitat A, while the losers go to habitat B. The probability of going to habitat A is given by;

$$P_i = a(X_i - \overline{X}) + 0.5 \qquad , \qquad (1)$$

where $\underline{X}$ is the mean size of males in the original population, $\underline{a}$ is the slope of the relationship between size differences and the probability of winning an encounter, and $\underline{x}$ is the size of individual i. The mean size of birds in habitat A is;

$$\overline{X}_A = \frac{\Sigma \ X_i P_i}{\Sigma \ P_i} \ . \tag{2}$$

Which simplifies to;

$$\overline{X}_A = \overline{X} + 2a\sigma^2 \ . \tag{3}$$

where sigma-squared is the variance with respect to size of the initial population. Therefore, the mean size of birds in habitat A, the good habitat, depends upon the initial population mean and variance, and the effect of size on winning (slope). Solving for $\underline{a}$,

$$a = \frac{\overline{X}_A - \overline{X}}{2\sigma^2} \ . \tag{4}$$

With this model, we can estimate $\underline{a}$ for pied flycatchers

using the information given in Lundberg et al. (1980, table 4).
The mean size of males in deciduous and coniferous plots, is
50.16 mm2-gm and 48.95 mm2-gm, respectively. (units derive from
a discriminant score based on wing and tarsus length, and
weight). Since this model depends on the actual data, the
observed mean size of birds in each habitat is assumed to equal
the parametric mean, and the mean size of the initial population
is taken as the unweighted average of the two observed means.
The variance of the initial population is estimated as the sums
of squares within habitats plus the sums of squares between
group means, divided by the total sample (Sokal and Rohlf 1969).

Using these figures, $\underline{a}$ is 0.24. For great tits, using the
same procedure, and with figures from Ulfstrand et al. (table
1, 1980), $\underline{a}$ is 0.33. These figures estimate the size advantage
needed to produce the mean size differences between habitats
observed by Lundberg et al. (1980) and by Ulfstrand et al.
(1980). The estimates rely on two assumptions about the
character of agonistic encounters: first, that encounters are
random with respect to size, and second, that the initial
population is large.

Lundberg et al. (1980) and Alatalo et al. (1984) provide
information which suggests that for pied flycatchers, each
assumption · is incorrect. Lundberg et al. show that the
deciduous plots are occupied earlier than are the coniferous
plots. Alatalo et al. found that in the same population, large

males arrive earlier than smaller males. Therefore, the population of competing males is smaller early in the season. Furthermore, the mean size of competing birds will change as the season progresses, since large birds are settling as smaller birds arrive. Competitors will also be more alike in size than expected if birds met at random.

A small population will make chance differences in the size of birds between habitats a more common occurrence. Non-random contests between birds of similar size will reduce the realized variance of the competitor population. Thus, the slope calculated above will be too small (see equation 4). Parallel considerations apply to great tits, but I can not evaluate my assumptions for that species.

Given that these slopes are realistic, or are under-estimated for pied flycatchers, they represent much stronger effects of size on the outcome of encounters than I found among song sparrows. In song sparrows, the largest positive slope observed was 0.031 (Table 15), an order of magnitude less than that calculated for great tits. There were no consistent effects of size on the outcome of encounters among song sparrows, and for birds in 1982, these effects were negative (Table 15). These results suggest that some other factor than dominance led to the differences in the size of males between habitats observed by Lundberg et al. (1980) and Ulfstrand et al. (1980). For pied flycatchers, the relationship between

arrival time and body size observed by Alatalo et al. (1984) could be sufficient to explain the difference between habitats.

DISCUSSION

Four points are made in the preceding sections. First, sex and age are tightly linked to body size in many species, and they may independently influence dominance. Ketterson (1979) found that wing length was a better predictor of dominance in juncos than was sex. My results were opposite to this finding. Female song sparrows won no more encounters when they were larger than males than when they were smaller. These opposite results may be due to the fact that Ketterson's conclusion was based on the results of a stepwise multiple regression in which sex was the last of four variables entered, and wing length was the first. She did not control for the strong correlation that exists between wing length and sex in juncos (Balph 1975), and thus much of the effect of sex on dominance would have appeared to have been 'explained' by wing length.

We know that sex and age are key determinants of dominance, and that size covaries with these factors. If size and dominance are linked via an extra 'X' chromosome in birds, size is important, but not per se. Experimental evidence suggests that males may dominate females largely because of a hormonal influence on behavior. Male birds typically have higher circulating levels of testosterone than females (Wingfield and

Farner 1978), and testosterone is known to directly influence aggressive behavior and the dominance status of birds (Rohwer and Rohwer 1978, Moss et al. 1979, Searcy and Wingfield 1980, Watson and Parr 1981, Moore 1984).

Second, studies that have found effects of size on dominance have either failed to control for factors known to affect both size and dominance, or have used morphological measures of size, such as wing length, that are unrelated to the mass of individuals within populations. Thus, no strong empirical evidence exists to support the notion that large size is advantageous in agonistic encounters in birds.

Third, this conclusion is supported by the study of dominance among song sparrows presented here, in which age, sex, and size could all be accurately measured. In this study, I found both positive and negative correlations between morphology and the probability of winning agonistic encounters. No significant effect of morphology on the outcome of encounters was consistent across years, or even among the sexes. These results show that large size confers no consistent advantage in agonistic encounters in the song sparrow, and that large size may sometimes be a disadvantage. Furthermore, they show that studies over a single year, or the observation of only one sex, may lead to spurious conclusions about the effect of size on dominance.

Finally, ecological processes that have been explained in terms of size-related dominance, such as the distribution of territorial male birds observed by Lundberg et al. (1980) and Ulfstrand et al. (1980), require a much stronger effect of size on dominance than was found in the song sparrow. While this does not exclude the possibility that size affects dominance more strongly in other species, it does suggest that other processes may explain the observations.

If dominance were unaffected by size, what factors could account for the habitat distribution of male great tits and pied flycatchers? There are at least two possibilities: 1) birds in better habitats may be older, and therefore larger (Table 13); 2) larger birds may be physiologically more able to withstand poor weather that might be associated with early arrival. If the proportion of older, more experienced males was higher in deciduous plots, than in poorer coniferous plots, this could explain the difference. However, for both species, males in deciduous plots also had slightly longer bills than those in coniferous plots. In great tits at least, bill length does depend upon age (Ulfstrand et al. 1981). Thus, some real size differences, uncorrelated with age, may exist. A second possibility was suggested by work on pied flycatchers by Alatalo et al. (1984). As discussed above, they found that tarsus length was negatively correlated with the arrival time of territorial males in spring. Lundberg et al. (1981) found that male pied flycatchers occupied deciduous plots before coniferous

plots. This being so, we should expect birds in deciduous plots to be larger on average. Large males might survive better during periods of adverse weather than smaller birds (e.g. Ketterson and King 1975, Piersma 1984). Therefore, large males might arrive early to aquire superior territories in the relative absence of competitors. For smaller males, the benefits of early arrival may not outweigh the associated risk. In any case, this difference in arrival time suggests that the observed habitat distribution did not result from size-related dominance. If it did, two questions need to be asked. First, where and when do competitive interactions occur? Second, why should the effect of size be strong in these species, but weak in others of similar size and life history (e.g. Moore 1972, Glase 1973, Schneider 1979, Kikkawa 1981)?

Why does body size have little influence on dominance in some birds? First, the character of aggressive encounters changes from species to species, and this may affect the influence of large size. Over 90% of the agonistic encounters observed between song sparrows in this study involved no bodily contact. When contact did occur, birds flew up against each other and used their feet, wings, and beaks in a brief, acrobatic flurry. I observed tumbling fights between birds on the ground only two or three times in over 5,000 encounters. Size could be more important in species that engage in shoving matches, where agility, speed and fighting skill may yield to bulk (e.g. Chum salmon, Schroder 1981; elephant seals, LeBoeuf

and Peterson 1969; red deer, Appleby 1982, Suttie 1983).

Second, the narrow size range within most bird species may preclude large asymmetries in dominance based on size. Song sparrows interacted randomly with respect to size in this study (Arcese unpublished data). Thus for wing length, 95% of of all sex-specific agonistic ecounters involved birds that differed by less than five percent in size. In species other than birds, there is much evidence that demonstrates that differences in size of ten percent were large enough to significantly favor larger contestants in agonistic encounters (male chum salmon, Schroder 1981; mantis shrimp, Caldwell and Dingle 1979; the anemone Actina equina, Brace and Pavey 1978) .

Intrasexual competition is frequently invoked to explain sexual size dimorphism in birds (e.g. Wiley 1973, Searcy 1979d), especially for polygamous species where variation in individual reproductive success may be much greater than in monogamous species (e.g. Searcy and Yasukawa 1983). This explanation is strongly supported by correlations within taxonomic families that demonstrate that the degree of dimorphism between males and females is much larger in polygamous species than in monogamous species (e.g. Selander 1972, Payne 1984). Within species, however, I have shown that the assumption that large size confers an advantage in agonistic encounters is generally unsupported in studies of birds. Yet, intrasexual competition makes this assumption to explain sexual

size dimorphism.

How can we resolve this paradox? I suggest three possibilities. First, intrasexual competition should be less important in monogamous species, since the variance in the reproductive success of individuals is lower than in polygamous species. The two most detailed studies of the effect of morphology on dominance in birds are Kikkawa's study of silvereyes (1981) and this study. Neither study showed an advantage of large size, and both were conducted on monogamous species. The results of these studies strongly suggest that sexual size dimorphism in these species is not the result of intrasexual competition. Price (1984a,b) showed that sexual selection favored large males in Geospiza fortis, a monogamous Galapagos finch, but that this resulted from female choice of large males, rather than through male-male competition. He found no evidence for size-related dominance in this species (Price 1984a). Price (1984a,b) and Downhower (1978) each found that selection favored small females in Galapagos finches, because small females produce eggs more efficiently and thus begin laying more quickly than larger ones. These studies, and others reviewed by Payne (1984), show that sexual size dimorphism in monogamous birds may be explained without invoking size-related dominance.

Second, the studies of monogamous birds may not accurately model the relationship between size and dominance that might

exist in polygamous species. If polygamous species were morphologically more variable than the monogamous species studied thus far, larger asymmetries in the size of contestants could occur more often. This might enhance the advantage of large size in agonistic encounters. Or, the character of aggressive encounters may differ between monogamous and polygamous species (see above).

Third, an advantage of large size in agonistic encounters may be real, but be slight and difficult to measure. However, even the slightest advantage to large individuals could be selected for, and thus cause sexual size dimorphism through intrasexual competition. This argument requires only evidence from comparative studies (e.g. Payne 1984) to support or or reject the assumption that large size is advantageous in agonistic encounters.

GENERAL SUMMARY

Dominance behavior is a widespread phenomenon both within and among species, and social dominance in animals has intrigued biologists for decades (e.g. Wilson 1975:279-297). Yet there is no consensus, and indeed there is little information, on the qualities of individuals that determine dominance status.

This study was undertaken to document the correlates of dominance status and consequences of dominance for the individual within one species. I first tested whether dominance could influence recruitment. If it does, then natural selection will operate on those characters which determine dominance. I therefore also sought correlations between several factors that had been found to, or that I thought could, influence dominance in the song sparrow.

The results of this investigation were strikingly clear. Individual song sparrows with high dominance status had superior survival and access to territory, as compared to subordinates. I found that only two factors consistently predicted dominant status. These were sex and date of hatch. Males were more often dominant than females, and males survived better than females overall. Thus, dominance could explain the skewed sex ratio favoring males on Mandarte Island (Smith et al. 1982).

Variation in the dominance of yearlings was largely explained by their age; birds hatched earlier in the season dominated those hatched later. I showed by experiment that this was not because early-hatched birds had a greater familiarity with local areas than others. Early-hatched birds that were deprived of this familiarity by confinement in groups, but were thus allowed experience in agonistic encounters, were as dominant as early-hatched birds that were not confined. However, they were dominant to late-hatched birds that lacked comparable experience in agonistic encounters. I propose that the amount of experience an individual has had in agonistic encounters is a key determinant of dominance.

Morphology only a weak influence on dominance among yearling sparrows. This result, along with others reviewed in Chapter Two, represents a serious challenge to current theories about the evolution of sexual size dimorphism in birds (e.g. Searcy and Yasukawa 1983). However, morphological variation in the monogamous song sparrow could be too low to observe asymmetries in the size of competitors large enough to produce a strong effect of size. More careful studies of the type described in this thesis are required in order to assess the importance of morphology in intrasexual competition. These are especially needed in species that are polygamous or are highly morphologically variable.

Few studies have investigated the correlates and

consequences of dominance behavior among so many individuals whose histories were known. A major contribution of this thesis was to show the importance of such complete information to the study of dominance.

This study was carried out in a population of monogamous territorial birds. However, dominance behavior is widespread among social animals, and the two factors identified in this study that influenced dominance, sex and age, are common attributes to many of them. I believe that this thesis suggests valuable avenues for further research into the origins and the significance of dominance behavior.

LITERATURE CITED

Alatalo, R.V., Lundberg,A.,& Stahlbrandt,K. 1984. Female mate
      choice in the pied flycatcher *Ficedula hypoleuca*. Behav.
      Ecol. Sociobiol. in press.

Amadon, D. 1943. Bird weights as an aid in taxonomy. Wilson
      Bull. 55:164-177.

Amadon, D. 1959. The significance of sexual differences in size
      among birds. Proc. Am. Phil.Soc. 103:531-536.

Appleby, M.C. 1982. The consequences and causes of high social
      rank in red deer stags. Behaviour 82:259-273.

Appleby, M.C. 1983. The probability of linearity in hierarchies.
      Anim. Behav. 31:600-608.

Bailey, R.O. 1979. Methods of estimating total lipid content in
      the redhead duck (*Aythya americana*) and an evaluation of
      condition indices. Can. J. Zool. 57:1830-1833.

Baker, M.C. and Fox, S.F. 1978. Dominance, survival, and enzyme
      polymorphism in dark-eyed juncos, *Junco hyemalis* .
      Evolution 32:697-711.

Baker, M.C., Belcher, C.S., Deutsch, L.C., Sherman, G.L., and
      Thompson, D.B. 1981. Foraging success in junco flocks and
      the effects of social hierarchy. Anim. Behav. 29:137-142.

Balph, M.H. 1975. Wing length, hood coloration, and sex ratio in
      dark-eyed juncos wintering in Northern Utah. Bird-banding
      46:126-130.

Blake, C.H. 1962. Wing length of the slate-colored junco. Bird-
      banding 33:97-99.

Boag, D.A. 1982. How dominance status of adult Japanese quail
      influences viability and dominance status of their
      offspring. Can. J. Zool. 60:1885-1891.

Boag, D.A. and Alway J.G. 1980. Effect of social environment within the brood on dominance rank in gallinaceous birds (Tetraonidae and Phasianidae) Can. J. Zool. 58:44-49.

Boag, D.A. and Alway J.G. 1981. Heritability of dominance status among Japanese quail: A preliminary report. Can. J. Zool. 59:441-444.

Boag, P. T. 1983. The heritability of external morphology in Darwin's ground finches (Geospiza) on Isla Daphne Major, Galapagos. Evolution 37:877-894.

Boersma, D. and Ryder J.P. 1984. Reproductive performance and body condition in nesting ring-billed gulls. J. Field Ornith. 54:374-380.

Brace, R.C. & Pavey, J. 1978. Size-dependent dominance hierarchy in the anemone Actina equina . Nature, Lond. 247:289-290.

Brawn,J.D. & Samson, F.B. 1983. Winter behavior of Tufted Titmice. Wilson Bull. 95:222-232.

Brian, A.D. 1949. Dominance in the great tit. Scot. Nat. 61:144-155.

Brown, J.L. 1963. Aggressiveness, dominance and social organization in the Stellar Jay. Condor 65:460-484.

Brown, J.L. 1975. The evolution of behavior. W.W. Norton and Company Inc., New York. 761pp.

Brown, J.L., Brown, E.R. & Brown, S.D. 1982. Morphological variation in a population of grey-crowned babblers: correlations with variables affecting social behavior. Behav. Ecol. Sociobiol. 10:281-287.

Caldwell, R.L. and Dingle, J. 1979. The influence of size differential on agonistic encounters in the mantis shrimp Gonodactylus viridus . Behavior 68:255-264.

Clark, G.A. 1979. Body weights of birds: a review. Condor 81: 193-202.

Clutton-Brock T.H., Guinness, F.H., and Albon, S.D. 1982. Red deer: behavior and ecology of two sexes. The University of Chicago Press, Chicago.

Collias,N.E. 1943. Statistical analysis of factors which make for success in initial encounters between hens. Am. Nat. 77:519-538.

Collias, N.E. & Taber, R.D. 1951. A field study of some grouping and dominance relations in ring-necked pheasants. Condor 53:265-275.

Connell, C.E., Odum, E.P. & Kale, H. 1960. Fat-free weights of birds. Auk 77:1-9.

Coutee, E.L. 1967. Agonistic behavior in the American goldfinch. Wilson Bull. 79:89-109.

Craig, J.V., Ortmann, L.L., and Guhl, A.M. 1965. Genetic selection for social dominance ability in chickens. Anim. Behav. 13:114-131.

Darwin, C.R. 1907. The descent of Man and selection in relation to sex. New York, New York:J.A.Hill and Company.

Dawkins, R. and Krebs, J.R. 1978. Animal signals: information or manipulation? In Behavioural Ecology. An evolutionary approach. Eds. Krebs, J.R. and Davies, N.B. Sinauer Associates, Inc. Sunderland, Massachusetts. pp 282-312.

De Vos, G.J. 1983. Social behavior of black grouse: an observational and experimental field study. Ardea 71:1-103.

Dhondt, A.A. 1979. Summer dispersal and survival of juvenile great tits in southern Sweden. Oecologia 42:139-157. .

Dhondt, A.A. and Huble, J. 1968. Fledging date and sex in relation to dispersal in young tits. Bird Study 15:127-134.

Dhondt,A.A., Eyckerman, R. & Huble, J. 1979. Will great tits become little tits? Biol. J. Linn. Soc. 11:289-294.

Dixon,K.L. 1965. Dominance-subordination relationships in the mountain chickadee (Parus gambeli) . Condor 67:291-299.

Downhower, J.F. 1976. Darwin's finches and the evolution of sexual size dimorphism in body size. Nature 263:558-563.

Ewald,P.W. & Rohwer, S.A. 1980. Age, coloration and dominance in non-breeding hummingbirds: a test of the asymmetry hypothesis. Behav. Ecol. Sociobiol. 7:273-279.

Fretwell, S.D. 1969. Dominance behavior and winter habitat distribution in juncos (Junco hyemalis) . Bird-banding 40: 1-25.

Fretwell, S.D. 1972. Populations in a seasonal environment. Princeton,New Jersey: Princeton University Press.

Gatti, R.C. 1983. Spring and Summer age separation techniques for the mallard. J. Wildl. Manage. 47:1054-1062.

Garnett, M.C. 1981. Body size, its heritability and influence on juvenile survival among great tits, Parus major . Ibis 123:31-41.

Gauthreaux, S.A. 1978. The ecological significance of behavioral dominance. In: Perspectives in Ethology vol.3 (eds. P.P.G. Bateson & P.H. Klopfer), pp.17-54.

Gilbert, N. 1973. Biometrical interpretation. Oxford University Press, London. 125pp.

Glase, J. 1973. Ecology and social organization of the black-capped chickadee. Living Bird 12:235-267.

Greenberg, R.E., Etter, S.L. & Anderson, W.L. 1972. Evaluation of proximal primary feather criteria for aging wild pheasants. J. Wildl. Manage. 36:700-705.

Greenwood, P.J., Harvey, P.H., and Perrins, C.M. 1979. The role of dispersal in the great tit: the causes, concequences, and heritability of dispersal. Jour. Anim. Ecol. 48:123-142.

Halse, S.A. & Skead D.M. 1983. Wing moult, body measurements and condition indices of spur-winged geese. Wildfowl 34,108-114.

Hamilton, T.H. 1961. The adaptive significance of intraspecific trends of variation in wing length and body size among bird species. Evolution 15:180-195.

Hannon, S.J. & Roland, J. 1984. Physiological factors influencing territory acquisition and retention in the Willow Ptarmigan. Can. J. Zool. in press.

Helms, C.W., Aussiker, E.B., Bower, E.B. & Fretwell, S.D. 1967. A biometrical study of the major body components of the slate-colored junco, Junco hyemalis . Condor 69:560-578.

Hinde, R.A. 1956. A comparative study of the courtship of certain finches (Fringillidae) . Ibis 98:1-23.

Howard, R.D. 1983. Sexual selection and variation in reproductive success in a long-lived organism. Am. Nat. 122:301-325.

Hrdy, S.B. 1977. The langurs of Abu. Harvard University Press. Cambridge Massachusetts. 360pp.

James, F.C. 1970. Geographic size variation in birds and its relationship to climate. Ecology 51:365-390.

Jehl, J.R. 1970. Sexual selection for size differences in two species of sandpipers. Evolution 24:311-319.

Ketterson, E.D. 1979. Aggressive beahvior in wintering dark-eyed juncos: determinants of dominance and their possible relation to geographic variation. Wilson Bull. 91:371-383.

Ketterson, E.D. and King, J.R. 1979. Metabolic and behavioral responses of fasting in the white-crowned sparrow (Zonotrichia luecophrys gambelii). Physiol. Zool. 50:115-129. .

Kikkawa, J. 1961. Social behavior of the white-eye Zosterops lateralis in winter flocks. Ibis 103:428-442.

Kikkawa, J. 1981. Winter survival in relation to dominance classes among silvereyes, Zosterops lateralis chlorocephala , of Heron Island, Great Barrier Reef. Ibis 122:437-446.

Knapton, R.W. 1973. Some ecological aspects of social beahvior in the song sparrow, Melospiza melodia). M.Sc. thesis, University of British Columbia, Vancouver.

Knapton, R.W. 1976. Dominance hierarchies in winter song sparrows. Condor 78:567-569.

Knapton, R.W. & Krebs, J.R. 1974. Settlement patterns, territory size, and breeding density in the song sparrow (Melospiza melodia) . Can. J. Zool. 52:1413-1420.

Krebs, J.R. 1983. Territorial defence in the great tit (Parus major): do residents always win? Behav. Ecol. Sociobiol.

LeBoeuf, B.J. and Peterson, R.S. 1969. Social status and mating activity in elephant seals. Science 1633:91-93.

Lill, A. 1976. Lek behavior in the golden-headed manakin (Pipra erythrocephala) in Trinidad (West Indies). Fortstschrift Verhaltenstorschung, heft 18.

Lundberg, A., Alatalo, R.V., Carlson, S. & Ulfstrand, S. 1981. Biometry, habitat distribution and breeding success in the Pied Flycatcher, Ficedula hypoleuca . Ornis Scand. 12:68-79.

Marler,P. 1955. Studies of fighting in chaffinches. 1. Behaviour in relation to the social hierarchy. Brit. J. Anim. Behav. 3:111-117.

Mayr, E. 1972. Sexual selection and natural selection. In Sexual selection and the descent of man, ed. B.G. Campbell, pp.87-104. Chicago:Aldine. 378pp.

Moore, M.C. 1984. Changes in territorial defense produced by changes in circulating levels of testosterone: a possible hormonal basis for mate-guarding behavior in white-crowned sparrows. Behavior 88:215-226.

Moore, N.J. 1972. Ethology of the Mexican junco (Junco phaenotus pallidus) . Ph.D. thesis, University of Arizona, Arizona.

Moss, R., Watson, A., Rothery, P., and Glennie, W.W. 1982. Inheritance of dominance and aggressiveness it captive red grouse Lagopus lagopus scoticus. Aggressive Behav. 8:1-18.

Morse, D.H. 1980. Behavioral mechanisms in ecology. Harvard University Press, Cambridge, Mass.

Mueller, H.C., Berger, D.D., and Allez, G. 1976. Age and sex variation in the size of goshawks. Bird-Banding 47:310-318.

Mueller, H.C., Berger, D.D., and Allez, G. 1979. Age and sex differences in the size of sharp-shinned hawks. Bird-Banding 50:34-44.

Mueller, H.C., Berger, D.D., and Allez, G. 1981. Age, sex, and seasonal differences in size of Cooper's hawks. J. Field Ornith. 52:112-126.

Murchison, C., Pomerat, C.M. & Zarrow, M.X. 1935. The experimental measurement of a social hierarchy in Gallus domesticus . V. The post-mortem measurement of anatomical features. J. Soc. Psychol. 6:172-181.

Newton, I., Marquiss, M. & Village, A. 1983. Weights, breeding and survival in European sparrow hawks. Auk 100:344-354.

Odum, E.P. 1942. The annual cycle of the black-capped chickadee. 12:113-119.

Parker, G.A. 1974. Assessment strategy and the evolution of fighting behavior. J. Theor. Biol. 47:223-243.

Perrins, C. 1963. Survival in the great tit, Parus major. Proc. XIII Intern. Ornith. Congr.:717-728

Peters, Wm. D. & Grubb, T.C. 1983. An experimental analysis of sex-specific foraging in the downy woodpecker, Picoides pubescens . Ecology 64:1437-1443.

Piersma, T. 1984. Estimating energy reserves of great crested grebes Podiceps cristatus on the basis of body dimensions. Ardea 72:119-126.

Power, D.M. 1969. Evolutionary implications of wing and size variation in the red-winged blackbird in relation to geographic and climatic factors: a multiple regression analysis. Syst. Zool. 18:363-373.

Price, T.D. 1984a. Sexual selection on body size, territory and plumage variables in a population of Darwin's Finches. Evolution, in press.

Price, T.D. 1984b. The evolution of sexual size dimorphism in Darwin's finches. Am. Nat. 123, in press

Rand, A.L. 1961. Some size gradients in North American birds. Wilson Bull. 73:46-56.

Richards, S.M. 1974. The concept of dominance and the methods of assessment. Anim. Behav. 22:914-930.

Rohwer, S.A. 1975. The social significance of avian winter plumage variability. Evolution 29:593-610.

Rohwer, S.A. and Rohwer, F.C. 1978. Status signaling in Harris' sparrows: experimental deceptions achieved. Anim. Behav. 26:1012-1022.

Rohwer, S.A., Ewald, P.W. and Rohwer, F.C. 1981. Variation in size, dominance and appearance within and between sex and age classes of Harris' sparrows. J. Field Ornithol. 52: 291-303.

Rolhf, F.J. and Sokal, R.R. 1969. Statistical tables. W.H. Freeman and Company. San Francisco.

Sabine, W.S. 1959. The winter society of the Oregon junco: intolerance, dominance, and the pecking order. Condor 61: 110-135.

Safriel, U.N. 1981. Social hierarchy among siblings in broods of oystercatchers, Haematopus ostralegus . Behav. Ecol. Sociobiol. 9:59-64.

Schneider, K.C.J. 1979. Dominance hierarchies, foraging and predation in winter flocks of the white-throated sparrow (Zonotrichia albicollis) . Ph.D. thesis Princeton University, New Jersey.

Schroder, S.L. 1981. The role of sexual selection in determining overall mating patterns and mate choice in chum salmon. Ph.D. thesis, University of Washington, Seattle, Washington.

Searcy, W.A. 1979a. Morphological correlates of dominance in captive male red-winged blackbirds. Condor 81:417-420.

Searcy, W.A. 1979b. Male characteristics and pairing success in red-winged blackbirds. Auk 96:353-363.

Searcy, W.A. 1979c. Size and mortality in male yellow-headed blackbirds. Condor 81:304-305.

Searcy, W.A. 1979d. Sexual selection and body size in male red-winged blackbirds. Evolution 33:649-661.

Searcy, W.A. 1982. The evolutionary effects of mate selection. Ann. Rev. Ecol. Syst. 13:57-85.

Searcy, W.A. and Wingfield, J.C. 1980. The effects of androgen and antiandrogen on dominance and aggressiveness in male red-winged blackbirds. Horm. Behav., 14:126-135.

Selander, R.K. & Johnston, R.F. 1967. Evolution of the house sparrow. I. Intrapopulation variation in North America. Condor 69:217-258.

Selander, R.K. 1972. Sexual selection and dimorphism in birds. In: Sexual selection and the descent of man 1871-1971(ed. B.G. Campbell), pp.180-230. Chicago:Aldine Atherton.

Shawcross, J.E. 1982. Agonistic behavior over food and perch space in the male Quelea quelea. Anim. Behav. 30:901-908.

Shoemaker, H.H. 1939. Social hierarchy in flocks of the canary. Auk 56:381-406.

Slagsvold, T. 1982. Criteria for estimating the condition of birds: relationship between fat content and body size dimensions in the hooded crow Corvus corone cornix. Ornis Scand. 13:141-144.

Smith, J.N.M. 1981. Cowbird parasitism, host fitness, and age of the host female in an island song sparrow population. Condor 83:152-161.

Smith, J.N.M. & Zach, R. 1979. Heritability of some morphological characters in a song sparrow population. Evolution 33:460-467.

Smith, J.N.M. and Dhondt, A.A. 1980. Experimental confirmation of heritable morphological variation in a natural population of song sparrows. Evolution 34:1155-1158.

Smith, J.N.M. and Roff, D.A. 1980. Temporal spacing of broods, brood size, and parental care in song sparrows (Melospiza melodia). Can. J. Zool. 58:1007-1015.

Smith, J.N.M., Montgomerie, R.D., Taitt,M.J. & Tom-Tov, Y. 1980. A winter feeding experiment on an island song sparrow population. Oecologia 47:164-170.

Smith, J.N.M., Yom-Tov, Y, and Moses, R. 1982. Polygyny, male parental care, and sex ratio in song sparrows: an experimental study. Auk 99:555-564.

Smith, S.M. 1976. Ecological aspects of dominance hierarchies in black-capped chickadees. Auk 93:95-107.

Smith, S.M. 1978. The "Underworld" in a territorial sparrow: adaptive stratagy for floaters. Am. Nat. 112:571-582.

Smith, S.M. 1984. Flock switching in chickadees: why be a winter floater? Am. Nat. 123:81-98.

Sokal, R.R. & Rohlf, F.J. 1982. Biometry. San Francisco, Calif.,:W.H. Freeman and Company.

Stiles, G. and Wolf, L. 1979. Ecology and evolution of lek mating behavior in the long-tailed hermit hummingbird. Ornith. Mongr. pp.27-88.

Suttie, J.M. 1983. Body size: dominance relationships in red deer stag calves. Anim. Behav. 31:610-611.

Syme, G.J. 1974. Competetive orders as measures of social dominance. Anim. Behav. 22:931-940.

Syme, G.J., Pollard, J.S., Syme, L.A., and Reid, R.M. 1974. An analysis of the limited access measure of dominance in the laboratory rat. Amin. Behav. 22:486-500.

Thompson, W.L. 1960. Agonistic behavior in the house finch part 2: factors in aggressiveness and sociality. Condor 62:378-402.

Tompa, F.S. 1964. Factors determining the numbers of song sparrows (Melpspiza melodia, Wilson) on Mandarte Island, B.C., Canada. Acta. Zool. Fenn. 109:3-68.

Tordoff, H.B. 1954. Social organization and behavior in a flock of captive non-breeding red crossbills. Condor 56:346-358.

Ulfstrand, S., Alatalo, R.V., Carlson, A. & Lundberg, A. 1981. Habitat distribution and body size of the great tit, _Parus major_. Ibis 123:494-499.

Watson, A,. & Parr, R. 1981. Hormone implants affecting territory size and aggressive and sexual behavior in red grouse. Ornis Scand. 12:55-61.

Watt, J.D., Ralph, C.J. & Atkinson, C.T. 1984. The role of plumage polymorphism in dominance relationships of white-throated sparrows. Auk 101:110-120.

Wiley, R.H. 1973. Territoriality and non-random mating in sage grouse, _Centrocercus urophasianus_.

Wilson, E.O. 1975. Sociobiology: the New Synthesis. Cambridge, Mass.,Harvard University Press.

Wishart, R.A. 1981. Wing-feather criteria for age separation of american wigeon. J.Wildl. Manage. 845:230-235.

Yasukawa, K. 1979. Territory establishment in red-winged blackbirds: importance of aggressive behavior and experience. Condor 81:258-264.

APPENDIX

Researchers have used several different methods to estimate dominance (reviewed by Syme 1974). Two methods, however, are most commonly employed by fieldworkers. Each of these uses the outcome of agonistic encounters over some resource, typically food, to determine the dominance of individuals. The individual that achieves a supplant (the winner) is said to dominate the one that is supplanted (the loser; Brown 1975). The Hierarchical Rank Method uses the outcome of paired encounters to construct dominance matrices (e.g. Sabine 1959, Brown 1963), within which individuals are ranked from one to n, where n equals group size. The Wins/Total Method simply divides the total number of wins per individual by the total number of encounters that the individual was observed in (e.g. Fretwell 1969, Kikkawa 1980). A variation on this method is the win/loss ratio employed by Searcy (1979).

Each of these methods has drawbacks. The Hierarchical Rank Method assumes that dominance is transitive, and this assumption is not always justified (Appleby 1983). In addition, when the number of individuals being sampled is large, dominance matrices are difficult to construct because the number of possible pair combinations increases as one half the square of the group size. This method also precludes the use of parametric statistics. On the other hand, the Wins/Total method, as I shall show here, is a very inaccurate measure of

dominance when the number of samples per individual is low. This method does, however, allow the use of parametric statistics, and it makes no assumption about the transitivity of dominance relations. Baker and Fox (1978) compared these two methods using data from captive and free-living juncos (Junco hyemalis) and found that the Wins/Total method provided unambiguous results, whereas the rank method sometimes produced more than one equally valid hierarchy. Baker and Fox (1978) did not, however, consider the effect that sample size has on estimation error.

I studied dominance in a population of song sparrows (Melospiza melodia) where the number of interacting birds exceeded 100. Thus, more than 5,000 pair combinations were possible in any one season. I therefore chose the Wins/Total method as the only feasible one for estimating dominance in the field among large groups of birds. After choosing this method, I had to devise a scheme to account for estimation error. Previous researchers have simply excluded from their analyses birds with less than five observations in order to reduce error in dominance estimates (e.g. Fretwell 1969, Kikkawa 1980). However, the 95% confidence limits for a value of 50% based even on ten observations are plus or minus 31.3%. Such a large error is unacceptable. Here, I account for the effect that estimation error has on least-squares type analyses, using standard statistical techniques.

The accuracy of any individual percentage increases with the number of samples upon which it is based. Thus, the confidence interval for a value of 50% is reduced from plus or minus 31.3% to plus or minus 10.1% as sample size increases from ten to 100 (Rohlf and Sokal 1969). Gilbert (1973) points out that the variance of a percentage, based upon N observations, is proportional to 1/N. He therefore recommended that percentage data based on radically different samples be weighted by one over the variance of the estimate. In the case of percentages based on N successive binomial trials, the appropriate weight is simply N (Gilbert 1973). Weighting has the effect of increasing the relative contribution of estimates based on larger, more accurate samples to the total (weighted) sums of squares.

My data were distributed approximately normally, and the angular transformation did not improve their fit. I therefore wished to determine the appropriate weight empirically, rather than immediately accepting the theoretical solution suggested above. I did this by estimating the relationship between the variance of the estimate and the number of observations it was based on. The data used for this purpose were obtained by observing the outcomes of agonistic encounters between color-marked yearling song sparrows at feeding tables. Details of the study site and methods employed are given in Chapter One. To estimate the variance of the Wins/Total dominance measure, I used data from twenty-five birds which had been observed in over

100 encounters (range 112-200), and whose sequence of interactions in time was fully known. Then, assuming that the variance is proportional to the mean-squared error of the estimates, I calculated the deviation of each successive estimate from the final estimate as indicated by:

Deviation = (wins/total) - (wins/total)
         N,bird   N observation   final

Where N is the observation number from one to 100. This generated 2,500 deviations. I summed the squared deviations for all birds over each observation number, and then multiplied this sum of the squares by 1/N to obtain the mean-squared error of the estimate which corresponded to observation N. A curve fitted to these points had the equation:

$$Y = .24 * X^{-.93}, \text{ r-squared} = 0.98 .$$

Where Y is the mean-squared deviation and X is the observation number. The weight is simply one over the X-term, which is very close to the theoretically predicted weight of N suggested by Gilbert (1973). I therefore accepted N as the appropriate weight.

I next wished to test the validity of this weighting scheme using the actual data. To do this, I first assumed that a sample dominance estimate more accurately reflected a bird's average chances of winning an encounter as the sample size of the estimate increased. I then chose a variable (hatch date) that was found to be highly correlated with the weighted dominance estimate. If the weighted correlation is correct, then similar results should be reached if only the best estimated samples are used to approximate the correlation, as if the weighted analysis were used.

As expected, when the acceptable minimum number of samples per estimate is increased from zero to one hundred, the correlation coefficient between dominance and hatch date increases linearly from 0.21 to 0.86 respectively (1983 data, n=112). The second figure is very similar to those obtained from weighted analyses (Table 6, Chapter One). The same effect of sample size on the correlation between two variables was also observed for correlations between morphology and dominance (Table 4, Chapter One). In cases where no significant correlations were found between dominance and an independent variable in weighted analyses, they were also absent when only estimates based on large samples were used.

These results confirm that this weighting scheme is a valuable tool to account for errors in dominance estimates based on win/loss data. It is important to note, however, that this

procedure is no alternative to the rigorous collection of data. If all estimates are based on very small samples, errors in sample estimates may prevent a statistical correlation from being found when a correlation of biological significance does indeed exist.

In summary, researchers that have used win/loss data to estimate the dominance of individuals have not seriously considered the effect that estimation error may have had on their analyses. The common procedure to deal with this problem has been to exclude from analyses all estimates based on fewer than five samples, and to treat all those based on more than five as equally good. The analyses presented here show that this is not a valid assumption. This failure to account for estimation error in this case means that biological relationships may be partially or totally obscured. The effect that error in estimates has can be accounted for using the standard statistical procedures reviewed here. I justify this procedure for the analyses presented in this thesis.