

THE UNIVERSITY OF CALGARY

DIFFERENTIAL MIGRATION IN THE EVENING GROSBEAK
(COCCOTHRAUSTES VESPERTINUS): A TEST OF HYPOTHESES

BY

DAVID R. C. PRESCOTT

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SUBMITTED TO THE FACULTY OF GRADUATE STUDIES
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DEGREE OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF BIOLOGICAL SCIENCES

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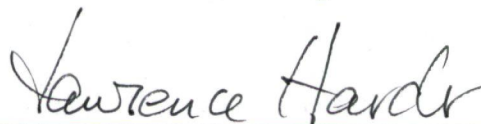


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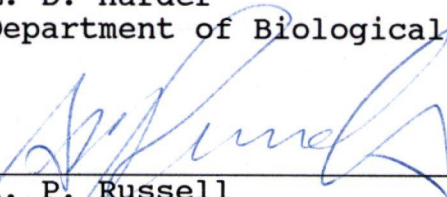
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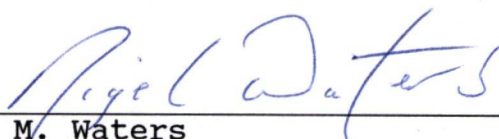
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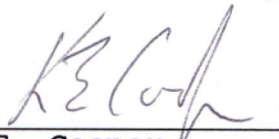
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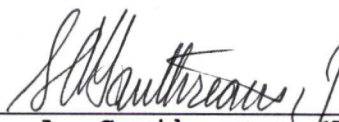
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ABSTRACT

Age or sex differences in winter distribution characterize many bird species migrating within temperate North America. Such "differential migration" could result from: (1) selection for early arrival by territorial individuals on the breeding grounds ("arrival time hypothesis"); (2) variable ability, resulting from age or sex differences in body size, to tolerate cold temperatures or periods of food shortage ("body size hypothesis"); and (3) differences in social-dominance rank, with subordinate classes making longer migrations from breeding grounds ("social dominance hypothesis"). This study tests predictions of these hypotheses in a suspected differential migrant, the Evening Grosbeak (Coccothraustes vespertinus).

Analyses of banding data confirmed that the Evening Grosbeak is a differential migrant. Males comprised 53 to 65% of wintering individuals in the north, but only 18 to 27% in the south. Neither sex showed age differences in distance migrated.

The chronology of northward movement in spring was similar for both sexes, suggesting that males should arrive earlier on the breeding grounds. However, southern-wintering males begin migrating earlier than males in the north. Therefore, the timing of migration may be as important for early arrival as is proximity to breeding

areas. The applicability of the arrival time hypothesis was further questioned by the lack of territory defence, and observations that pair bonds may form before migration is terminated. Sex differences in body size (males > females) were consistent with the body size hypothesis, but age differences (adults > immatures) were not. Males endured severe cold stress longer than females, but this difference was independent of body size. There was no age difference in cold tolerance, nor any effects of age, sex or body size on fasting endurance. Thus, the body size hypothesis was unsupported, but cold tolerance may influence the winter distribution of the sexes. Males were socially dominant over females. Dominant individuals gained priority of access to food, accruing a net energetic advantage over subordinates (as indicated by doubly-labelled water). Females may therefore be forced to undertake longer migrations than males in order to survive the winter. Age differences in rank (immatures > adults) were inconsistent with the social dominance hypothesis, but the strength of this tendency may be insufficient to influence the distribution of age classes during winter.

Sexual differences in dominance and cold tolerance may be the most important selective forces in the evolution of differential migration in Evening Grosbeaks. The relationship of these factors to winter movements, and their fitness consequences, should be investigated further.

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CHAPTER 1

INTRODUCTION

1. Patterns of Migration in Birds

In its broadest sense, migration can be defined as "the act of moving from one spatial unit to another" (Baker 1978). This definition encompasses all locomotory movements made by animals, and most biologists have emphasized that "true" migration should be defined as those movements that occur with some degree of temporal regularity (Heape 1931, Ricard 1969, Street 1976). A variety of temporal scales can be considered (Gauthreaux 1982, 1985), but migration usually occurs either on a daily basis (e.g., regular movements between feeding and resting areas) or with seasonal cyclicity (e.g., movements between breeding and nonbreeding ranges).

Both types of migration have been observed in a wide variety of animal types, but seasonal migrations are perhaps most prevalent among the vertebrates. Such movements have been well documented in species of fish, amphibians, reptiles, and mammals (see reviews in Baker 1978 and Rankin 1985), but are undoubtedly most prevalent in birds (Orr 1970, Street 1976). Almost all of the 33 orders of birds contain migratory species (Pettingill 1970), and about half of all bird species have been

described as being migratory (Jarman 1972). The diversity of avian migration systems, coupled with the high probability that the migratory habit in birds has evolved independently on many different occasions (Evans 1985), provides an unparalleled opportunity to investigate the proximate and ultimate factors responsible for the evolution of animal migration. It is therefore not surprising that birds have been the predominant subjects of investigations of migration (Dorst 1962, Orr 1970, Gauthreaux 1982).

Although a bird species may be designated as being "migratory" or "non-migratory", it is clear that individuals within a species may pursue different migration strategies. Two such strategies have been identified. In partial-migrant species, some individuals migrate from the breeding area while other individuals remain on the breeding grounds for the winter. In differential migrants, all individuals leave the breeding grounds during winter, but the distance migrated differs among individuals (Gauthreaux 1982, Ketterson and Nolan 1985, Terrill and Able 1988). In some cases, different populations of the same species may exhibit different types of migratory behavior. For example, Mead (1983) reported that populations of the Blackcap (Sylvia atricapilla) breeding at high latitudes in Europe are differential migrants, but

mid-latitude populations are partial migrants and those at the lowest latitudes are sedentary.

The tendency to migrate is often associated with differences in age and sex in both partial and differential migrants. For example, in partial migrants, adult males tend to remain on the breeding grounds during winter, whereas females and immatures (individuals less than 1 year of age) of both sexes tend to winter at more southerly sites (Lack 1944, Gauthreaux 1982, Hilden 1982, Ketterson and Nolan 1985, Smith and Nilsson 1987). In differential migrants, males usually winter farther north¹ than females (Howell 1953, Ketterson and Nolan 1976, 1979, Nichols and Haramis 1980, Myers 1981, Dolbeer 1982, Alexander 1983, Morton 1984), although the reverse pattern has been documented in several species (Johnston 1970, Mueller et al. 1977, Myers 1981, Kerlinger and Lein 1986). Differences in the latitudinal distribution of age classes during winter have also been documented in differential migrants. In most species, adults tend to winter north of immatures (Gauthreaux 1978). However, the tendency for

¹ Virtually all evidence for differential migration in birds has been accumulated from species that inhabit the northern hemisphere throughout the year. Throughout this dissertation, the phrases "farther north" and "closer to the breeding grounds" are therefore used synonymously.

immatures to winter north of adults has also been reported (Ketterson and Nolan 1982, 1985, Morton 1984, Prescott and Middleton 1990).

Partial and differential migrants differ only in the extent to which some individuals remain year-round on breeding areas, and both patterns have been identified in a wide range of bird species (see Gauthreaux 1982). This dissertation focuses on the ecology and evolution of differential migration, which appears to be the prevalent pattern among north-temperate zone migrants in North America. To date, at least 28 species of North American birds have been identified as being differential migrants with respect to either sex or age (Table 1). Although the strength of evidence provided (i.e., number of individuals and proportion of the nonbreeding range considered) and type of data analyzed for age and sex differences in distance migrated differs widely for each species, it is clear that differential migration is a widespread phenomenon among North American birds. Even so, detailed investigation has failed to detect age or sex differences in winter distribution for a number of species, including the Mallard (Anas platyrhynchos, Nichols and Hines 1987), American Black Duck (A. rubripes, Diefenbach et al. 1988), Lesser Scaup (Aythya affinis, Alexander 1983), Red Phalarope (Phalaropus fulicarius, Myers 1981), American

TABLE 1. Literature accounts of differential migration in North American birds, and hypothesis(es) proposed to account for differences in distance migrated among age or sex classes.

Species	Class Farthest North		Favored Hypothesis ^a		Type of ^b Evidence	Source ^c
	Sex	Age	Sex	Age		
Wood Duck (<u>Aix sponsa</u>)	None	Adult	-	?	BR	1
Canvasback (<u>Aythya valisineria</u>)	Male	?	SD	-	FO	2
	Male	?	SD,BS	-	BR	3
Redhead (<u>A. americana</u>)	Male ^d	?	?	-	FO	2
Ring-necked Duck (<u>A. collaris</u>)	Male	?	SD	-	FO	2
Greater Scaup (<u>A. marila</u>)	Male ^d	?	?	-	FO	2
Common Goldeneye (<u>Bucephala clangula</u>)	Male	?	SD,BS,AT	-	FO	4
Sanderling (<u>Calidris alba</u>)	Female ^e	None	AT	-	M	5

TABLE 1, con't

Least Sandpiper (<u>C. minutilla</u>)	Male	?	AT	-	L	5
Western Sandpiper (<u>C. mauri</u>)	Male	?	AT	-	L	5
Herring Gull (<u>Larus argentatus</u>)	?	Immature	-	?	BR	6
Northern Goshawk (<u>Accipiter gentilis</u>)	Female?	Adult	SD?	SD	FO	7
Rough-legged Hawk (<u>Buteo lagopus</u>)	Female	?	SD	-	M	8
American Kestrel (<u>Falco sparverius</u>)	Male	?	AT	-	FO	9
Mourning Dove (<u>Zenaida macroura</u>)	Male	Adult	?	?	BR	10,11
Snowy Owl (<u>Nyctea scandiaca</u>)	Female	Adult	SD	SD	M	12
Yellow-bellied Sapsucker (<u>Sphyrapicus varius</u>)	Male	?	SD,BS,AT	-	M	5,13
European Starling (<u>Sturnus vulgaris</u>)	None	Adult	-	SD	BR	14

TABLE 1, con't

Palm Warbler (<u>Dendroica palmarum</u>)	Male	?	SD	-	M	8
Indigo Bunting (<u>Passerina cyanea</u>)	Female	?	?	-	FO	15
Savannah Sparrow (<u>Passerculus sandwichensis princeps</u>)	Male ^f	?	SD	-	M	8
Song Sparrow (<u>Melospiza melodia</u>)	Male	?	?	-	FO	16
American Tree Sparrow (<u>Spizella arborea</u>)	Male	?	?	-	M	17,18
Dark-eyed Junco (<u>Junco hyemalis</u>)	Male	Immature	None	None	B, BR, FO	19,20,21
White-crowned Sparrow (<u>Zonotrichia leucophrys</u>)	Male	Immature	SD, BS, AT	?	L, FO, M	5,22,23
Red-winged Blackbird (<u>Agelaius phoeniceus</u>)	Male	Adult?	BS	SD	BR	14
	Male	Immature	?	?	M	24
Common Grackle (<u>Quiscalus quiscula</u>)	Male	Adult	BS	SD	BR	14

TABLE 1, con't

American Goldfinch (<u>Carduelis tristis</u>)	Male	Immature	SD,BS	None	B,BR	25
House Finch (<u>Carpodacus mexicanus</u>)	Male	?	BS	-	B,BR	26

^a SD = Social dominance hypothesis; BS = Body size hypothesis; AT = Arrival time hypothesis

^b B = Banding data; BR = Band recovery data; FO = Field observations; L = Literature surveys; M = analysis of museum specimens or locally-collected birds

^c (1) Hepp and Hines 1991; (2) Alexander 1983; (3) Nichols and Haramis 1980; (4) Sayler and Afton 1981; (5) Myers 1981; (6) Moore 1976; (7) Mueller et al. 1977; (8) Russell 1981; (9) Arnold 1991; (10) Tomlinson et al. 1988; (11) Dunks et al. 1982; (12) Kerlinger and Lein 1986; (13) Howell (1953); (14) Dolbeer 1982; (15) Johnston 1970; (16) Nice 1937; (17) Heydweiller 1936; (18) Heydweiller 1942; (19) Ketterson and Nolan 1976; (20) Ketterson and Nolan 1979; (21) Ketterson and Nolan 1983; (22) King et al. 1965; (23) Morton 1984; (24) James et al. 1984; (25) Prescott and Middleton 1990; (26) Belthoff and Gauthreaux 1991

^d Western North America only

^e Immature birds only

^f Rising (1988) found no differential migration by sex in a continent-wide sample of Savannah Sparrows

Woodcock (Philohela minor, Diefenbach et al. 1990), and Brown-headed Cowbird (Molothrus ater, Dolbeer 1982).

2. Hypotheses for Differential Migration

At least seven hypotheses have been proposed to account for latitudinal segregation of age and sex classes during the nonbreeding season (see below). All of the hypotheses implicitly or explicitly assume that the costs of migration (in terms of energy expenditures, mortality, or time unavailable for breeding) increase with distance travelled from the breeding grounds, and that natural selection favors individuals that migrate only as far south as necessary to survive the winter (see Nichols and Haramis 1980). In energetic terms, this assumption is undoubtedly true because flight costs must accumulate as the distance travelled increases. The importance of the other potential costs of migration is unclear, mainly because it is difficult to determine the origin, destination, and life histories of individual migrants. Ketterson and Nolan (1982) found some support for a relationship between distance travelled and mortality. They calculated that northern- and southern-wintering Dark-eyed Juncos had approximately equal annual survivorship, but that within-winter survival was higher for birds in the south. This suggests that southern-wintering birds must experience higher mortality at other times of the year, and most

likely during their longer migrations. In short, the assumption that the costs of migration increase with distance travelled seems justified.

For convenience, the hypotheses for differential migration can be divided into three "major" and four "minor" hypotheses, based on the frequency with which they have been invoked to account for the evolution of differential migration of various avian species. The three "major" hypotheses (which are the focus of the present study) are as follows:

(1) Arrival Time Hypothesis: - This hypothesis argues that competition for resources (territories, mates) during the breeding season places a premium on early arrival on the breeding grounds for certain sex and/or age groups (Myers 1981). Therefore, the class with most to gain from early arrival should winter as close to breeding sites as possible (i.e., at higher latitudes). In most avian species, males defend breeding territories and should therefore winter farthest north. The relative advantages of early arrival by different age classes is less clear. Ketterson and Nolan (1983) argued that young birds, which are breeding for the first time, might gain more from early arrival than experienced breeders, which can usually regain former nesting territories if they are already occupied.

(2) Body Size Hypothesis: - This hypothesis states

that there is a relationship between body size and survival, such that larger-bodied individuals (or age/sex classes) are better able to tolerate harsh climatic conditions that occur during winter. The most often-cited mechanism for size differences in survival is fasting endurance (Ketterson and King 1977, Ketterson and Nolan 1978, Lindstedt and Boyce 1985). Larger individuals can store more fat than smaller individuals, and because mass-specific metabolic rate declines with body size, fat is catabolized at a slower rate in large-bodied individuals (Kendeigh 1945, Calder 1974). Thus, when snowfall restricts food availability, large individuals should have a higher probability of survival. Within temperate regions, such conditions should occur most frequently in northern areas, because snowfall tends to increase with latitude (Potter 1965, Ruffner and Bair 1987).

A second mechanism for the hypothesized relationship between body size and survival is cold tolerance (Kendeigh 1969). Large individuals have a smaller surface-area-to-volume ratio than do smaller individuals. That is, the volume of heat-producing tissues increases faster than the surface area of the body (across which heat is lost) as body size increases (Hamilton 1961, Kendeigh 1969, Calder 1974). Therefore, larger-bodied individuals (or age/sex classes) should be best able to endure periods of extreme

cold. In the northern hemisphere, mid-winter temperatures decrease with increasing latitude (Bryson and Hare 1974, Ruffner and Bair 1987). Accordingly, large individuals should tend to occupy the most northerly areas during winter.

(3) Social Dominance Hypothesis: - The social dominance hypothesis posits that competition for resources (especially food) on the wintering grounds forces subordinate individuals (usually immatures and females) to undertake longer migrations than dominants. As a result, socially-subordinate age and sex classes should be found farther south during the winter (Gauthreaux 1978, 1982). This hypothesis assumes that subordinate individuals are at an energetic disadvantage when in the company of dominants, and can more easily meet their energy requirements by migrating to areas where more dominant birds are less common.

The four "minor" hypotheses are as follows:

(4) Sexual Dimorphism Hypothesis: - Selander (1966) proposed that in sexually-dimorphic species, males and females (or different age groups) may be morphologically adapted to exploit different resources. Such differences could lead to geographic differences in the winter range of age and sex classes. Although males and females of some migratory species are known to occupy different habitats

during winter (e.g., Mills 1976, Lynch et al. 1985, Smallwood 1988), sexual dimorphism has rarely been considered as a factor influencing differential migration by birds. Russell (1981) argued that morphological differences among age and sex classes in most differential migrants are probably too small to influence resource partitioning.

(5) Physiological Readiness Hypothesis: - In many species of birds, migration begins soon after nesting is completed. Immature birds therefore have a relatively short period of time in which to complete development and prepare for their first migration. Prescott and Middleton (1990) proposed that, in some species, immature birds may be physiologically unprepared to migrate as far south as adults of the same species. This hypothesis could apply only to the few species (Table 1) where immatures winter farther north than adults, and might be especially applicable to species with relatively late breeding seasons (Prescott and Middleton 1990).

(6) Migration Costs Hypothesis: - Ketterson and Nolan (1983) suggested that natural selection would favor shorter migrations by individuals of particular age and sex classes if the risk of mortality during migration also differs among classes. It is often assumed that birds undertaking their first migratory journey suffer higher rates of

mortality than adults (Greenberg 1980, Ketterson and Nolan 1983, 1985). If so, then the migration costs hypothesis could apply to species where immature birds winter farther north than adults. Unfortunately, migration mortality is difficult to quantify (Owen and Black 1989), and interclass differences in the risks of migration are almost impossible to detect. Accordingly, this hypothesis has rarely been discussed in studies of differential migration.

(7) Migration Threshold Hypothesis: - Baker (1978) proposed a multifactorial model for the evolution of differential migration. He proposed that all individuals have a "migration threshold" determined by the relative costs and benefits (in terms of potential reproductive success) of migrating to different areas. The position of the threshold can be affected by numerous environmental variables which differ between alternate habitats (e.g., food availability, local climate, competitor density), as well by the age and experience of the individual. Each individual has a threshold determined by natural selection, and migration must occur if the threshold value is exceeded. Once migration is initiated, individuals should migrate until benefits (relative to costs) are maximized. Differential migration should result if this distance differs consistently among age and sex classes.

To date, only Ketterson and Nolan (1983) have

evaluated the importance of the migration threshold hypothesis in a differential migrant. They concluded that latitudinal differences in winter distribution by age and sex classes of the Dark-eyed Junco were better explained by the multifactorial model than by any single-factor hypothesis. However, they acknowledged that the model was extremely complex and lacked predictive powers. It is therefore questionable whether the migration threshold model could be of broad utility in determining the major factors responsible for the evolution of differential migration in birds.

During the past decade, virtually all studies that have detected age or sex differences in winter distribution for a particular species have attempted to evaluate the relative importance of the arrival time, body size and social dominance hypotheses to the evolution of differential migration. Support for all three hypotheses has been provided (Table 1) but, in almost all cases, the evidence used to support or reject each hypothesis has been descriptive in nature. For example, the observation that larger-bodied age or sex classes winter farthest north has been interpreted as support for the body size hypothesis. Similarly, the tendencies for behaviorally-dominant classes, or for individuals of the sex that establishes territories, to winter closest to the breeding grounds have

been cited as support for the social dominance and arrival time hypotheses, respectively. The major flaw in this approach is that, for most species, predictions from competing hypotheses are not mutually exclusive. For example, in most species studied to date, males are the larger sex, are socially dominant, and also establish breeding territories before the arrival of females. All three hypotheses therefore make the same prediction, that males should winter in the northern parts of the range. Thus, it has been difficult to identify single-factor hypotheses to account for differential migration (Ketterson and Nolan 1983) if, indeed, a single hypothesis is tenable for a given species. In order for competing hypotheses to be decoupled, a more complete knowledge of the importance and interaction of the factors influencing the choice of wintering sites is required. Furthermore, a larger comparative database is needed in order to generalize about the importance of each factor in the evolution of avian migration systems (King et al. 1965, Myers 1981).

Detailed attempts to unravel the relative importance of body size, social dominance and arrival time for differential migration have so far concentrated on a single species, the Dark-eyed Junco, in which males winter farther north than females, and birds in their first year of life winter north of adults of the same sex (Ketterson and Nolan

1976, 1979, 1983). Male juncos are larger than females (Nolan and Ketterson 1983) and, under conditions of food deprivation in the laboratory, can survive for longer periods of time (Stuebe and Ketterson 1982). Sexual differences in winter distribution are therefore consistent with the body size hypothesis. However, immature birds are smaller than adults of the same sex (Nolan and Ketterson 1983), yet have a more northerly distribution. Furthermore, there are no latitudinal trends in body size within any age/sex class during winter (Nolan and Ketterson 1983). Thus, body size differences alone do not appear to be responsible for differential migration in this species (Ketterson and Nolan 1983). As predicted by the social dominance hypothesis, male juncos are dominant over females (Balph 1977, Ketterson 1979), and subordinates are less likely to survive when food is in short supply (Baker and Fox 1978). However, immatures are subordinate to adults of the same sex (Ketterson 1979), and northern-wintering birds (presumed to be dominants under this hypothesis) do not dominate southern-wintering individuals under experimental conditions (Rogers et al. 1989, Cristol and Evers 1992). Social dominance is therefore of questionable importance in the migration system of the junco. Finally, the tendency for males (and particularly, immature males) to winter farthest north is consistent with the idea that individuals

of the territorial sex, and particularly those breeding for the first time, may winter closest to the breeding grounds to gain early access to reproductive resources. However, Ketterson and Nolan (1983) downplayed the importance of the arrival time hypothesis. They reasoned that the advantages of early arrival should not differ between age classes of females, yet these classes tend to winter at different latitudes.

In the absence of strong support for any single hypothesis, Ketterson and Nolan (1983) concluded that differential migration of the Dark-eyed Junco might best be explained by a model in which individuals of different age/sex classes select wintering sites based on an optimum balance of a multitude of factors (e.g., Baker 1978). They acknowledged that identifying the components of this multifactor model, and their relative importance, may prove to be impossible. Furthermore, the a posteriori nature of such a model would render it of weak predictive power.

3. Objectives

It is unreasonable to assume that differential migration can always be explained by single-factor hypotheses, or that the same factor(s) can account for age and sex differences in migration by different species (Ketterson and Nolan 1983). Nevertheless, the evaluation

of single-factor hypotheses provides a useful starting point for understanding the relative importance of different selective pressures to the evolution of differential migration for particular species (Myers 1981). The present study investigates the winter distribution of a North American finch, the Evening Grosbeak (Coccothraustes vespertinus), and attempts to evaluate the three major hypotheses as they apply to geographical differences in winter distribution of age and sex classes of this species. Specific objectives of this investigation are as follows:

- (1) To quantify the geographic distribution of age and sex classes of Evening Grosbeaks during winter in order to determine the patterns of differential migration in this species, and the annual consistency of such patterns.
- (2) To examine the timing and rates of spring migration by male and female Evening Grosbeaks from different wintering latitudes in order to determine whether the choice of wintering latitude influences the timing of arrival on the breeding grounds in spring.
- (3) To examine age, sex and geographical patterns of morphological variation in Evening Grosbeaks, in order to determine whether observed patterns of body size are consistent with predictions of the

body size hypothesis.

- (4) To evaluate the hypothesized relationships of fasting endurance and cold tolerance with body size in Evening Grosbeaks, in order to determine whether observed patterns of winter distribution can be attributed to physiological mechanisms.
- (5) To describe dominance relationships among age and sex groups in nonbreeding flocks of Evening Grosbeaks, in order to relate patterns of dominance to patterns of winter distribution by these groups.
- (6) To quantify the costs and benefits of flock membership to individual Evening Grosbeaks of different social rank, in order to determine whether subordinates are at an energetic disadvantage relative to dominants.

4. The Biology of the Evening Grosbeak

The Evening Grosbeak breeds throughout the coniferous forest regions of North America, including the boreal forests of Canada and the northern United States, and the cordilleran forests of the west (American Ornithologists' Union 1983). Three subspecies are recognized: C. v. vespertinus, which breeds in boreal forests east of the continental divide, C. v. brooksi which breeds in most of

the mountainous regions of the western United States and Canada, and C. y. montana, which breeds in the southwestern United States and northwestern Mexico (American Ornithologists' Union 1957). In general, the western subspecies are darker in color, and have longer, thinner bills than does C. y. vespertinus (Grinnell 1917).

The Evening Grosbeak is a sexually-dichromatic species. Males are mostly bright yellow, with black wings and a prominent white wing-patch, whereas females are dull yellow with grey-black wings (Peterson 1980). There are also slight differences in plumage among age classes. Both males and females in their first year of life have duller-colored wings than adults of the same sex. In addition, young males have black edging on the otherwise white tertial feathers (Yunick 1977). Males tend to have longer wings and are heavier than females (Balph 1976, Lago 1979). Size differences between age groups have not been investigated.

Nesting activity begins in late May or early June (Bekoff et al. 1987, Scott and Bekoff 1991). Unlike most other passerine birds, Evening Grosbeaks are not territorial during the breeding season (Scott and Bekoff 1991), and have been described as being semicolonial nesters (Hope 1947). Pair bonds are typically monogamous, but one instance of polygyny has been described (Fee and Bekoff

1986). Nests are constructed high up in a variety of trees, with coniferous species being preferred (Bekoff et al. 1989). Females do most of the nest construction. Males feed females during incubation, and both sexes feed the young (Scott and Bekoff 1991). Clutch size is typically two to five eggs (Speirs 1968, Scott and Bekoff 1991), and young leave the nest as early as late June (Shaub and Shaub 1953, Shaub 1956, Downs 1958). Evening Grosbeaks are primarily insectivorous while breeding (Dahlsten et al. 1985), with the preferred food being larvae of the spruce budworm, Choristoneura fumiferana (Blais and Parks 1964, Speirs 1968). Evening Grosbeaks shift their breeding areas from year to year (Shaub 1956), apparently in response to outbreaks of this insect (Morris et al. 1958, Blais and Parks 1964, Parks 1965).

Evening Grosbeaks are irruptive migrants, in which large-scale movements away from the breeding grounds occur in some years, but not in others (Bock and Lepthien 1976). In some winters, individuals may be found as far south as the Gulf of Mexico (Michael 1970, Jackson 1974). Although irruptive movements are known in C. y. brooksi, most birds wintering in non-breeding areas of eastern and central North America belong to the vespertinus subspecies (American Ornithologists' Union 1957, Bock and Lepthien 1976), suggesting that eastern birds may be more migratory

than those in the west (see also Balph and Lindahl 1978, Yunick 1983). The timing of fall migration varies but, during invasion years, large numbers of birds typically appear south of the breeding range between October and December (Shaub 1960, 1963, Dexter 1969). Return movements to the breeding grounds occur in April and May (Shaub 1960, 1963, Yunick 1983). Courtship is frequently observed before spring migration is terminated (Shaub 1956, 1963, Downs 1958, Jackson 1974).

During winter, grosbeaks occur in flocks numbering up to several hundred members (Mason and Shaub 1952). Individuals are reported to move freely among flocks (Parks 1945, Fast 1962), although studies of banded birds indicate that some flock members, despite travelling large distances, may remain together for several years (Magee 1930, Mason and Shaub 1949, Carrier 1957, Parks and Parks 1963). Wintering grosbeaks are almost exclusively vegetarian, and have been reported to eat a wide variety of seeds and fruits (Speirs 1968, Jackson 1974). Evening Grosbeaks are common visitors to bird feeders in winter, where they feed primarily on sunflower (Helianthus annuus) seeds. Intense aggression is commonly observed among flock members at feeders, and males are reported to be socially dominant over females (Balph and Balph 1976, Bekoff and Scott 1989).

5. The Evening Grosbeak as a Differential Migrant

Several authors have suggested that female Evening Grosbeaks may migrate farther than males during irruption years (Mason and Shaub 1949, Parks 1953, Shaub 1960, 1963, Balph and Balph 1976). This conclusion is based primarily on samples gathered by bird banders operating in restricted geographic areas and, to date, there has been no detailed investigation of geographic variation in age and sex composition of grosbeak populations over the entire winter range. However, a synthesis of literature accounts of sex ratios in different areas shows that the pattern described by previous authors may be real. Populations at northern latitudes are predominantly male, while those at more southerly sites are composed primarily of females (Table 2). It must be noted that these data were gathered during many different winters, and there is likely much annual variation in the latitudinal extent of migration, and in the number of individuals participating in these movements. Thus, although these data strongly suggest that differential migration of the sexes occurs, they provide only a weak assessment of the strength of the relationship between sex ratio and latitude, and provide no information about the annual consistency of differential migration nor the relationship between age ratios and latitude.

The suggested relationship between sex ratio and

TABLE 2. Literature accounts of sex ratios of Evening Grosbeaks during winter.

Location	Latitude (°N)	Proportion Male	n	Source
Rouyn-Noranda, QB	48	0.60	216	Prescott, unpubl.
Sault Ste. Marie, MI	46	0.54	185	Magee 1939
Ottawa, ON	45.5	0.38	708	Poulin and Blacquiere 1983
S. Londonderry, VT	42.5	0.76	314	Downs 1958
Northampton, MA	42.5	0.43	774	Mason and Shaub 1949 Shaub and Shaub 1950
Hartford, CT	42	0.42	923	Parks 1945, 1947
Logan, UT	42	0.41	300	Balph and Balph 1976
Northeastern OH	41.5	0.36	133	Dexter 1969, 1979
Carlisle, PA	40.5	0.51	408	Grimm 1954
Whiting, NJ	40	0.46	4087	Pharo 1978, 1979
Arlington, VA	39	0.29	1039	Fast 1962
Nacogdoches, TX	31.5	0.30	132	Michael 1970

latitude described above forms the basis for studying the factors responsible for differential migration in the Evening Grosbeak. In addition, several aspects of the biology of this species make it an ideal candidate for investigation. It occupies a wide geographical range during winter, so there is potential for latitudinal segregation of age and sex classes to occur. Age and sex can accurately be determined for most individuals, and data on the distribution of age and sex classes are readily available in computerized bird-banding databases. Large numbers of study skins are available in museum collections, which permits assessment of intraspecific and geographic variation in morphology of wintering individuals. Finally, individuals can be captured from the wild and maintained in captivity easily (e.g., Dawson and Tordoff 1959, West and Hart 1966). This offers the potential for captive studies of physiology and social behavior which are essential to understanding the mechanisms underlying differential migration.

Because of subspecific differences in morphology and migratory tendency (see Section 4, above), the present study is restricted to birds occurring east of the continental divide, and presumably of the nominate ("eastern") subspecies, *C. y. vespertinus*. By eliminating

the western subspecies, the complicating effects of altitude on the selection of wintering latitude are also minimized.

CHAPTER 2

GENERAL METHODS

The methodologies used in each section of this dissertation are generally distinct from each other. Specific methodologies will therefore be described in the chapters where they are used. Here, I describe only those procedures which are common to more than one chapter of this study.

1. Capture and Maintenance of Birds

Live Evening Grosbeaks used in social dominance, cold tolerance and fasting endurance trials were captured between 9 December 1989 and 23 January 1990, and between 11 November 1990 and 19 January 1991. All birds were captured from free-living flocks in one of four locations in south-central Alberta: Sundre (51°40'N, 114°30'W), Red Deer (52°10'N, 113°40'W), Water Valley (51°20'N, 114°30'W), or the Kananaskis Centre For Environmental Research, near Seebe (51°00'N, 115°00'W). All birds were either captured using traps baited with sunflower, green ash (Fraxinus pennsylvanica), or Manitoba maple (Acer negundo) seeds, or caught in mist nets erected in baited areas.

Upon capture, all birds were sexed, and aged as being either "immature" (first-winter) or "adult" (> first-winter) based on plumage criteria (Yunick 1977, Pyle et al.

1987) or by the extent of skull ossification (Pyle et al. 1987). Individuals were weighed using a portable spring balance (± 0.2 g), measured (see Section 2, below), and scored for subcutaneous fat deposits. The magnitude of fat deposits was classified on a scale of 0 (no visible fat) to 3 (extremely fat) in increments of 0.5 (after McCabe [1943], Helms and Drury [1960]). This nondestructive procedure has been widely used in ornithological research, and is known to give a reliable index of total body-fat in birds (Krementz and Pendleton 1990). All birds were then color-marked with plastic leg-bands for individual identification. If transportation was required, birds were housed individually in darkened 25 x 25 x 20 cm boxes constructed of plywood.

Captive birds were housed in a 4.0 x 8.0 x 2.5 m outdoor aviary at the Kananaskis Center for Environmental Research (where all experiments were conducted). The aviary was supplied with perches and a variety of coniferous vegetation for roosting cover. Water was available at all times for drinking and bathing, except during very cold weather when birds used snow as a source of drinking water. While in captivity, birds fed primarily on the same seeds used during trapping operations. These seeds were supplemented at various times with millet (Panicum sp.), cracked corn (Zea mays), apple (Malus sp.),

pin cherry (Prunus pensylvanica) and meal worms (Tenebrio molitor) to ensure a balanced diet. All food was dispensed from a centrally-located feeding tray.

In some experiments, birds were housed indoors for up to several days. In such cases, birds were removed from the aviary after being caught in hand nets or with baited traps. When indoors, birds were housed individually in 60 x 25 x 33 cm cages (hereafter, "individual cages"), and provided with food (as above) and water. It was noted early in the study that some birds sustained minor injuries when confined to small cages. This problem was remedied by lining each cage with cardboard. Holes were cut in the cardboard liner to permit light to enter the cage, and to allow for air circulation. Individual cages were usually placed inside environmental chambers at a constant 2°C temperature. Unless otherwise noted, the photoperiod in the chambers was adjusted (± 0.5 h) to correspond with naturally-occurring conditions.

At the termination of experiments, color bands were replaced with aluminum U. S. Fish and Wildlife Service bands, and birds were released to the wild. All individuals were released from captivity at least two hours before sunset, so that birds could locate food and roosting cover before nightfall.

2. Measurement of Overall Body Size

A measure of overall body size for individual birds was required for testing aspects of both the social dominance and body size hypotheses. There has been much recent discussion about the validity of various techniques to measure body size in birds. In most cases, researchers have used wing length as a measure of size, because it tends to be correlated with other univariate body measurements, and because it is easily and routinely recorded on captured birds (James 1970, Zink and Remsen 1986). However, many biologists have questioned whether wing length, or any other univariate measure, can adequately be used as a measure of body size (Zink and Remsen 1986, Rising 1988, Rising and Somers 1989, Freeman and Jackson 1990). It is now generally acknowledged that, when possible, body size should be estimated using a multivariate statistic derived from several univariate metrics which can be reliably and repeatably measured (Zink and Remsen 1986). Such a technique is used in this study.

Six external measurements (following Pettingill [1970] and Pyle et al. [1987]) were taken from all birds used in this study. Digital calipers (Mitotoyu model #500-321) were used to take five measurements, as follows: unflattened wing chord, bill length (exposed culmen), maximum bill width (width of lower mandible plus

ramphotheca measured at its junction with the facial feathers), maximum bill depth (measured from points on the midline of the upper and lower mandibles at their junctions with the forehead and chin feathers), and tarsometatarsus (hereafter, "tarsus") length (from the joint of the tibiotarsal/metatarsal bones to the distal end of the last undivided scute). In addition, I measured tail length by inserting a ruler between the middle retrices. All morphological variables were tested for normality (Shapiro-Wilks test, Conover 1980), and transformed if required to meet the assumptions of parametric statistical analyses.

Principal components analysis (PCA, Tabachnick and Fidell 1983) was used to assess the major axes of variation in the morphological data set. The first principal component (PC1) is considered to represent a body size axis if it correlates positively with all univariate measures from which it is derived (Zink and Remsen 1986). There has been recent discussion about the relative merits of extracting principal components from correlation or variance-covariance matrices (McGillivray 1985, Rising and Somers 1989, James and McCulloch 1990). Analysis of the variance-covariance matrix weights variables according to their variance. Measures with large means (e.g., wing and tail length) tend to have large variances, and will therefore tend to be overemphasized in the extracted

components (Rising and Somers 1989, Freeman and Jackson 1990). I extracted components from the correlation matrix because all variables are weighted equally, and the resulting PC1 should be representative of absolute body size, rather than allometric size (Freeman and Jackson 1990). Factor scores on PC1 were computed for all individuals in the morphological data set and were used as a measure of overall body size.

3. Statistical Considerations

Statistical procedures specific to the testing of various hypotheses are detailed in the appropriate chapters. All statistics were computed using PC-SAS (SAS Institute 1988), and unless otherwise stated, all statistical tests observe a Type I error rate of $\alpha = 0.05$. All mean values are presented with their associated standard errors (SE).

CHAPTER 3

GEOGRAPHIC PATTERNS OF AGE AND SEX DISTRIBUTION IN THE
EVENING GROSBEAK DURING WINTER

1. Introduction

As a first step to understanding the migratory behavior of the Evening Grosbeak, it is necessary to quantify the extent to which age and sex classes differ in their choice of wintering latitude. Several authors have suggested that male Evening Grosbeaks winter farther north than females (Mason and Shaub 1949, Parks 1953, Shaub 1960, 1963, Balph and Balph 1976, see Chapter 1). This suggestion is consistent with the patterns found in two other fringillid finches, the American Goldfinch (Prescott and Middleton 1990) and the House Finch (Belthoff and Gauthreaux 1991). However, there has been no previous attempt to quantify distributional differences between male and female Evening Grosbeaks on a continent-wide scale. In this chapter I use bird-banding data to test the prediction that male Evening Grosbeaks winter farther north than females, and to examine year-to-year consistency of such patterns.

I also use bird-banding data to examine age differences in winter distribution of Evening Grosbeaks. It is difficult to predict a priori the age distribution in

this species. In other irruptive species, immature birds tend to migrate longer distances than adults (Svardson 1957, Gauthreaux 1982). However, this pattern is reversed in emberizine and fringillid finches that migrate with annual regularity (Ketterson and Nolan 1983, Morton 1984, Prescott and Middleton 1990, Belthoff and Gauthreaux 1991). I therefore test the general prediction of differential winter distribution of age classes in the Evening Grosbeak.

2. Methods

Computerized records of Evening Grosbeaks banded between 1955 and 1988 were obtained from the Canadian Wildlife Service, Ottawa. All records with status codes indicating that birds were transported, maintained in captivity or released in poor health were eliminated from the database. Records of birds banded in provinces and states west of and including British Columbia, Montana, Wyoming, Colorado and New Mexico were also eliminated (i.e., birds presumably belonging to C. v. brooksi or C. v. montana). Records obtained during the breeding season (1 June to 31 August) were also excluded. Preliminary analysis of the remaining data indicated that 97.8% of all birds were of known sex. Unsexed birds were omitted from further analyses. Data from all available years were used to investigate sexual differences in winter distribution. However, because criteria for aging Evening

Grosbeaks were developed only recently (Yunick 1977), only data from 1977-78 to 1987-88 were used to test for age differences in distribution during winter. Individuals were aged as being either "immature" (first winter) or "adult" (second winter or older).

The first step in the analysis was to determine the period of the nonbreeding season during which the latitudinal distribution of Evening Grosbeaks reaches its southernmost point, and remains relatively stable (i.e., migration has terminated). To this end, I calculated the 25% quantile (Q25) latitude (i.e., the latitude north of which 75% of all grosbeaks were banded) for birds of all age and sex classes for half-month periods during each migration year from 1960-61 to 1986-87. Migration years between 1955-56 and 1959-60 were eliminated from this analysis because banding data were available only as monthly summaries during this period. The mean Q25 latitude for each half-month period was then calculated for all years. The period during which the latitudinal distribution of nonbreeding populations stabilized was then subjectively determined. This period, hereafter referred to as "winter", was used in all subsequent analyses of sex and age distribution.

Because of the binary nature of the dependent variables (age and sex), analysis of covariance (ANCOVA)

with a logistically-transformed dependent variable (Neter et al. 1985) was used to test the prediction that male Evening Grosbeaks winter farther north than females, and to investigate age differences in winter distribution. For each winter, the total numbers of birds of each sex and age were calculated in each 10-minute latitude/longitude block (blocks containing < 5 birds of known age or sex were omitted). The proportion of males, or adults within each sex, was calculated using the logit transformation, $\text{logodds} = \ln[p/(1-p)]$, where $p = n/N$ if $0 < n < N$; $p = 0.5N$ if $n = 0$; and $p = 1-(0.5N)$ if $n = N$ (where n = number of males or adults, and N = total number sexed, or total number aged within each sex). Logit-transformed proportions were then included as dependent variables in a multiple regression with year (YEAR), latitude (LAT) and longitude (LONG) as independent variables. Proportions were weighted by $w = Np(1-p)$ to adjust for inequalities in the variances of the error terms (Neter et al. 1985). When appropriate, the number of interaction and main effects in the regression model was reduced by backward elimination of terms (Neter et al. 1985). After testing for annual and longitudinal effects, predicted proportions of males and adults (of each sex) were calculated from $p = e^{a+b[LAT]}/1+e^{a+b[LAT]}$, where a and b are the intercept and slope estimated from the regression of logodds sex or age against latitude.

3. Results

The analysis of movements of grosbeak populations during the nonbreeding season included 544,666 individuals of known sex (overall sex ratio = 0.82 male:1 female; annual range of sex ratios = 0.54:1 to 1.31:1). Birds reach the southernmost latitude by early January, and remain there until the northward migration begins in mid-April (Figure 1). Thus, "winter" is defined as the period between 1 January and 15 April for all subsequent analyses. Because records obtained between 1955 and 1959 were summarized on a monthly basis, "winter" during 1955-56 to 1958-59 was considered to be January-March, inclusive. Figure 2 provides the sample size and Q25 latitude for each winter, emphasizing the annual variability of Evening Grosbeak migrations.

3.1 Sex Distribution

A total of 336,318 grosbeaks (61.7% of total sample) of known sex (overall sex ratio = 0.77 male:1 female; annual range of sex ratios = 0.48:1 to 1.19:1) were banded during winter. ANCOVA indicated a significant YEAR*LAT*LONG interaction effect on the proportion of wintering males ($F_{30, 3107} = 3.8, p < 0.0001$). To clarify the longitudinal effect, the analysis was repeated within each of two longitudinal regions: "east" ($< 85^{\circ}\text{W}$) and

FIGURE 1. Mean Q25 latitude ($\pm$ SE) by half-month periods between 1 September and 31 May, 1960-61 to 1987-88. Numbers on error bars represent number of years used in calculation of mean values, if < 27 .

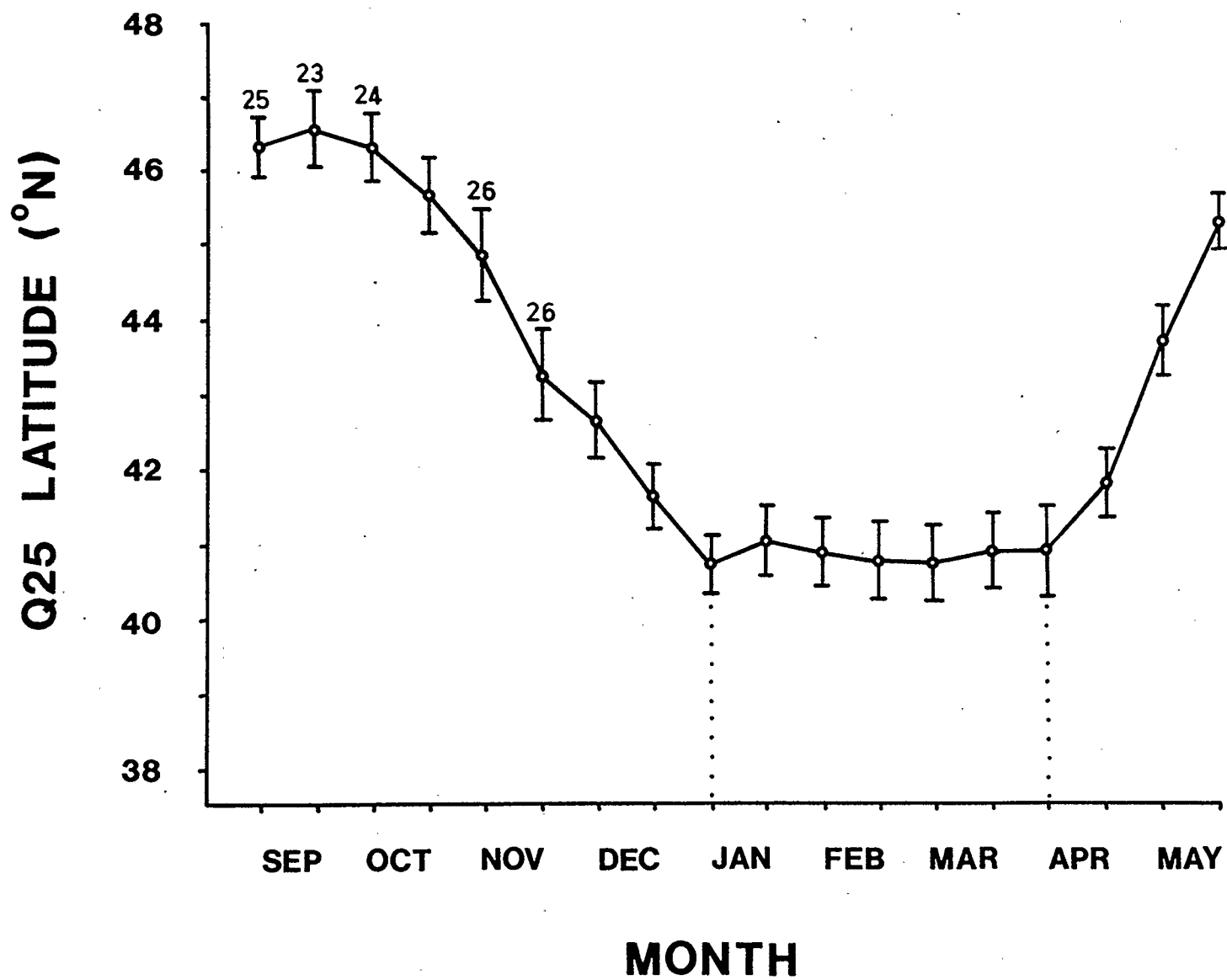
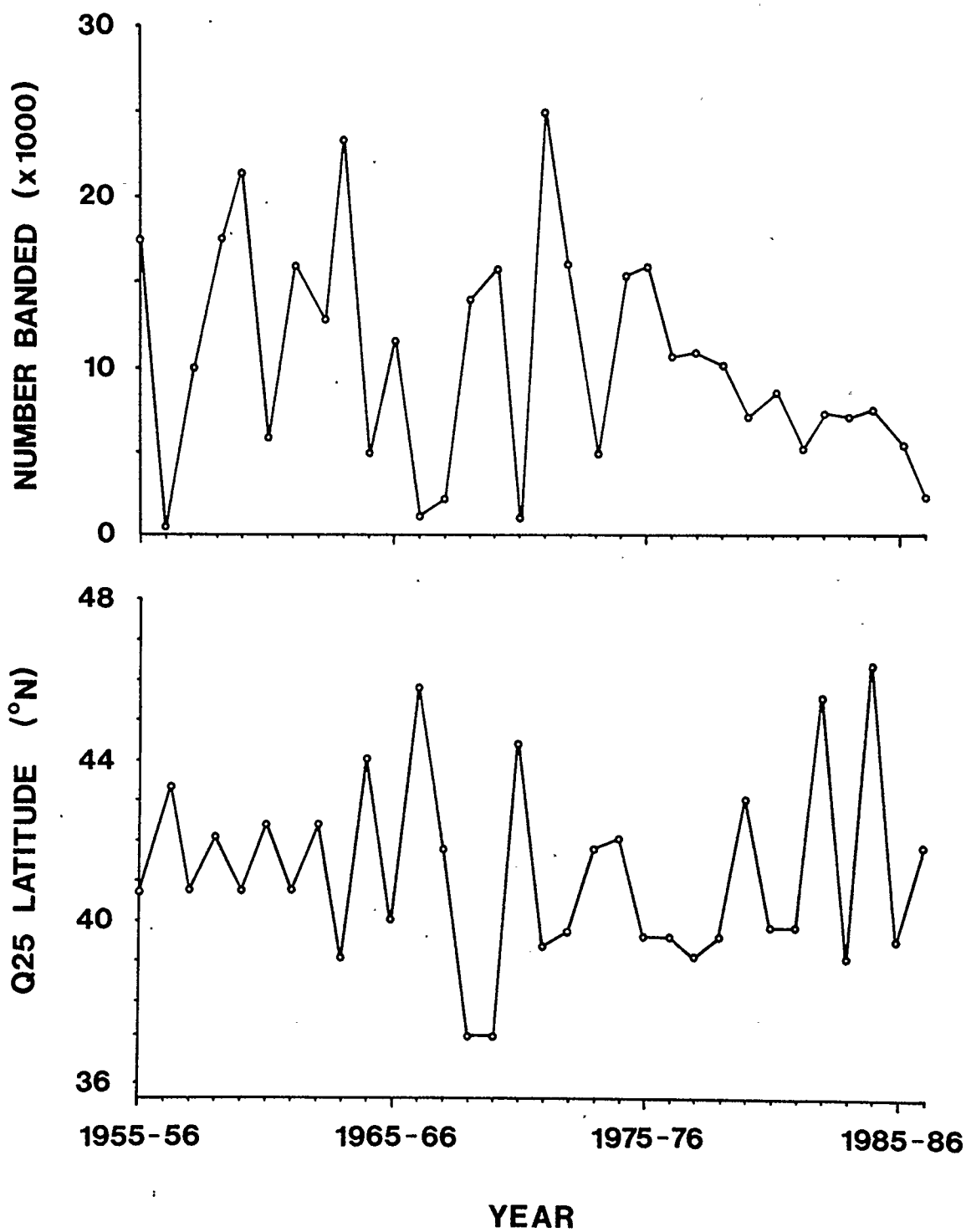


FIGURE 2. Number of Evening Grosbeaks banded (top), and Q25 latitude of grosbeak populations (bottom) during winter, 1955-56 to 1987-88.



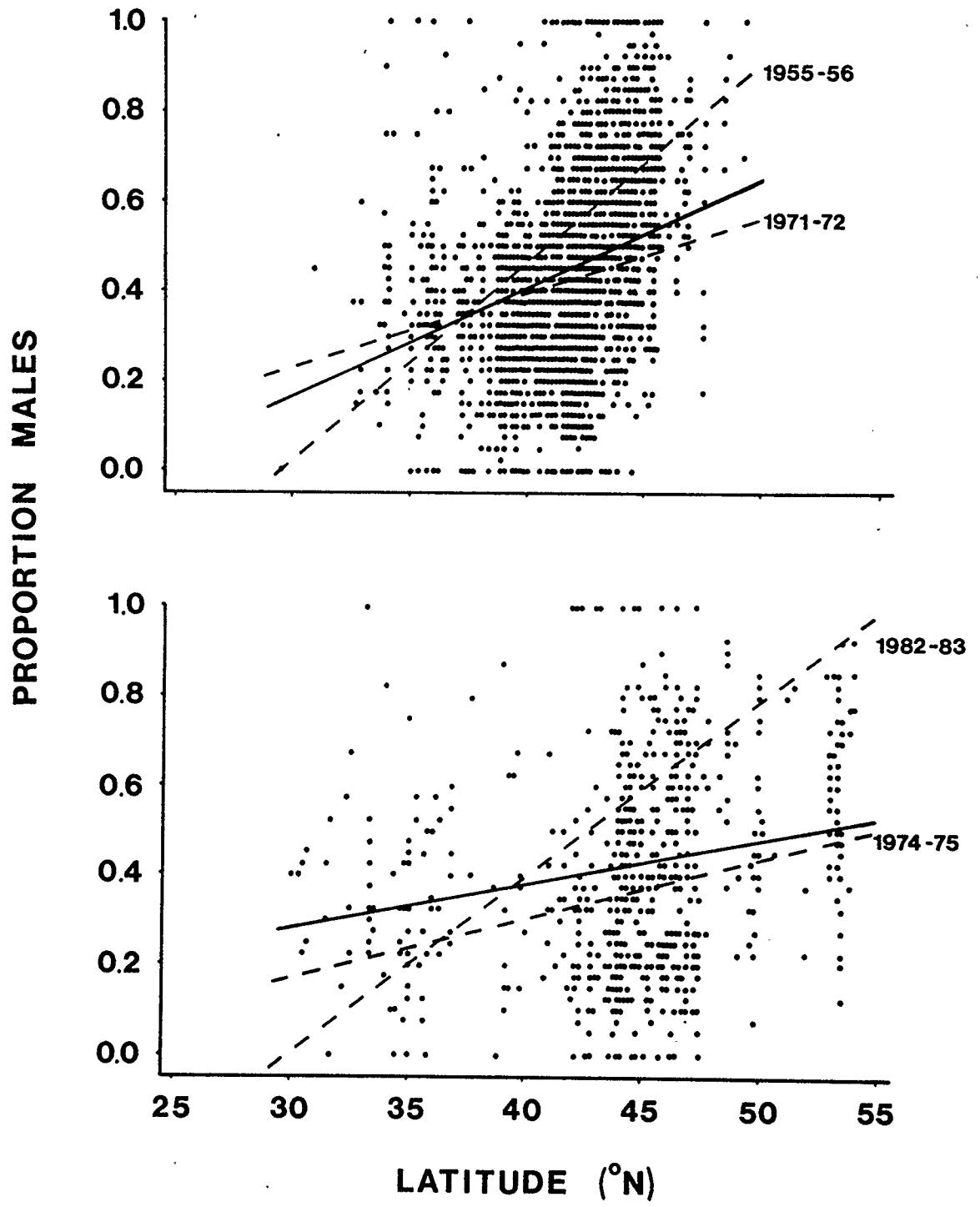
"central" ($\geq 85^{\circ}\text{W}$). In both regions, there was a significant YEAR*LAT effect (east: $F_{31, 2506} = 7.2$, $p < 0.0001$; central: $F_{30, 601} = 2.2$, $p < 0.001$). Regression slopes were significantly greater than 0 ($p < 0.05$, one-tailed tests) in 28 of 31 years in the east, and in 12 of 31 years in the central region. The overall regression of logodds sex on latitude (east: $\text{logodds } Y = -4.66 + 0.11[\text{LAT}]$, $F_{1, 2568} = 558.7$, $p < 0.0001$; central: $\text{logodds } Y = -2.32 + 0.04[\text{LAT}]$, $F_{1, 662} = 54.0$, $p < 0.0001$), along with minimum and maximum annual slopes, are shown in Figure 3. Over all years, the predicted proportion of males in the eastern region declined from 65% in the north (50°N) to 18% in the south (30°N). In the central region, the proportion of males declined from 53% at 55°N to 27% at 30°N .

3.2 Age Distribution

During the winters of 1977-78 to 1987-88, 15,857 males (53.9% of total) and 7,190 females (16.9%) of known age were reported. The overall age ratio (adult:immature) was 0.96:1 for males (range, 0.69:1 to 1.32:1), and 0.66:1 for females (range, 0.39:1 to 1.16:1).

Following the elimination of insignificant terms, the ANCOVA model for both sexes reduced to contain LAT, YEAR and their interaction (males: $F_{19, 329} = 1.6$, $p = 0.06$; females: $F_{19, 147} = 1.8$, $p < 0.03$). Regression

FIGURE 3. Overall regressions (solid line), and minimum and maximum annual slopes (dashed lines) of the proportion of males versus latitude in eastern (top) and central (bottom) North America.



slopes for males were significantly different from 0 (two-tailed tests) only in 1982-83 ($F_{1, 19} = 8.5$, $p < 0.0001$), where the proportion of adults increased with latitude (logodds $Y = -11.73 + 0.26[\text{LAT}]$). For females, only the regression slope for 1984-85 was significantly different from 0 ($F_{1, 12} = 13.5$, $p < 0.01$), when the proportion of adults decreased with increasing latitude (logodds $Y = 15.93 - 0.07[\text{LAT}]$).

4. Discussion

Despite the annual variability in Evening Grosbeak migrations, male grosbeaks, like other North American finches (King et al. 1965, Ketterson and Nolan 1976, Morton 1984, Prescott and Middleton 1990, Belthoff and Gauthreaux 1991), tend to winter farther north than females. However, evidence for distributional differences between the age classes is equivocal. First-winter Evening Grosbeaks of both sexes do not show a tendency to migrate farther than adults, as reported for other irruptive species (Svardson 1957, Gauthreaux 1982, Kerlinger and Lein 1986), nor to winter farther north like non-irruptive finch species (Ketterson and Nolan 1983, Morton 1984, Prescott and Middleton 1990).

This study adds the Evening Grosbeak to the ever-increasing list of North American migrants that show age or

sex differences in winter distribution. In the following chapters, I turn to the problem of evaluating which of the three major hypotheses (if any) is most consistent with the patterns of winter distribution I observed. As an initial step in this process, it might be useful to ask why differential migration of the sexes is more pronounced in eastern than in central North America. It is unlikely that benefits to early arrival on the breeding grounds would differ between eastern and central regions, so the arrival time hypothesis does not explain the longitudinal patterns of differential migration that I observed. If differences in body size are a factor in the selection of wintering latitude, then conditions in the east must either be colder, or food supplies more unpredictable, than in central regions. If social dominance is important, then intraspecific competition must be more intense in the east. Long-term, mean temperatures recorded during January show that locations in the east average 1 to 3°C warmer than comparable latitudes in the central region (Bryson and Hare 1974), which is inconsistent with the body size hypothesis. Christmas Bird Count data show that Evening Grosbeaks winter in higher numbers in the east (at least in areas south of the breeding range, Root 1988a), suggesting that competition may be more intense in this area. Unfortunately, information on regional differences in the

predictability and abundance of food, necessary for a full evaluation of both the body size and social dominance hypotheses, are not available.

CHAPTER 4

THE ARRIVAL TIME HYPOTHESIS

1. Introduction

Males of many species of migratory birds return to the breeding grounds earlier in spring than do females (Gauthreaux 1982, Francis and Cooke 1986). Such differences in arrival schedules presumably result because, early in the breeding season, intrasexual competition is most intense in the sex (usually males) that defends resources such as territories (Myers 1981, Jakobsson 1988). Earlier arrival by males than by females could be accomplished in two ways. First, the chronology of spring migration could differ between the sexes, with males beginning northward movements earlier than females, or migrating at a faster rate of travel. Second, males could make shorter migrations from the breeding grounds in autumn than females (i.e., differential migration), and thereby achieve earlier arrival even in the absence of sexual differences in the timing or rate of spring migration.

There is evidence that both of these mechanisms might be important in explaining differences in arrival schedules. In the Rose-breasted Grosbeak (Pheucticus ludovicianus), males return to the breeding grounds from their winter range in the neotropics several days before

females, despite a similar pattern of winter distribution in both sexes (Francis and Cooke 1990). This indicates that early arrival by males results from sexual differences in the chronology of northward migration. An increasing number of species are known to exhibit sexual differences in winter distribution, with males tending to winter closer to the breeding grounds (Chapter 1). Although there may be physiological or social differences between the sexes that could account for this pattern (Myers 1981, Ketterson and Nolan 1983), such distributional differences are consistent with the idea that males benefit most from early arrival on the breeding grounds. Consequently, the "arrival time hypothesis", which states that individuals of the territorial sex should winter closest to the breeding grounds because of advantages associated with early arrival in spring, has frequently been cited in discussions about the evolution of differential migration in birds (Ketterson and Nolan 1976, 1983, Myers 1981).

The Evening Grosbeak is an irruptive migrant in which males tend to winter farther north than do females (Chapter 3). There is little information on sexual differences in arrival schedules on the breeding grounds, although both Shaub (1956), and Scott and Bekoff (1991) noted that some birds are already paired when they arrive at breeding sites. In this chapter, I use banding and recovery data

collected during spring migration to test predictions of the arrival time hypothesis. If males winter closer to the breeding grounds than females in order to gain early access to breeding resources, then (1) males should initiate spring movements at the same time as, or earlier than, females, (2) males should migrate at the same rate as, or faster than, females, and (3) southern-wintering males should not begin migrating before males in the north. Rejection of any of these predictions would suggest that individuals migrating from southerly latitudes in spring may "catch up" with those wintering in the north, thereby reducing any advantages associated with early arrival by northern-wintering individuals.

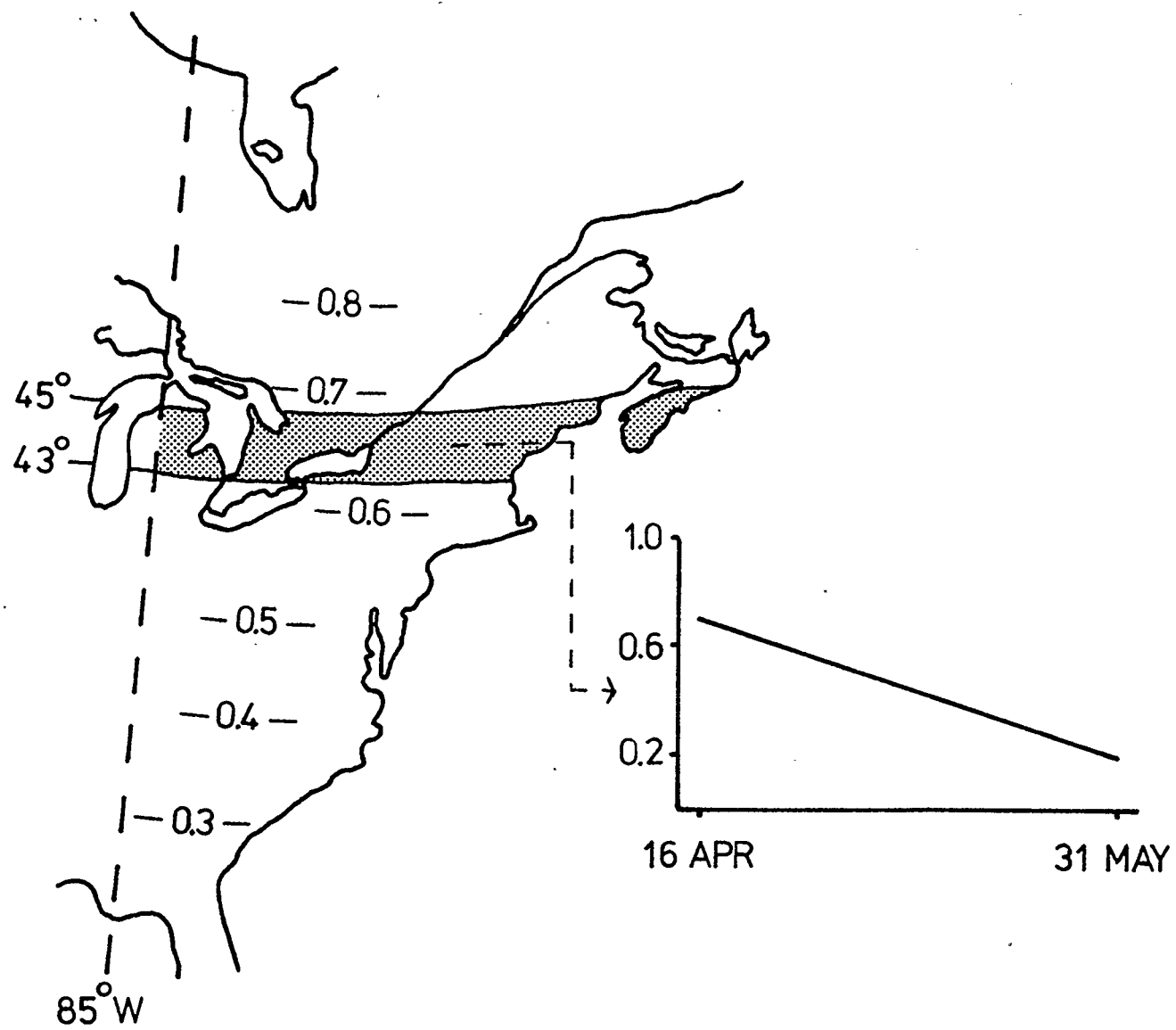
2. Methods

Inferences concerning sexual differences in the timing or rates of migration typically are made by observing the passage of males and females at some point on the migratory route (Chandler and Mulvihill 1990). Interpreting differences in the timing of migration observed through this procedure is complicated in differential migrants. Suppose, for example, that the observation point is located in the northern part of the winter range, where males are more common than females. Even in the absence of sexual differences in migratory chronology, males will outnumber females early in the migratory period. Unless sexual

differences in the latitudinal origin of northward-migrating individuals are taken into account, it might be erroneously concluded that males migrate sooner, or faster, than females. Thus, to investigate sexual differences in the timing and rate of spring migration in Evening Grosbeaks, I used the method described by Chandler and Mulvihill (1990). This technique uses knowledge of the relative abundance of males and females at different winter latitudes to predict temporal changes in sex ratios that would be observed at a reference point during spring migration, if there were no sexual differences in migration schedules (Figure 4). Expected values can then be compared with observed changes in the proportion of the sexes moving past a reference point at different times during migration to test for sexual differences in migratory chronology.

Banding (1955-1988) and recovery (1944-1988) records for Evening Grosbeaks were obtained from the Canadian Wildlife Service, Ottawa. The tendency for Evening Grosbeak populations to show differential migration varies longitudinally (Chapter 3). Therefore, I restricted the analysis to birds banded east of 85°W, the region where the tendency for males to winter north of females is most pronounced, and where sample sizes of banded birds are largest (Chapter 3). To monitor the northward migration of

FIGURE 4. Schematic representation of how the temporal passage of males and females through the reference band (shaded area) during spring migration was estimated from a hypothetical winter distribution of the sexes. Numbers on the map represent the proportion of males wintering at different latitudes. Numbers on the ordinate of the graph represent the predicted proportion of males moving through the reference band at different dates (abscissa), assuming that the onset and rate of northward movement is identical for males and females (see text).



birds in spring, I sought a band of reference near the northern edge of the wintering range during irruption years, but south of the normal summer range in the boreal forest (southern boundary of approximately 45°N). Banding locations are summarized in $10'$ blocks of latitude and longitude (Canadian Wildlife Service 1984), and preliminary inspection of the data indicated that no single $10'$ band of latitude contained sufficient numbers of banded grosbeaks during the spring migration (16 April to 31 May, see Chapter 3) for analysis. I therefore selected a reference band between 43° and 45°N . The numbers of males and females banded within the reference band during nine, five-day intervals between 16 April and 31 May were tallied. The proportion of males was then calculated for each time period, and these numbers were used as "observed" values in subsequent analyses (see below). Only those years in which more than five birds of either sex were banded during each of the nine time periods were considered further.

Expected values for the proportion of males in the reference band at different time periods during spring migration were calculated as follows. For each year, the number of males and females banded between 1 January and 15 April in each $10'$ band of latitude was summed. All latitudes above 44°N (the midpoint of the reference band) were omitted, because only birds that would move northward

in spring through the reference band were of interest. Latitudes below 44°N where grosbeaks were banded during each winter were converted into continuous values from 1 (at 44°N) to 9 (at the southernmost winter latitude during each year). These values are assumed to correspond to the temporal sequence of passage of birds from different wintering latitudes through the reference band in spring, assuming that northern-wintering birds move through earliest (i.e., during time period 1) and southern-wintering birds last (time period 9).

To describe the relationship between the observed and expected sex composition of the migrating population, linear regressions of logit-transformed proportion ($\text{logodds} = \ln[p/(1-p)]$) of males vs. time were performed (for both observed and expected values). Proportions were calculated as $p = n/N$ (where n = number of males and N = total number of birds) if $0 < n < N$, $p = 1 - [1/2N]$ if $n = N$, and $p = 1/2N$ if $n = 0$ (Neter et al. 1985). I used analyses of covariance (ANCOVA, Neter et al. 1985) to test the hypothesis of no difference in the relationship of observed and expected values at different time periods. I first inspected for similarity in rates of travel by the sexes by testing for homogeneity of expected and observed regression slopes. Tests for differences in intercepts (i.e., at time = 1) of the regression lines were performed to determine

whether one sex began migration earlier than the other. To visualize the relationship between observed and expected proportion of males at different time periods, I back-transformed the regression equations using $p = e^{a+b[TIME]}/1 + e^{a+b[TIME]}$, where p is the proportion of males predicted from the regression equation, and a and b are the intercept and slope estimated by the regression.

Differences in intercepts between observed and expected regression lines could result from one sex moving into the reference band in early spring from regions to either the north or south. The same effect could result from the other sex departing northward or southward from the reference band in early spring. To interpret differences in intercepts, I used band recovery data to test for differences in the timing or direction of travel by males and females wintering at different latitudes. To assure that there were sufficient recoveries for this analysis, I divided the winter range into "north" ($\geq 43^{\circ}\text{N}$) and "south" ($< 43^{\circ}\text{N}$). I then extracted records of birds of known sex banded during five, half-month periods (between 1 March and 15 May), and recovered during the same year in the subsequent half-month period (between 16 March and 31 May). Mann-Whitney U-tests (Conover 1980) were used to compare the distance travelled (degrees) in a northerly direction by males and females in each region and between

time periods (hereafter, time "intervals" 1 through 5). In addition, Fisher's Exact Tests (Conover 1980) were used to compare the number of males and females moving north or south from their point of banding in different regions and time intervals.

The same "north" and "south" regions and time intervals were used to test the null hypothesis of no difference in the timing of northward movement between northern- and southern-wintering males. Mann-Whitney U-tests compared the northward distance travelled by males from different regions in each time interval. Fisher's Exact Tests compared the number of males moving north and south from their point of banding in each region.

3. Results

Five irruption years (1965-66, 1972-73, 1973-74, 1975-76 and 1981-82) met the criterion for analysis (> 5 birds banded in each time period, Table 3, Figure 5). For simplicity, these years are hereafter referred to by the calendar year in which the spring migration occurred (e.g., 1965-66 = 1966). There was no significant difference between observed and expected slopes in any year (ANCOVA, all $p > 0.3$), indicating that male and female Evening Grosbeaks move northward in spring at similar rates of travel. However, the intercepts of observed and predicted regression lines differed significantly in all five years

TABLE 3. Regression equations for observed and expected logit-transformed proportion of males versus time period in the reference band (43 - 45°N) between 16 April and 31 May.

Year	Regression	N	Regression Equation ^a	d. f.	F
1966	Observed	748	$Y = 0.97 - 0.08(\text{TIME})$	1,8	4.6 ^b
	Expected	9831	$Y = 0.54 - 0.17(\text{TIME})$	1,41	7.9 ^b
1973	Observed	1535	$Y = 0.77 - 0.12(\text{TIME})$	1,8	7.3 ^b
	Expected	10820	$Y = 0.30 - 0.13(\text{TIME})$	1,48	10.5 ^c
1974	Observed	2144	$Y = -0.10 - 0.03(\text{TIME})$	1,8	0.3
	Expected	2291	$Y = -1.14 - 0.02(\text{TIME})$	1,36	0.1
1976	Observed	1528	$Y = 1.26 - 0.14(\text{TIME})$	1,8	13.9 ^c
	Expected	13153	$Y = 0.76 - 0.23(\text{TIME})$	1,42	15.8 ^c
1982	Observed	1217	$Y = 0.30 - 0.02(\text{TIME})$	1,8	0.4
	Expected	3336	$Y = 0.13 - 0.12(\text{TIME})$	1,36	3.6 ^b

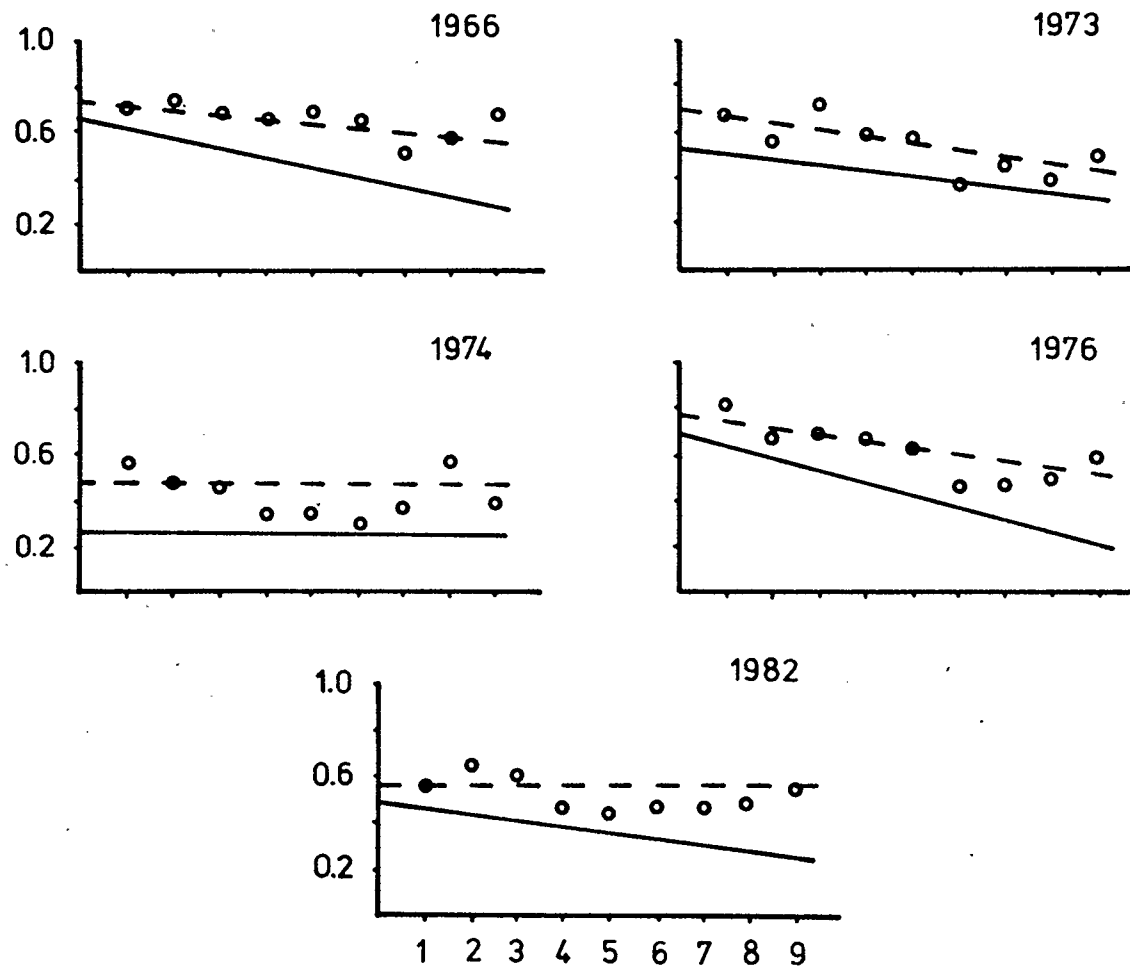
^a Y is logodds proportion of males (see text)

^b $p < 0.05$

^c $p < 0.01$

FIGURE 5. Observed proportion of male Evening Grosbeaks (open circles), and regressions of observed (dashed line) and expected (solid line) proportion of males in the reference band (43° - 45° N) during nine, five-day time periods between 16 April and 31 May.

PROPORTION MALES



TIME PERIOD

(ANCOVA, all $p < 0.05$). In all cases the observed proportion of males in the reference band was higher than that predicted from the known winter distribution of the sexes (Figure 5).

There was no difference between the sexes in the distance moved during any of the five time intervals in the northern region (Mann-Whitney U-tests, all $p > 0.2$, Table 4), nor in the frequency of northerly or southerly movements by either sex (Fisher's Exact Tests, all $p > 0.5$). In the southern region, males banded in late April and recovered in early May (interval 4) moved farther north than did females during the same interval. Also, a greater proportion of males than females were recovered north of the point of banding during this interval (Fisher's Exact Test, $p < 0.05$). Thus, the consistently higher proportion of males observed in the reference band in spring can be explained by the tendency for southern-wintering males to begin migrating sooner than females wintering in the same area. A comparison between the movements of males in the two regions supports this result. More southern- than northern-wintering males moved northward between late April and early May (Fisher's Exact Test, $p < 0.05$), and the distance travelled by southern males during this period was greater ($U = 134$, $p < 0.001$).

TABLE 4. Distance moved northward in degrees (mean $\pm$ SE) by male and female Evening Grosbeaks during half-month time intervals during spring migration. Numbers in parentheses are sample sizes.

Time Interval ^a	Northern Region ($> 43^{\circ}\text{N}$)		Southern Region ($\leq 43^{\circ}\text{N}$)	
	Males	Females	Males	Females
1	-0.18 ± 0.15 (19)	0.06 ± 0.16 (6)	-0.01 ± 0.09 (16)	-0.01 ± 0.05 (20)
2	0.06 ± 0.06 (6)	-0.10 ± 0.31 (7)	-0.17 ± 0.13 (11)	0.05 ± 0.04 (13)
3	0.07 ± 0.13 (12)	0.10 ± 0.13 (12)	0.11 ± 0.11 (14)	0.24 ± 0.16 (17)
4	0.21 ± 0.02 (13) ^b	0.50 ± 0.38 (8)	1.88 ± 0.35 (20) ^{b,c}	1.13 ± 0.47 (20) ^c
5	0.15 ± 0.17 (8)	0.22 ± 0.25 (6)	2.60 ± 0.60 (8)	2.00 ± 0.65 (4)

^a 1 = Early March - Late March; 2 = Late March - Early April; 3 = Early April - Late April; 4 = Late April - Early May; 5 = Early May - Late May. "Early" refers to ≤ 15 th day of the month, "late" refers to > 16 th day of the month

^b Two-tailed Mann-Whitney U-test of differences between regions (males only),
 $p < 0.001$

^c Two-tailed Mann-Whitney U-test of differences between sexes (southern region),
 $p < 0.05$

4. Discussion

The results failed to reject two of three predictions arising from the arrival time hypothesis. First, I predicted that males should begin spring migrations no later than do females. Two lines of evidence suggest that males may actually start moving first: (1) the proportion of males in the reference band in early spring is higher than the proportion predicted from the known winter distribution of the sexes, and (2) southern-wintering males begin migrating northward sooner than southern-wintering females. Second, I predicted that males and females should show similar rates of northward travel after 15 April, when most migratory movements occur (Chapter 3). The similarity of regression slopes for expected and observed proportion of males over time in the reference band supports this prediction. Taken together, these results suggest that birds that winter closest to the breeding grounds (predominantly males, Chapter 3) could achieve the earliest arrival in spring. However, my third prediction, that southern-wintering males should not begin migrating before males wintering at more northerly latitudes, was rejected. Latitudinal differences in the onset of spring migration may therefore compensate for the increased distance travelled, and males that make longer migrations in autumn need not arrive on the breeding grounds later than males

that winter farther north. Thus, it is doubtful that early arrival is an important factor in the choice of wintering latitude by Evening Grosbeaks.

Although data on spring movements suggest that males may precede females to the breeding grounds, the advantages of early arrival to males are not clear. Male Evening Grosbeaks do not defend territories during the breeding season (Bekoff and Scott 1989, Scott and Bekoff 1991), so early-arriving males should not benefit from exclusive access to breeding resources such as food and nest sites. It is possible that males arrive early in order to compete with other males for access to the later-arriving females. The observation that inter-male aggression in flocks is most intense when courtship begins in April (Bekoff and Scott 1989) supports this idea. However, courtship is frequently observed far south of the breeding range (Shaub 1956, Jackson 1974, pers. obs.), and at least some birds are already paired upon reaching the breeding site (Shaub 1956, Scott and Bekoff 1991). Although it is not known if all birds pair before migration is terminated, these observations suggest that early arrival on the breeding grounds by males may not influence the probability of acquiring a mate. Therefore, an explanation for the observed tendency of males to arrive first in spring is unclear, and requires further information on the ecology of

male and female grosbeaks early in the breeding season.

Evidence from other migratory species suggests that the timing and location of pair formation can influence the winter distribution of the sexes. Mallards, American Black Ducks and Redheads pair on the wintering grounds (Diefenbach et al. 1988, Rohwer and Anderson 1988), and show no sexual differences in winter distribution (Alexander 1983, Perdeck and Clason 1983, Nichols and Hines 1987, Diefenbach et al. 1988). Conversely, Canvasbacks and Ring-necked Ducks pair late in migration or after arrival on the breeding grounds (Bluhm 1988, Rohwer and Anderson 1988). In both these species, males winter farther north than do females (Nichols and Haramis 1980, Alexander 1983), and presumably benefit from early arrival at breeding sites. If the timing of pair bonding alone was an important determinant of winter distribution of the sexes in Evening Grosbeaks, then males and females should winter at similar latitudes. The strong tendency for males to winter north of females in this species (Chapter 3) suggests that factors other than early arrival must be important.

CHAPTER 5

THE BODY SIZE HYPOTHESIS

PART 1: INTRASPECIFIC AND GEOGRAPHIC PATTERNS OF BODY SIZE

1. Introduction

The body size hypothesis states that larger-bodied individuals should make the shortest migrations from the breeding grounds because large size confers a survival advantage in regions that are either cold or subject to periods of severe food limitation. In temperate regions of the northern hemisphere, temperatures are generally colder, and snowfall (which can cover food and thereby limit its availability) is heaviest at higher latitudes (Potter 1965, Bryson and Hare 1974). In migratory species, the body size hypothesis therefore predicts that larger-bodied individuals should winter farthest north. This argument should apply to the geographic distribution of age and sex classes during winter, as well as to the latitudinal distribution of individuals within each class.

The body size hypothesis is based on the observation that in some closely-related species with allopatric ranges, larger-bodied species tend to have a more northerly distribution than those inhabiting more southerly sites. Although this pattern, termed "Bergmann's Rule", was originally derived from interspecific comparisons (James

1970), it has been extended to intraspecific trends in body size as well (Mayr 1963, James 1970). The generality of this ecogeographic "rule" has been questioned widely (Scholander 1955, McNab 1971, Zink and Remsen 1986, Geist 1987), but it is clear that, in some species, observed geographic differences in body size are consistent with the idea that larger-bodied birds inhabit more northerly regions (see below).

In general, studies of geographic variation in body size have focused on sedentary species, or on breeding populations of migratory species. Summarizing 92 studies for which data on the relationship between wing length and latitude for such species could be determined, Zink and Remsen (1986) found that latitudinal trends in body size were at least weakly consistent with Bergmann's Rule in 20 (74 %) of the 27 sedentary species considered. Although the mechanism responsible for this pattern is not clear, geographic trends in body size correlate closely with winter temperatures in North American populations of the Downy Woodpecker (Picoides pubescens, James 1970) and House Sparrow (Passer domesticus, Johnston and Selander 1971). This suggests that, at least in some sedentary species, body size may have evolved in response to climatic conditions encountered during the winter. Support for Bergmann's Rule is weaker among breeding populations of

migratory species. Zink and Remsen (1986) found that wing length increased from south to north in only 30 (46%) of 65 such species. Wiedenfeld (1991) noted that the pattern of variation in body size in breeding populations of male Yellow Warblers (Dendroica petechia) is opposite to that predicted by Bergmann's Rule. In short, there is little evidence to suggest a relationship between breeding latitude (and therefore climate) and body size in migrant species.

There have been few studies of geographic variation in body size of migratory species during the winter (Zink and Remsen 1986). In both the Townsend's Warbler, Dendroica townsendi (Morrison 1983) and Painted Bunting, Passerina ciris (Storer 1951, in Zink and Remsen 1986), smaller-bodied individuals are reported to winter farthest north. European Starlings are largest at mid-latitudes of their winter range (Blem 1981), and Savannah Sparrows show no geographic variation in body size during winter (Rising 1988).

Despite a lack of evidence among migrants that larger individuals winter farthest north, the body size hypothesis has frequently been cited as a possible explanation for differential migration in birds (Myers 1981, Ketterson and Nolan 1983, 1985). Most support for this hypothesis is derived from the observation that the larger-bodied sex or

age class tends to winter closest to the breeding grounds (Nichols and Haramis 1980, Sayler and Afton 1981, Dolbeer 1982, Prescott and Middleton 1990). This approach offers only weak support for the hypothesis, because it fails to distinguish between body size effects per se, and other effects such as social dominance or the benefits of proximity to the breeding grounds that may be associated with age and sex differences (Zink and Remsen 1986).

A more rigorous test asks whether trends in body size within age and sex classes are consistent with predictions of the body size hypothesis. To date, only two studies have addressed body-size variation within age or sex classes of differential migrants during the winter. Nolan and Ketterson (1983) found that although male Dark-eyed Juncos are larger than females and winter farther north, there are no latitudinal differences in body size within any age or sex class during winter. Conversely, James et al. (1984) found that both male and female Red-winged Blackbirds (a species in which the larger-bodied males winter farther north than females) show an increase in size from south to north during winter (James et al. 1984). Unfortunately, James et al. (1984) apparently sampled both migratory and sedentary populations during winter, and it is therefore difficult to distinguish latitudinal trends in morphology for birds of different migratory status.

Furthermore, both of these studies (and most others which have considered body size) suffer because "size" was determined from a single morphological measure (wing length), and univariate measures are often poor indicators of overall body size in birds (Rising 1988, Rising and Somers 1989, Freeman and Jackson 1990).

In this chapter, I test predictions of the body size hypothesis as they apply to intraspecific differences in winter range of the Evening Grosbeak. In this species, males winter farther north than do females, but there are no differences in distribution between age classes of either sex (Chapter 3). If the body size hypothesis can account for differential migration in this species, then (1) males should be larger-bodied than females, but (2) adults and immatures of both sexes should be of similar body size. Furthermore, I predict that (3) within each age and sex class, larger-bodied individuals should be found farthest north during winter. These predictions are tested using a multivariate assessment of body size for individuals collected over a wide geographic area (museum skins), as well for live-caught birds wintering in southern Alberta.

2. Methods

Between December 1988 and December 1989, I examined study skins of Evening Grosbeaks contained in 59 North

American museum collections (see Appendix 1). Because this study deals exclusively with the eastern subspecies (C. v. vespertinus), only birds collected in provinces and states east of British Columbia, Montana, Wyoming, Colorado and Arizona were considered. The location and date of capture were recorded from museum tags. Latitude/longitude coordinates were later assigned (using Anonymous 1966, and regional gazeteers) to specimens where the county or municipality of collection was recorded. Individuals were aged and sexed according to plumage characteristics (see Chapter 2). Birds collected during the breeding season (1 June to 31 August) were not included in the present study because molt during this period could introduce error to wing and tail measurements, and because of difficulties in accurately determining the age of breeding males. The molt from immature to adult plumage occurs at approximately one year of age (Dwight 1900), so males hatched during the previous summer could be designated as either immature or adult, depending on whether the molt had been completed at the time of collection. Similarly, males in immature plumage collected between June and August could either be young of the year, or birds hatched during the preceding summer which had not yet molted to adult plumage. Attempts to assign ages to study skins of females were abandoned because soiling and fading of many museum specimens made

age criteria difficult to apply.

To quantify the relative body sizes of adult and immature females, and to verify other age and sex-specific patterns of body size observed in the museum data, I supplemented museum measurements with similar data from free-living Evening Grosbeaks captured in southern Alberta from December 1989 to March 1990, and November 1990 to April 1991. Because of possible shrinkage in museum specimens (e.g., Harris 1980, Bjordal 1983), separate analyses were conducted on data from live and museum specimens.

Six external measurements (see Chapter 2) were taken from each bird by a single investigator. To verify that measurements were repeatable over time, 77 museum specimens measured during the first month of the study (December 1988) were remeasured during August and September 1989. At this time, approximately 65% of the available study skins had been examined. Initial and final measurements on the same individuals were compared using a repeated-measures multivariate analysis of variance (MANOVA). Principal components analysis was then used to quantify the body size of each bird (see Chapter 2).

Two methods were used to compare body measurements of age and sex classes. MANOVA was used to compare overall differences in body measurements among age and sex

classes. Overall body size was compared by performing t-tests on PC1 scores for individuals of each class. A one-tailed test was used to test the prediction that males should be larger than females. A two-tailed test was used to examine for differences in body size between age classes of males and females.

The prediction that larger individuals should be found farthest north during winter was tested using data from museum specimens collected between 1 January and 15 April. During this period, Evening Grosbeak populations are at the southernmost limit of their migration (Chapter 3). Individuals were included in this analysis only if latitude/longitude coordinates could be assigned to their collection sites. The data were analysed in two ways. First I combined data from all years to test for broad geographic trends in body size. Because the Evening Grosbeak is an irruptive migrant and the winter range changes from year to year, this approach might obscure geographic patterns of body size occurring in different years (Rising 1988). Therefore, I also performed separate analyses of the relationship between body size and location of capture for winters in which ≥ 15 individuals of any age or sex class were collected. For the overall analysis, PC1 scores for each individual were entered as dependent variables in a multiple regression analysis, with latitude

(LAT) and longitude (LONG) as independent variables. I included longitude in the analysis because the tendency for vespertinus males to winter north of females is stronger in eastern North America than it is central regions (Chapter 3). Because of the smaller sample sizes, longitude was not included as an independent variable when considering each year separately. All analyses were performed separately on adult males, immature males, and females. One-tailed tests of significance were used in all cases.

3. Results

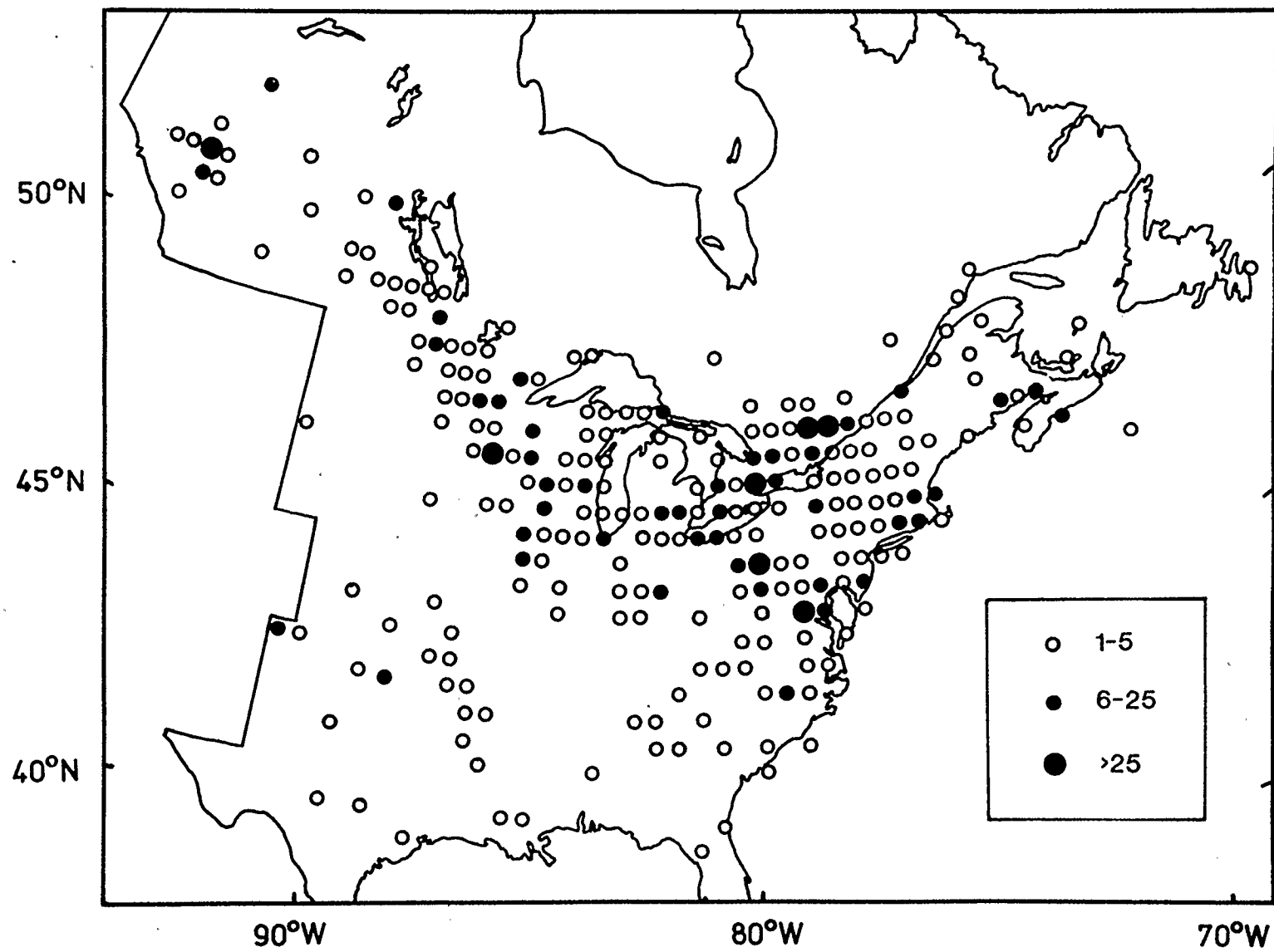
3.1 Age and Sex Differences in Morphology

3.1.1 *Museum Specimens*

A total of 1739 museum specimens (955 male, 784 female) were examined. The distribution of samples of known geographical origin ($n = 1729$) is shown in Figure 6. Of the males, 896 (93.8%) were aged as being either immature or adult. Males of undetermined age were included in calculation of principal component scores and in comparisons of sexual differences in body size, but were excluded from comparisons between male age groups.

All univariate measures except tail length were normally distributed in all age and sex groups. Attempts to normalize tail-length measurements by transformations were unsuccessful, so raw values of this variable were

FIGURE 6. Geographical origin of Evening Grosbeak study skins used in morphological analyses. Numbers are total specimens in each one-degree latitude/longitude block. All specimens were collected between 1 September and 31 May.



retained for all analyses.

There was no evidence that any measurements made by the same observer varied over the study period (repeated measures MANOVA, $F = 0.7$, d. f. = 1, 73, $p > 0.6$).

I initially performed PCA separately for each age and sex class to check that patterns of morphological covariation were similar in each group. In all cases, two components with eigenvalues > 1 were extracted (Table 5). Loading patterns were similar among age and sex classes. I therefore repeated the analysis and extracted factor scores from the entire dataset. This procedure again produced two eigenvectors, which accounted for 58.4% of the total variance (Table 5). PC1 (40.0%) correlated positively with all univariate measures and was therefore interpreted as representing overall body size. PC2, which accounted for 18.4% of the variance, was characterized by individuals with long wings and tails relative to bill and leg measurements. This component incorporates a shape element, and will not be discussed further.

Univariate measurements and PC1 scores for each age and sex class are given in Table 6. Males were larger than females in all measurements (MANOVA, $F = 77.6$, d. f. = 6, 1595, one-tailed $p < 0.0001$), and also had significantly higher PC1 scores ($t = 15.4$, d. f. = 1527, one-tailed $p < 0.0001$). Among males, adults were larger than immatures in

TABLE 5. Correlations between morphological measurements and principal component scores for study skins of Evening Grosbeaks collected between 1 September and 31 May. In all analyses, only PC1 and PC2 were statistically significant (eigenvalues > 1.0).

Character	Immature Males (n = 368)		Adult Males (n = 423)		Females (n = 691)		All Birds (n = 1602)	
	PC1	PC2	PC1	PC2	PC1	PC2	PC1	PC2
Wing Length	0.63	0.53	0.55	0.64	0.60	0.57	0.69	0.49
Bill Length	0.63	-0.37	0.64	-0.33	0.61	-0.24	0.62	-0.36
Bill Width	0.77	-0.32	0.70	-0.18	0.73	-0.32	0.76	-0.22
Bill Depth	0.70	-0.42	0.69	-0.32	0.67	-0.37	0.71	-0.32
Tarsus Length	0.49	0.32	0.56	-0.14	0.58	-0.05	0.45	-0.20
Tail Length	0.49	0.59	0.34	0.80	0.43	0.75	0.45	0.74
Eigenvalue	2.36	1.15	2.10	1.29	2.24	1.18	2.40	1.10
% Variation	39.4	19.1	35.0	21.6	37.3	19.7	40.0	18.4

TABLE 6. Univariate measurements (in mm) and PC1 scores for age and sex classes of the Evening Grosbeak. All data are from museum study skins collected between 1 September and 31 May. All t-tests between age (two-tailed) and sex (one-tailed) classes are significant at $p < 0.0001$, unless otherwise indicated. Values are mean $\pm$ SE (sample size).

Character	Immature Males	Adult Males	All Males	All Females
Wing Length	109.4 $\pm$ 0.1 (410)	111.3 $\pm$ 0.1 (472)	110.4 $\pm$ 0.09 (935)	108.1 $\pm$ 0.1 (753)
Bill Length	15.1 $\pm$ 0.03 (403)	15.3 $\pm$ 0.03 (464)	15.2 $\pm$ 0.02 (918)	15.1 $\pm$ 0.03 (738)
Bill Width	13.9 $\pm$ 0.02 (409)	14.0 $\pm$ 0.02 (469)	14.0 $\pm$ 0.02 (930)	13.7 $\pm$ 0.02 (752)
Bill Depth	14.9 $\pm$ 0.03 (403)	15.0 $\pm$ 0.03 (463)	15.0 $\pm$ 0.02 (916)	14.6 $\pm$ 0.02 (743)
Tarsus Length ^{a, b}	20.9 $\pm$ 0.03 (408)	20.9 $\pm$ 0.03 (467)	20.9 $\pm$ 0.02 (928)	21.0 $\pm$ 0.02 (744)
Tail Length	62.2 $\pm$ 0.1 (407)	63.0 $\pm$ 0.1 (468)	62.6 $\pm$ 0.09 (927)	61.3 $\pm$ 0.1 (751)
PC1	0.1 $\pm$ 0.07 (393)	0.9 $\pm$ 0.07 (443)	0.5 $\pm$ 0.05 (884)	-0.6 $\pm$ 0.05 (718)

^a differences between male age classes not significant (two-tailed $p > 0.7$)

^b difference between sexes is significant (one-tailed $p < 0.05$)

all univariate measures (MANOVA, $F = 22.2$, d. f. = 6, 829, two-tailed $p < 0.0001$) except tarsus length ($t = 0.1$, d. f. = 834, two-tailed $p > 0.3$), and also had higher PC1 scores ($t = 7.7$, d. f. = 789, two-tailed $p < 0.0001$).

3.1.2 *Live Birds*

Measurements were obtained for 33 male (16 immature and 17 adult) and 40 female (14 immature, 25 adult, one unknown age) Evening Grosbeaks wintering in southern Alberta. Complete measurements were obtained for most of these birds. However, knemidokoptiasis ("scaly leg"), which is common in Alberta populations of Evening Grosbeaks (McNicholl 1977), prevented tarsal measurements being taken for three males and five females. All univariate measures were normally distributed, with the exception of bill width in immature females (Shapiro-Wilks test, $W = 0.86$, $p < 0.05$). Transformations did not improve normality, and original values for this variable were retained for all analyses.

Because of the relatively small sample size of live birds, I did not attempt separate principal component analyses for each age and sex group. When all birds were considered simultaneously, the analysis identified two eigenvectors which summarized 44.7 and 20.9% of the morphological variation, respectively (Table 7). All univariate measures loaded positively on the first

TABLE 7. Correlations between principal component scores and six morphological measures obtained from free-living Evening Grosbeaks wintering in southern Alberta.

Character	Correlation Coefficient	
	PC1	PC2
Wing Length	0.38	-0.46
Bill Length	0.42	0.15
Bill Width	0.50	0.18
Bill Depth	0.52	0.18
Tarsus Length	0.23	0.57
Tail Length	0.33	-0.60
Eigenvalue	2.68	1.25
% Variation	44.7	20.9

component, indicating that PC1 represented an overall size vector. PC2 was interpreted as being a shape vector, being characterized by individuals with relatively short wings and tails.

Males were larger than females when all univariate measurements were considered simultaneously (MANOVA, $F = 5.1$, d. f. = 6, 58, one-tailed $p < 0.001$), but were no larger than females in either wing length ($t = 1.4$, d. f. = 63, one-tailed $p > 0.1$) or tail length ($t = 1.7$, d. f. = 63, one-tailed $p > 0.1$, Table 8). Males were larger than females along the body size vector (PC1, $t = 11.6$, d. f. = 63, one-tailed $p < 0.001$). There were no overall differences in measurements between age classes of males (MANOVA, $F = 2.3$, d. f. = 6, 23, two-tailed $p > 0.05$; PCA, $t = 0.8$, d. f. = 28, two-tailed $p > 0.3$), and the only univariate measurement found to be larger in adults was wing length ($F = 10.4$, d. f. = 1, 28, two-tailed $p < 0.01$). MANOVA indicated no overall differences in univariate measurements between age classes of females ($F = 0.3$, d. f. = 6, 27, two-tailed $p > 0.2$), although adults had longer wings ($F = 4.2$, d. f. = 1, 32, two-tailed $p < 0.05$) and deeper bills ($F = 4.4$, d. f. = 1, 32, two-tailed $p < 0.05$) than did immatures. PC1 scores were larger for adult females than for immatures ($t = 5.5$, d. f. = 32, two-tailed $p < 0.05$, Table 8).

TABLE 8. Univariate measures (in mm) and PC1 scores calculated from live-caught Evening Grosbeaks in southern Alberta. T-tests between age classes are one-tailed; tests between sex classes are two-tailed. Values are mean $\pm$ SE.

Character	Males		Females		All Males (n = 33)	All Females (n = 40)
	Immatures (n = 16)	Adults (n = 17)	Immatures (n = 14)	Adults (n = 25)		
Wing Length	107.1 $\pm$ 0.6	110.1 $\pm$ 0.6 ^b	106.5 $\pm$ 0.6	108.6 $\pm$ 0.6 ^b	108.6 $\pm$ 0.5	107.5 $\pm$ 0.5
Bill Length	15.6 $\pm$ 0.2	15.8 $\pm$ 0.2	15.2 $\pm$ 0.1	15.4 $\pm$ 0.1	15.7 $\pm$ 0.1	15.4 $\pm$ 0.1 ^b
Bill Width	14.4 $\pm$ 0.1	14.3 $\pm$ 0.1	13.8 $\pm$ 0.1	14.0 $\pm$ 0.1	14.3 $\pm$ 0.1	13.9 $\pm$ 0.1 ^c
Bill Depth	14.9 $\pm$ 0.2	14.9 $\pm$ 0.2	14.1 $\pm$ 0.2	14.5 $\pm$ 0.1 ^b	14.9 $\pm$ 0.1	14.4 $\pm$ 0.1 ^c
Tarsus Length ^a	21.1 $\pm$ 0.2	20.8 $\pm$ 0.2	21.0 $\pm$ 0.1	21.2 $\pm$ 0.1	21.0 $\pm$ 0.1	21.2 $\pm$ 0.1
Tail Length	64.5 $\pm$ 0.6	65.4 $\pm$ 0.5	63.2 $\pm$ 0.9	63.7 $\pm$ 0.8	64.8 $\pm$ 0.4	63.4 $\pm$ 0.5 ^b
PC1 ^a	0.4 $\pm$ 0.3	1.0 $\pm$ 0.5	-1.3 $\pm$ 0.4	-0.2 $\pm$ 0.2 ^b	0.7 $\pm$ 0.3	-0.6 $\pm$ 0.2 ^c

^a because tarsal measurements could not be obtained for all birds (see text), sample sizes for tarsus length and PC1 are as follows: immature males and adult males = 15; immature females = 13; adult females = 21; all males = 35; all females = 30

^b differences between age or sex groups are significant ($p < 0.05$)

^c differences between age or sex groups are significant ($p < 0.001$)

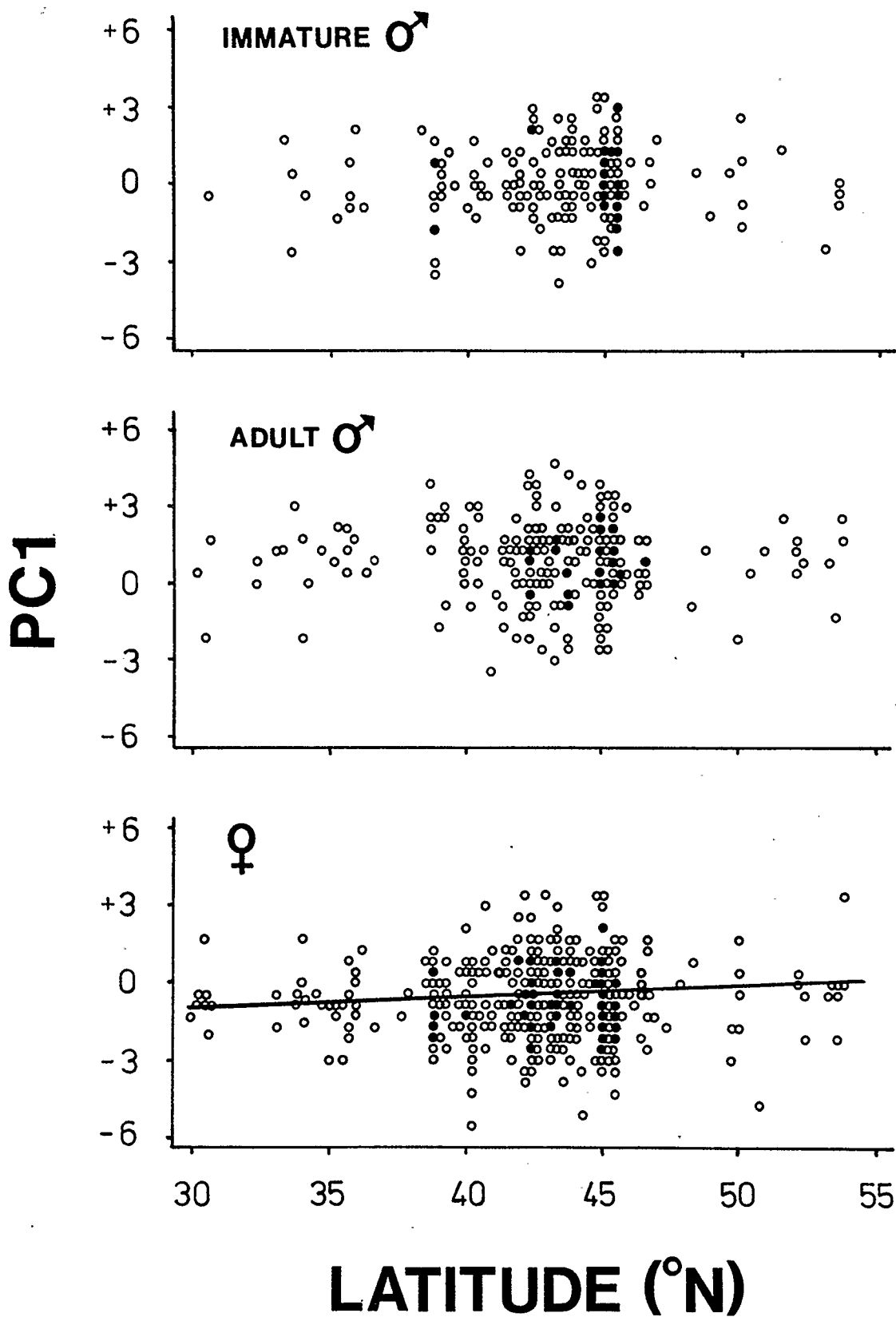
3.2 Latitudinal Variation in Body Size

When all years were combined, there was no evidence within either of the male age groups that larger individuals winter farther north (immatures: $F = 0.6$, d. f. = 1, 219, one-tailed $p > 0.2$; adults: $F = 0.1$, d. f. = 1, 280, one-tailed $p > 0.4$). However, there was weak tendency for body size to increase from south to north in females ($F = 2.7$, d.f. = 1, 472, one-tailed $p = 0.05$, Figure 7). In none of the regressions was longitude a significant main or interaction effect ($p > 0.05$). Data were sufficient to analyze geographic trends in body size for adult males in 1886 ($n = 15$) and 1889 ($n = 45$), for immature males in 1889 ($n = 23$) and 1971 ($n = 15$), and for all females in 1889 ($n = 78$), 1961 ($n = 19$), 1968 ($n = 16$), and 1971 ($n = 24$). There was no relationship between body size and latitude of capture for any age or sex class in any year (all $p > 0.1$).

4. Discussion

Based on analyses of museum specimens from a wide geographic range, and of birds from a local population of wintering individuals, male Evening Grosbeaks are larger-bodied than females. When coupled with the known tendency for males of this species to winter farthest north (Chapter 3), the size difference is consistent with predictions of the body size hypothesis. In contrast, both adult males and females are larger than immatures of the same sex, but

FIGURE 7. Relationships between body size (PC1) and wintering latitude for age and sex classes of the Evening Grosbeak. The regression of PC1 on latitude was significant only for females ($Y = -1.91 + 0.03$ [LAT], $p = 0.05$). Solid circles are points comprised of ≥ 3 individuals.



there are no distributional differences among age groups (Chapter 3). For males, this conclusion is based only on the analysis of museum specimens, because populations of live birds wintering in southern Alberta show no age differences in size.

There are two possible reasons for this discrepancy. Size differences between age classes of males may be sufficiently small that they could not be detected from the sample size of live birds obtained in this study. Alternatively, adult and immature males in this population may not differ in body size. This could result if the local population consisted of relatively small adults and relatively large immatures as compared to other wintering populations. Whatever the reason for the disagreement between results obtained from live birds and museum specimens, I consider the museum sample to be most representative of species-wide differences, and these data show size differences among age classes of males.

The analysis of geographic variation in body size within age and sex classes also offers conflicting support for the body size hypothesis. In neither age class of males was there a latitudinal trend in body size, but larger-bodied females tended to winter farther north than smaller individuals. If the assumption that climatic conditions can influence the choice of wintering latitude

by birds of different body size is correct, then males must be sufficiently large that intrasexual differences in size do not confer differential tolerance to winter conditions. Females, on the other hand, are smaller-bodied than both age classes of males, and may be more influenced by conditions occurring on the wintering grounds. However, if body size differences alone could produce the observed latitudinal trend in females, then the larger-bodied adults should winter farther north than immatures. This pattern does not occur (Chapter 3). Observed sexual differences in the relationship between body size and latitude could also result if the variation in body size differed between the sexes. That is, males might be less variable than females in terms of body size, and individual differences in size might be too small to affect the choice of wintering location. Tests for homogeneity of variances (Ostle and Mensing 1979) showed that this was not the case. PC1 scores for males were no less variable than scores for females (one-tailed tests, museum sample: $F = 1.1$, d. f. = 884, 717, $p > 0.2$; live birds: $F = 1.3$, d. f. = 32, 39, $p > 0.2$).

Taken together, the results suggest that that sexual differences in winter distribution could result because males are larger than females, but it is not clear whether relative size differences between the sexes are sufficient

for males to realize physiological benefits. Comparisons of body-size distribution within age and sex classes suggest this is unlikely, because only females show a geographic trend in size that is consistent with the body size hypothesis. To explain adequately the observed patterns of distribution of age and sex classes in terms of the body size hypothesis, the assumption of physiological advantages to large body size must be verified (see Chapter 6). Direct investigation of the relationship between body size and fasting endurance or cold tolerance in birds has been limited (but see Ketterson and King 1977, Stuebe and Ketterson 1982, Perry et al. 1988), but evidence from field studies indicates that winter survival is not always related to large size. Directional selection for large body size during severe winters has been observed in Canvasbacks (Haramis et al. 1986) and Great Tits, Parus major (Lehikoinen 1986), but not in American Black Ducks (Krementz et al. 1989). In the House Sparrow, both large and small individuals survive better than intermediate-sized birds (Johnston et al. 1972, Johnston and Fleischer 1981, Fleischer and Johnston 1984). In this case, large birds may survive better because of advantages associated with thermoregulation or fasting endurance, or because size confers a high dominance status and priority of access to food. Small individuals might survive well because their

food requirements are lower, and they can more easily meet energy demands when food is in short supply. Also, small, subordinate individuals may avoid aggressive encounters, and thereby have more time available for feeding.

Intermediate-sized birds gain neither of these advantages, and might therefore have a low probability of survival when conditions are severe (Johnston and Fleischer 1981, Fleischer and Johnston 1984). Thus, large size need not always be an advantage, and there might be counteracting selection pressures which could eliminate the relationship between body size and latitude predicted for male Evening Grosbeaks.

Even in the absence of physiological advantages to large size, distributional differences between males and females, and latitudinal trends in body size of females could result if size is a determinant of social rank. Numerous studies have shown that social status is positively related to body size in birds (Searcy 1979, Watt 1986, Richner 1989), and large individuals may winter farther north simply because they are more successful in competition for resources such as food. Male grosbeaks are larger than females, and are the socially-dominant sex (Balph and Balph 1976, Bekoff and Scott 1989). However, there are no data that specifically address the importance of body size on social status in Evening Grosbeaks,

although such a relationship has been implied (Bekoff and Scott 1989). If the relationship between social rank and body size can explain geographic patterns of distribution observed here, then such a pattern should occur among females, but not within either age class of males.

The analysis of morphological variation in wintering Evening Grosbeaks provides only weak support for the body size hypothesis. Clearly, the physiological and social implications of intraspecific variation in body size must be understood before the mechanisms responsible for the patterns observed here can be identified. In the following chapter, I test the assumption that large body size confers a metabolic advantage to wintering Evening Grosbeaks, either through enhanced fasting endurance, or by increased tolerance to cold temperatures. The relationship between body size and social-dominance rank is evaluated in Chapter 7.

CHAPTER 6

THE BODY SIZE HYPOTHESIS

PART 2: THE RELATIONSHIP OF COLD TOLERANCE AND FASTING
ENDURANCE TO BODY SIZE IN EVENING GROSBEAKS**1. Introduction**

Birds that live in temperate regions periodically experience conditions that can challenge physiological tolerances. For example, cold temperatures during winter require that metabolic heat production be increased to maintain a core body-temperature that is constant. In order to sustain an elevated metabolic rate, energy intake must also be increased. Procuring sufficient food to meet energy demands may sometimes be difficult because short day-lengths during winter limit the time available for foraging, and heavy snowfall can periodically cover food supplies (Kendeigh 1945, Ketterson and King 1977). Thus, mechanisms that enhance tolerance of cold temperatures or periods of food deprivation are clearly advantageous to animals living in northern climates. Furthermore, the ability to tolerate severe conditions has important implications for migration, distribution and abundance of individuals of different species (Kendeigh 1945, Root 1988b).

Birds inhabiting northern regions show a wide variety

of adaptations for acquiring and conserving energy. Behavioral adaptations include migration (i.e., avoidance of harsh climates), flocking (which might increase the probability that individuals locate patchily-distributed food; Cody 1971, Krebs et al. 1972), selection of microhabitats that minimize exposure to cold temperatures and wind (Buttemer 1985, Reinertsen 1986), and food storing (Smith and Reichman 1984, Sherry 1985). There are also a number of physiological mechanisms that enhance survival in cold climates. Most birds store body fat during winter for use as metabolic fuel (Helms and Drury 1960, King 1972). In some species, fat deposits during winter may attain 15% of lean body mass (Helms et al. 1967, Clark 1979). Many birds show seasonal shifts in metabolism, including an increased capacity for thermogenesis during winter (Hart 1962, Marsh and Dawson 1986). The physiological basis for these seasonal changes is not clear, but may involve shifts in the ability to mobilize substrates which are catabolized to produce energy (Marsh and Dawson 1982, 1986). Finally, many species of birds that winter in northern areas can depress body temperatures between 2° and 12°C at night (Reinertsen 1983, Wang 1986). Nocturnal hypothermia can result in daily energy savings of up to 30% (Steen 1958, Saarela et al. 1991).

In theory, large-bodied individuals should be best

able to endure periods of physiological stress during winter. As body mass increases, there is a proportionate (1:1) increase in the mass of heat-producing tissues (muscles), but the increase in surface area of the body (through which heat is dissipated) is proportional to body mass raised to the $2/3$ power (Calder 1974). Therefore, smaller individuals have a higher surface area-to-volume ratio, and lose body heat at a faster rate (on a per-gram basis) than do larger-bodied individuals. In other words, cold tolerance should be positively related to body size (Kendeigh 1969, Calder 1974). Large size should also confer an advantage during periods of food shortage. As body size increases, more metabolic substrates (fat) can be stored. Furthermore, metabolic rate increases with body mass raised to the 0.6 or 0.7 power (Kendeigh 1969, Calder 1974, Nagy 1987), so that large individuals catabolize fat stores at a comparatively slower rate than do smaller individuals. Because the ratio of energy stores to power consumption therefore increases with body size, large-bodied individuals should survive longer if food is temporarily unavailable (Calder 1974).

The theoretical relationship of body size to fasting endurance and cold tolerance has frequently been cited as a mechanism producing latitudinal gradients in the body size of homeotherms (see Chapter 5). In birds, large-bodied

species tend to survive for longer periods than smaller ones under laboratory conditions which simulate winter environments (Kendeigh 1945), as well as in the wild (Errington 1939). However, there has been little investigation of whether small intraspecific differences in body size are sufficient to influence physiological tolerances during winter, and this possibility has been questioned (Scholander 1955, 1956, Irving 1957). Most intraspecific investigations have considered sexual differences in size-dimorphic species, and all have focussed on fasting endurance rather than cold tolerance. In general, individuals of the larger sex (usually males) tend to endure food deprivation for the longer duration (Kendeigh 1945, Latham 1947, Ivacic and Labisky 1973, Ketterson and King 1977), although the opposite trend has been observed occasionally (Latham 1947, Jordan 1953). The reasons for this pattern are not clear. Laboratory studies show that the rates and amount of mass (fat) loss during fasting typically are independent of both body size (estimated from wing length; Ketterson and King 1977, Ketterson and Nolan 1978, Lehikoinen 1987) and sex (Ketterson and Nolan 1978, Shapiro and Weathers 1981, Stuebe and Ketterson 1982, Lehikoinen 1987, Webster 1989, but see Ketterson and King 1977), suggesting that intraspecific variation in body size is insufficient to

influence the rate at which fuel reserves are catabolized. However, it is possible that individuals of the larger sex can endure longer periods without food simply because they are fatter initially (Ketterson and Nolan 1978, Stuebe and Ketterson 1982). In short, evidence to support the idea that small intraspecific differences in body size can influence survival during periods of food shortage is equivocal.

The possibility that intraspecific differences in cold tolerance are positively related to body-size differences has not, to my knowledge, been tested empirically. Swanson (1990) found that larger Dark-eyed Juncos endured severe cold stress longer than did smaller birds. However, size differences were based on body mass, so it is unclear whether heavier birds were of larger structural size, or whether they simply contained larger stores of body fat (Swanson 1990).

I have demonstrated previously that male Evening Grosbeaks winter farther north than do females (Chapter 3), and that males are the larger-bodied sex (Chapter 5). Adults are larger-bodied than immatures in both sexes (Chapter 5), but there are no geographical differences in distribution of age classes during winter (Chapter 3). Males (of either age class) show no latitudinal variation in body size during the winter, but females wintering in

the northern parts of the winter range are larger-bodied than those wintering at more southerly sites (Chapter 3). These patterns offer conflicting support for the body size hypothesis (see Chapter 5), which states that larger-bodied individuals (or age and sex classes) should winter farthest north because of advantages associated with their greater size (Ketterson and Nolan 1983, 1985). However, patterns of geographic distribution can not be interpreted adequately in light of this hypothesis until the assumption that intraspecific differences in body size confer differences in the ability to endure either cold temperatures, or periods of food limitation, is tested.

In this chapter, I test whether body size influences cold tolerance or fasting endurance in captive Evening Grosbeaks, and whether such physiological tolerances are influenced by age or sex. To test the hypothesized relationship of body size to cold tolerance, I subjected individual Evening Grosbeaks to severe cold stress and predicted: (1) that individuals of large-bodied age and sex classes should remain homeothermic ("survive") longer than would individuals of smaller-bodied classes; and (2) that large individuals within each class should "survive" longer than would smaller ones. To test the relationship of fasting endurance to body size, I monitored the body-mass loss of individuals during food deprivation trials. I

predicted: (3) that large-bodied individuals (or age and sex classes) should experience greater loss of mass over a fixed period of time than should smaller individuals (because of differences in energy requirements); but (4) that mass loss expressed as a percentage of lean mass (body size) should be comparatively less as body size increases.

2. Methods

Birds were captured from wild populations, measured, and housed in an outdoor aviary as described previously (Chapter 2). All birds were held for at least two weeks before being subjected to either fasting or cold endurance trials (see below). Most individuals were used in both experiments, and the order of the two experiments for each bird was determined by a coin toss. A minimum of four days elapsed before different trials were conducted using the same bird.

Principal components analysis (PCA), as described in Chapter 3, was used to determine the overall body size of each individual. The analysis was performed on all live birds captured during the period of study, whether or not they were subsequently used in cold tolerance or fasting endurance experiments. Because PC scores are not calculated for individuals with any missing measurements, and because "scaly leg" prevented accurate measurements of tarsometatarsus ("tarsus") length in some individuals

(Chapter 5), the present analysis differs from the previous PCA in that tarsus length was not included. As before, I considered the first eigenvector (PC1) to represent overall body size if it correlated positively with all univariate measures from which it was derived.

2.1 Cold Tolerance Experiments

Cold tolerance was defined as the duration over which individuals could remain homeothermic under conditions of severe cold stress (Dawson et al. 1983). I sought a temperature at which 50% of experimental birds would become hypothermic within approximately one hour of exposure (W. R. Dawson, pers. comm.). Evening Grosbeaks often experience temperatures below -40°C during winter, and the temperature required to induce hypothermia in air could not be attained using available equipment. However, cold temperatures can be simulated in the laboratory by exposing experimental individuals to more moderate temperatures in an atmosphere where the nitrogen component of normal air (79%) is replaced with helium (i.e., a 21% oxygen: 79% helium mixture, hereafter termed "helox"). Because helium is about six times more conductive than the nitrogen it replaces (Chemical Rubber Company 1986), heat is lost from the body at a faster rate than normal, and metabolic rate increases to augment

thermogenesis (Leon and Cook 1960, Rosenmann and Morrison 1974). Thus, experimental subjects respond as if they were encountering much colder temperatures than are actually experienced.

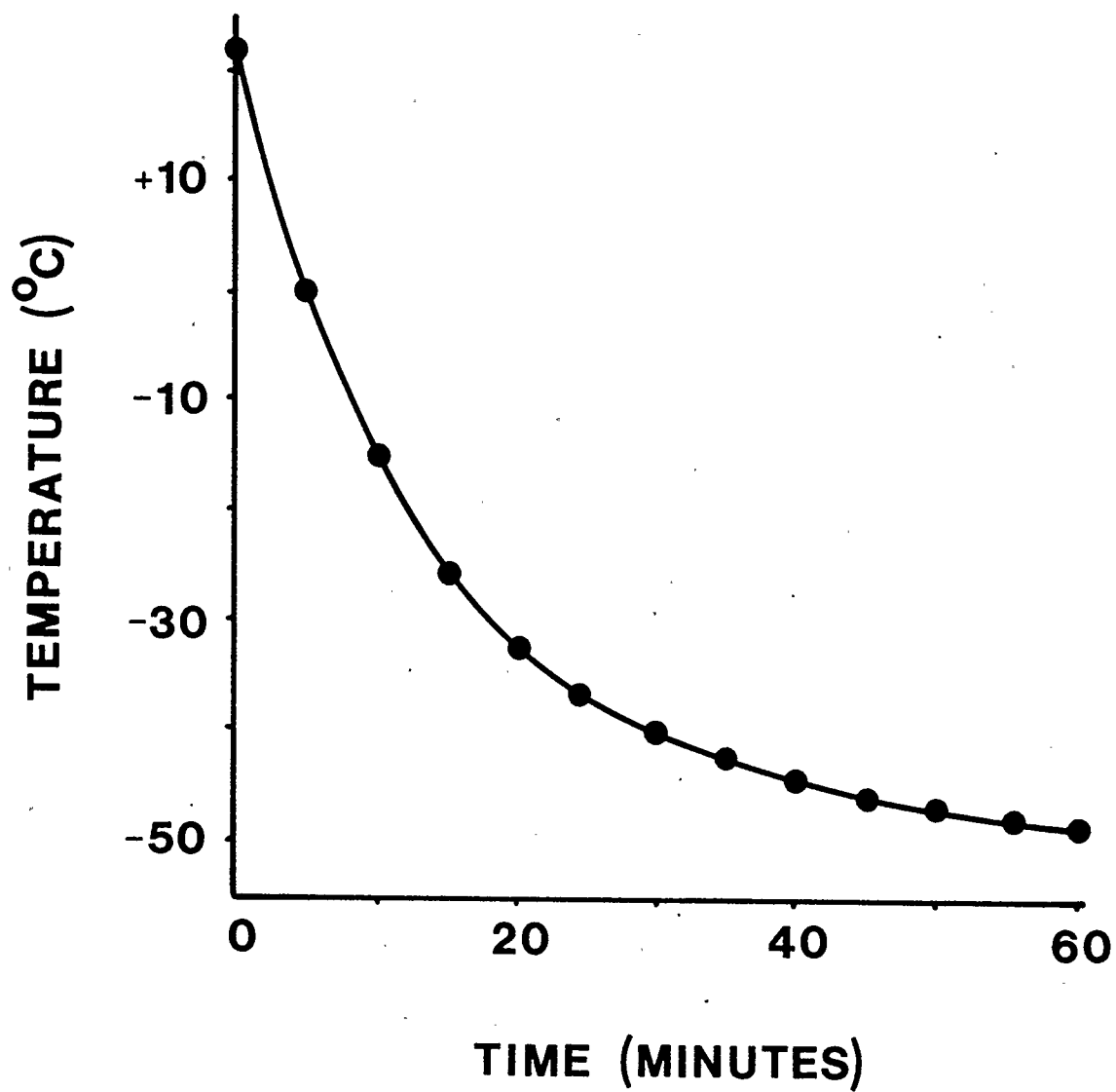
After preliminary trials, the following experimental procedure was established. Helox was delivered through Tygon tubing, and precooled through a 17-m coil of copper tubing placed in a chest freezer set to -28°C . The cooled gas was fed immediately into an experimental chamber placed inside an ultra-cold freezer set at -48°C . The chamber, in which experimental birds were placed, consisted of a four-litre paint can lined with a thin layer of cardboard and containing a plastic-mesh floor to prevent birds from contacting cold surfaces. Preliminary trials showed that all birds placed in this apparatus experienced hypothermia within 15 to 20 minutes. To increase the variation in "survival" time of subjects, heat loss from the chamber was reduced by wrapping the exterior with a 1 cm layer of fibreglass insulation.

Gases flowed through the system at a rate of 1.6 ± 0.1 l/min. This rate was calculated from the basal metabolic rate (BMR) of winter-acclimatized Evening Grosbeaks (0.042 ml $\text{O}_2/\text{g}/\text{min}$, Dawson and Tordoff 1959), assuming an average body mass of 60 grams, and a peak metabolic rate of five times BMR as observed in other cold-stressed finches

(Dawson and Carey 1976). The minimum required flow rate was calculated to be 1.26 l/min, so the rate used in these experiments should have provided a sufficient margin of safety against hypoxia. At this flow rate, the temperatures in the empty chamber dropped from room temperature (20°C) to approximately -48°C in about 45 minutes (Figure 8).

Cold tolerance experiments were conducted between 2 and 20 February 1990, and between 19 December 1990 and 29 January 1991. All trials commenced between 1100 and 1500 MST. Experimental birds were removed from the aviary two to three hours before trials were to begin, and housed individually in 60 x 25 x 33 cm cages. Cages were supplied with water (but no food), and placed in an environmental chamber at 2°C. Immediately before each trial, birds were weighed and scored for fat deposits (Chapter 2). The body mass obtained at this time was considered to be "gut-empty" mass, because the gastrointestinal tract of most small birds is voided within two to three hours of eating (Stevenson 1933, Ziswiler and King 1972). A 30-gauge copper-constantan (type T) thermocouple, which passed through a gas-tight port on the test chamber, was inserted 2.5 cm into the cloaca of each bird. Thermocouples were threaded through a small piece of cardboard, and paper-clipped to the tail to prevent removal by birds during

FIGURE 8. Temperature gradient to which Evening Grosbeaks were exposed in the experimental chamber during cold tolerance experiments. Mean temperatures at each five-minute interval are derived from seven trials using an empty chamber, and a air-flow rate of 1.6 l/min. Standard errors (not shown) on all mean values are $< 1.0^{\circ}\text{C}$.



trials. The sealed chamber was then placed in the ultracold freezer, and the inlet and outlet gas lines attached ("time 0"). The temperatures of both the chest and ultracold freezers were taken at this time, using thermocouples similar to those described above.

The system was ventilated with normal air for five minutes before the delivery of helox commenced. Body and chamber temperatures were recorded every minute, using a Cole-Parmer (model N-08500-40) thermocouple thermometer. In preliminary trials, most birds showed some thermoregulatory capacity (short bursts of heat production resulting in increased body temperature) when core temperatures exceeded 32°C , and several birds could maintain body temperatures of 34 to 36°C for up to 30 min. Core temperatures generally dropped rapidly after reaching 32°C , and birds quickly became lethargic. Thus, trials continued until body temperature dropped to 32°C from the normal 41°C (Dawson and Tordoff 1959, West and Hart 1966). When this body temperature was attained, the temperatures of the two freezers were recorded, and individuals were quickly moved to a warm area to revive. Birds resumed normal activity within five to 10 minutes. Birds were reweighed, scored again for fat deposits, and provided with food and water. All individuals were held for at least two hours before being released into the

aviary or to the wild.

Analysis of covariance (Neter et al. 1985) was used to test the prediction that large-bodied individuals (or age and sex classes) should be most cold tolerant. Because subcutaneous fat deposits varied widely among individuals (pers. obs.), and because these variations might influence the ability to produce heat (mobilization of fatty acids) or conserve heat (insulation), I included fat class (Chapter 2) as an independent variable in the analysis. I first tested the effect of all four independent variables (sex, age, PC1 and fat class) and their interactions on cold tolerance, and then used backwards elimination of insignificant effects (Neter et al. 1985) to fit a model containing the fewest number of significant terms.

2.2 Fasting Endurance Trials

Fasting endurance trials were conducted between 11 and 24 February 1990, and between 17 December 1990 and 25 January 1991. Birds were removed from the aviary between 0800 and 1000, weighed, scored for fat (Chapter 2), and housed in individual cages at 2°C (see above) with water but no food. After three hours, body mass ("gut-empty") was recorded. Birds were then returned to the environmental chamber, and left undisturbed for 24 ± 0.1 h on a 10:14 light:dark photoperiod (lights on at 0800). The temperature remained constant during the entire trial.

After 24 h, birds were weighed, scored for fat, and provided with food for at least one hour before being released into the aviary or to the wild.

I used analysis of covariance and backward elimination of terms (Neter et al. 1985) to test the hypothesis that larger-bodied individuals (or age and sex classes) should lose more mass (fat) during fasting.

To test the hypothesis that larger-bodied individuals should lose proportionately less fat during food deprivation than smaller-bodied individuals, I required a measure of lean body mass for each individual. This value was estimated by regressing gut-empty body mass on fat class, and calculating residual body mass for each individual (Piper and Wiley 1989, Mulvihill and Chandler 1990). Individual values of residual mass were then added to the intercept of the regression equation (i.e., the average mass of all birds at fat class 0) to estimate lean mass for each individual. This procedure assumes that body mass is a linear function of fat class. A test for lack-of-fit of the regression model (Neter et al. 1985) confirmed this assumption ($F = 0.5$, d. f. = 4, 37, $p > 0.2$, see also Rogers and Rogers 1990). Absolute mass loss during each trial was then divided by estimated lean mass for each individual to estimate relative mass loss (g fat lost/g lean mass). Analysis of covariance and backward

elimination of terms was used to test the predicted effects of body size (PC1), age and sex on relative mass loss.

Finally, I estimated the duration over which Evening Grosbeaks of different fat classes could survive without food at 2°C. This was accomplished by combining the observed rate of absolute mass loss during fasting with estimates of the average mass of fat represented by each fat class (from the regression of body mass versus fat class, see above). This procedure assumes that death occurs when fat reserves are depleted. In reality, the mobilization of protein and carbohydrate reserves could extend this period. However, these substrates are relatively minor sources of energy in fasting birds (Le Mayo et al. 1981, Cherel et al. 1988). Moreover, their contribution to fasting endurance should be independent of differences in fat reserves among individuals.

3. Results

Principal components analysis was performed on univariate measures of body size obtained from 73 individuals captured in southern Alberta during winter (see Chapter 5). PCA extracted two eigenvectors with eigenvalues > 1.0. The first component, which accounted for 51.2% of the variation in the data set, correlated positively with all univariate measures, and is interpreted

as being a body-size vector (Table 9). PC2 (21.1% of variation) was characterized by individuals with long wings and tails relative to other measures, and is not considered further. Factor scores for each individual bird were therefore calculated along PC1, and used as a measure of overall body size in subsequent analyses.

3.1 Cold Tolerance Trials

Forty-six individuals (10 immature males, 11 adult males, 12 immature females, 13 adult females) were used in cold tolerance trials. Initial temperatures ranged between -25.6°C and -29.5°C in the chest freezer (mean = -27.9 ± 0.1 [SE]) and between -45.6°C and -51.0°C in the ultracold freezer (mean = -47.9 ± 0.2). Final freezer temperatures ranged between -25.0°C and -29.4°C (mean = -27.9 ± 0.1), and between -45.9°C and -49.3°C (mean = -47.5 ± 0.1), respectively. Thus, all birds were subjected to similar temperature gradients during individual experiments. Minimum temperatures attained in the experimental chamber during trials averaged $-30.6 \pm 0.3^{\circ}\text{C}$ (range, -25.0 to -34.0).

The mean duration over which birds could endure the experimental temperatures was 49.3 ± 4.3 min (range, 15 to 157). Over the course of the trials, individuals lost an average of 0.7 ± 0.1 g (range, 0.1 to 2.3) of body mass. In only one instance did the initial and final fat class

TABLE 9. Correlations between principal component scores and five morphological measures obtained from 73 free-living Evening Grosbeaks wintering in southern Alberta.

Character	Correlation Coefficient	
	PC1	PC2
Wing Length	0.41	0.55
Bill Length	0.40	-0.42
Bill Width	0.51	-0.27
Bill Depth	0.51	-0.30
Tail Length	0.39	0.59
Eigenvalue	2.59	1.05
% Variation	51.2	21.1

differ. This occurred in an adult male which "survived" for the second-longest duration (140 min), and lost 2.1 g of mass and 0.5 of a fat class. All birds had visible fat remaining at the end of trials (minimum fat class 1.0).

The distribution of survival times was non-normal (Shapiro-Wilks test, $W = 0.77$, $p < 0.0001$), and was log-transformed for inclusion in the analysis of covariance (after transformation, $W = 0.96$, $p > 0.1$). Although fat class was measured as a discrete variable, its relationship with survival time was linear (lack-of-fit $F = 0.2$, d. f. = 4, 37, $p > 0.9$), and it was therefore included in the model as a covariate. After the elimination of nonsignificant terms (all $p > 0.2$), the covariance model contained only fat class ($F = 9.1$, d. f. = 1, 45, $p < 0.005$) and sex ($F = 6.4$, d. f. = 1, 45, $p < 0.05$). Thus, fat birds survived longer than leaner individuals regardless of sex, and males survived longer than females regardless of their fat class. Males survived for an average of 52.0 min (upper SE = 57.2 min; lower SE = 47.2 min [asymmetrical SE based on log-transformed data]), whereas females survived for 37.2 min (upper SE = 40.6; lower SE = 34.0).

3.2 Fasting Endurance Trials

Forty-six birds (10 immature males, 11 adult males, 11 immature females, 14 adult females) were used in fasting endurance trials. Individuals lost an average of 5.4 ± 0.2

g of mass and 0.6 ± 0.03 of a fat class when deprived of food for 24 h. All individuals had subcutaneous deposits of fat remaining at the termination of trials (minimum fat class = 0.5).

Absolute mass loss was not influenced by body size, age, or sex (all $F < 1.9$, d. f. = 1, 42, all $p > 0.1$).

I estimated the lean body mass of birds in the experimental population to be 48.6 ± 2.0 g (intercept of body mass versus fat class regression) with a range from 40.5 to 55.6 g. Individuals lost an average of 0.1 ± 0.03 g of mass/g of lean body mass during trials. There was no significant main or interaction effect of age, sex, or body size on relative mass loss (all $F < 0.6$, d. f. = 1, 42, all $p > 0.4$).

The estimated mass of fat deposits at different fat class was as follows: class 1.0, 4.9 g; class 1.5, 7.3 g, class 2.0, 9.8 g, class 2.5, 12.2 g; class 3.0, 14.4 g. From these estimates, and the average rate of absolute mass loss during fasting, I estimated that, at 2°C, the leanest birds (in these experiments, class 1.0) should survive food deprivation for 21.7 h, while the fattest birds (class 3.0) should survive for 64.0 h.

4. Discussion

4.1 Cold Tolerance

Contrary to expectation, there was no influence of body size on cold tolerance in Evening Grosbeaks. However, males survived significantly longer than females when exposed to extremely low temperatures. This trend is consistent with the tendency for males to winter farthest north (Chapter 3), where temperatures are coldest (Bryson and Hare 1974). Although males are larger-bodied than females (Chapter 5), factors other than size must be invoked to account for sexual differences in the ability to endure cold temperatures.

Previous studies have suggested that cold hardiness is related primarily to the ability to store, mobilize and metabolize fuels such as fat and glycogen (Carey et al. 1978, Marsh and Dawson 1982, Dawson et al. 1983), and to a minor extent, to the insulative value of the plumage (Dawson and Carey 1976, Dawson et al. 1983, Swanson 1991). To my knowledge, there is no information on physiological or plumage differences between male and female birds which could be related to the sexual differences in cold tolerance I observed in Evening Grosbeaks. However, differences in fat storage should not be an important factor, because there was no sex difference in mean fat score at the beginning of cold tolerance trials (Mann-

Whitney U-test, $T = 1.1$, $p > 0.2$). Birds of both sexes catabolized only a small proportion of fat stores during cold tolerance trials, and all birds had visible fat remaining when hypothermia was induced. This suggests that cold tolerance was not limited by the availability of lipid reserves. It is possible that sexual differences in the ability to use other metabolic fuels may be important in cold tolerance. Although glycogen accounts for less than one percent of fuel reserves in birds (Marsh and Dawson 1982, Cherel et al. 1988), seasonal shifts in thermogenic capacity of finches are closely related to the ability to restrict the catabolism of glycogen stores during winter (Marsh and Dawson 1982, 1989). Minor differences in glycogen metabolism between males and females could therefore have important implications for the ability to endure cold temperatures. Such information is currently lacking, and future research into mechanisms of heat production in males and females is required before the sexual differences in cold tolerance observed in Evening Grosbeaks can be explained adequately.

Although fat stores cannot account for sexual differences in cold tolerance, fat birds, regardless of sex, "survived" significantly longer than did leaner individuals under the same experimental conditions. There are at least two possible reasons for this. First, fat

birds may have been better able to mobilize fatty acids for thermogenesis than leaner individuals, and might therefore have been able to achieve or sustain a higher rate of heat production. Alternatively, fat deposits may serve an insulative function, thereby reducing the amount of metabolic heat dissipated from the body. In birds, subcutaneous fat is deposited primarily in the furcular and abdominal regions. Compared to the plumage, such deposits should be of minimal insulative value, because they do not cover the pectoralis muscle, where most metabolic heat is produced (Dawson et al. 1983). Nevertheless, fat deposits should reduce heat loss across the body surface, and prolong the ability of birds to resist extreme temperature gradients (Veghte 1964, Collins 1989).

4.2 Fasting Endurance

The absolute and relative rates of fat loss during food deprivation did not vary as predicted by the body size hypothesis. It is therefore unlikely that larger-bodied Evening Grosbeaks can survive for longer periods without food than smaller-bodied individuals. However, the possibility remains that larger birds may endure food deprivation for longer periods because, for a given fat class, large birds should have greater fuel reserves (in absolute terms) than smaller birds (Ketterson and King 1977, Ketterson and Nolan 1978). Based on the range of

fat-free masses of birds used in fasting endurance trials, there was a 15.7% variation in lean body size in this population of Evening Grosbeaks. Assuming that the absolute mass of fat varies proportionately with lean size (Calder 1974), then the predicted survival times of the largest and smallest birds should differ by 3.4 h for lean individuals (fat class 1.0), and by 10.0 h for the fattest birds (class 3.0). These estimates ignore the possibility that metabolic costs also increase with body size (Kendeigh 1970, Calder 1974), so the range of survival times calculated for the smallest and largest birds may be somewhat less than expected. Furthermore, body-size variations in the study population were insufficient to affect rates of fat loss, so it seems unlikely that observed differences in size would significantly affect the amount of fat that could be deposited.

4.3 The Body Size Hypothesis and Differential Migration

Taken together, the results suggest that small intraspecific differences in body size in Evening Grosbeaks are insufficient to influence tolerance to cold temperatures or the ability to survive prolonged periods without food. Thus, there is no evidence that size-mediated differences in physiological tolerances can explain the evolution of differential migration in this

species. This conclusion is largely consistent with patterns of latitudinal variation in body size of wintering individuals, where neither immature or adult males show north-south trends in body size across the winter range (Chapter 5). Females show a weak tendency to increase in overall size from south to north. However, the absence of a relationship between body size and fasting endurance or cold tolerance in females suggests that mechanisms other than physiological tolerances must be invoked to explain this trend.

During winter, Evening Grosbeaks occasionally must endure periods when ambient temperatures are well below the zone of thermoneutrality for extended durations. However, individuals of this species appear to be extremely tolerant of cold conditions, and it is possible that temperatures normally encountered within the winter range are insufficient to influence the distribution of individuals (regardless of body size). Because cold tolerance was tested in a helox atmosphere, it is difficult to determine the equivalent air temperature that was experienced by birds during trials. Rosenmann and Morrison (1974) found that peak metabolic rate in another fringillid finch, the Common Redpoll (Carduelis flammea) was reached at about -70°C in air, and at about -5°C in helox. Most Evening Grosbeaks in the present experiments became hypothermic

only if the temperature in the chamber dropped below -30°C . Thus, the equivalent temperature in air was probably well below -70°C in my experiments, which is much colder than temperatures normally encountered within the winter range. Even though temperatures of -40°C , when accompanied with moderate winds, might necessitate extremely high thermogenic requirements, free-living individuals could still resort to behavioral strategies that minimize exposure to such conditions (e.g., forage in protected microclimates, Grubb 1975, 1977) or augment heat production (e.g., locomotor activity, Webster and Weathers 1990). Therefore it seems reasonable to conclude that the capacity to produce sufficient metabolic heat should rarely, if ever, be exceeded in wild Evening Grosbeaks during winter.

Fasting endurance might also be of little importance to wintering Grosbeaks. Intuitively, the ability to endure periods of food shortage should be most important to ground-feeding birds, because snowfall can occasionally cover food (Graber and Graber 1979, Stuebe and Ketterson 1982, Lima 1986, Rogers 1987). Snowfall should have little effect on food availability for this species because Evening Grosbeaks are primarily arboreal foragers (Parks 1947, Speirs 1968, pers. obs.), and it is unlikely that their food supply would suddenly become unavailable during severe weather (see also Rogers 1987). Fasting could still

be important if food is patchily distributed and in limited supply. Even so, Evening Grosbeaks are reported to feed on a wide variety of vegetable matter during winter (Davis 1924, Speirs 1968, Jackson 1974), and may therefore be able to secure an adequate food supply regardless of prevailing weather conditions.

Finally, although fat reserves are clearly important for both cold tolerance and fasting endurance in this species, most birds examined for fat immediately upon capture from the wild during winter contained only intermediate levels of subcutaneous fat (mean fat class = 1.8 ± 0.1 , $n = 74$), and only two (2.7%) individuals were determined to have near-maximum reserves (fat class 3.0). Why do all Evening Grosbeaks not maintain large stores of fat during the winter? Perhaps birds are constrained from depositing large reserves because food resources are usually in short supply. If so, then captive birds should be fatter than those in the wild, because food was always abundant in the aviary. However, individuals scored for fat prior to fasting endurance and cold tolerance trials (mean duration in captivity 39.5 ± 2.6 days, $n = 92$ [data for individuals used in both trials treated as separate observations]) were not significantly fatter than free-living birds (Mann-Whitney U-test, $T = 1.4$, $p > 0.1$). Perhaps there are costs associated with maintaining large

reserves of fat. For example, fat birds may be less efficient fliers than leaner individuals, thereby rendering them more prone to predation (Stuebe and Ketterson 1982, Pienkowski et al. 1984, Lima 1986). However, the relatively small reserves of fat that I observed may further indicate that the ability to withstand low temperatures and periods of food shortage may not play an important role in the winter distribution of Evening Grosbeaks.

CHAPTER 7

THE SOCIAL DOMINANCE HYPOTHESIS

1. Introduction

In many group-living organisms, the social ranks of individuals can be arranged in a hierarchial sequence based on predictable dominance-subordination relationships with other group members (Huntingford and Turner 1987). Such "dominance hierarchies" have been identified in a wide variety of animals including molluscs, arachnids, crustaceans, insects, and all classes of vertebrates (see review in Gauthreaux 1978). The prevalence of dominance behavior among animals suggests that it has important ramifications for a broad spectrum of life-history traits (Allee 1939, Collias 1944, Wilson 1975, Gauthreaux 1978). Of interest for the present study is the fact that social dominance has been implicated as a factor responsible for the evolution of many types of animal movements, including both dispersal and migration (Cox 1968, Gauthreaux 1978). Consequently, dominance behavior can have a strong effect on the distribution of individuals, and therefore influences gene flow and population dynamics (Wilson 1975, Gauthreaux 1978).

Gauthreaux (1978) proposed a model whereby dominance behavior affects the distribution of dominant and

subordinate individuals during the nonbreeding season. According to this model, food resources available to populations occupying breeding areas are occasionally in short supply and intense intraspecific competition results. Socially-dominant individuals are most likely to obtain an adequate food supply under these conditions, while subordinate individuals are forced to migrate to areas where either food resources are more abundant or competition from dominants is relaxed. When food is sufficiently limiting so that all individuals must leave breeding areas, dominants should be able to secure adequate resources in areas that are closest to the breeding grounds, while subordinates must extend their movements to more distant areas. Because social rank is frequently associated with differences in age and sex, the result is either partial or differential migration.

In most species of birds, males are socially dominant over females (Balph 1977, Baker and Fox 1978, Ketterson 1979, Richner 1989), and tend to winter farthest north (Chapter 1). Accordingly, the social dominance hypothesis frequently has been cited as a proximate or ultimate factor in the evolution of differential or partial migration of the sexes in birds (Gauthaux 1978, Ketterson and Nolan 1983, Lundberg and Schwabl 1983, Lundberg 1985, Terrill 1987, Wiedenmann and Rabenold 1987). Typically, adults are

socially dominant over immatures of the same sex (Ketterson 1979, Ekman and Askenmo 1984, Desrochers et al. 1988, Hogstad 1988, Piper and Wiley 1989), which is consistent with the dominance hypothesis for species in which adults winter farther north than do immatures (Gauthreaux 1978, Dolbeer 1982, Kerlinger and Lein 1986). However, in several species, immatures winter farthest north (Chapter 1) despite being subordinate (e.g., Dark-eyed Junco, Ketterson and Nolan 1983; American Goldfinch, Prescott and Middleton 1990). In such species, an important role for dominance in the choice of wintering latitude by individuals of different age groups is unlikely.

Knowledge of dominance relationships and winter distribution of age and sex groups can be used to support or refute the social dominance hypothesis, but this approach relies on the widespread conception that the benefits of being dominant outweigh the benefits of being subordinate. There is some support for this idea. Dominant birds typically gain priority of access to food (Baker et al. 1981, Lundberg 1985, Millikan et al. 1985), or to habitats where the threat of predation is low (Ekman and Askenmo 1984, Schneider 1984, Ekman 1987, Hogstad 1988). In some cases, dominants have higher survival than subordinates when food is in limited supply (Fretwell 1969, Baker and Fox 1978, Kikkawa 1980, Arcese and Smith 1985).

These observations imply that dominants are at an energetic advantage relative to subordinates, and low-ranking individuals are seen as "hopeful dominants" (Rohwer and Ewald 1981, Ekman 1987) that will increase their social status later in life.

Although the benefits of being dominant are relatively clear, there has been little investigation into the costs of dominance, or the compensating benefits of being subordinate (Millikan et al. 1985, Huntingford and Turner 1987). There is some evidence that subordinates need not always be at a disadvantage. For example, dominants may have higher metabolic rates than lower-ranking individuals, suggesting that the energetic cost of being a dominant may be high (Farr and Andrews 1978, Roskaft et al. 1986, Hogstad 1987). Dominants often spend more time fighting than do subordinates (Balph 1977, Ketterson 1979, Kikkawa 1980, Ficken et al. 1990) and may therefore have less time available for foraging than do lower-ranking individuals, particularly when food sources are economically defendable (Rohwer and Ewald 1981, Theimer 1987). Thus, dominants may gain increased benefits at higher cost, while subordinates acquire reduced benefits at lower cost. In this scenario, dominance and subordination might be energetically-equivalent strategies (Rohwer and Ewald 1981, Whitfield 1987). If there is no energetic advantage to being

dominant, the possibility that asymmetries in social status can account for differences among age and sex groups in distance migrated is reduced. Thus, the relative costs and benefits to individuals of different social rank must be considered before the social dominance hypothesis can be invoked to explain differential migration in birds.

The Evening Grosbeak is a differential migrant, in which females make longer migrations than males, but there are no differences in distance migrated between age classes of either sex (Chapter 3). In this chapter, I ask whether these patterns of winter distribution are consistent with predictions of the social dominance hypothesis. At first glance, social dominance might appear to be an important determinant of intraspecific variation in migratory behavior of Evening Grosbeaks. This species is gregarious throughout the year, but particularly during winter when flocks of mixed age and sex may comprise up to several hundred individuals (Mason and Shaub 1952). Intense aggression among flock members at food sources is frequently observed, and males have been reported to aggressively exclude females from food (Balph and Balph 1976, Balph et al. 1979, Bekoff and Scott 1989).

If observed patterns of geographic distribution of age and sex groups can be explained by the social dominance hypothesis, I predict: (1) that males should be socially

dominant over females, but (2) that there should be no difference in social rank between age groups for either sex. I tested these predictions by observing interactions in captive flocks composed of individuals of different age and sex classes.

I also examined the influence of body size on dominance rank. Other studies have implicated the importance of size as a determinant of social dominance (Baker and Fox 1978, Searcy 1979, Watt 1986, Richner 1989). Because male Evening Grosbeaks are larger than females (Chapter 5; see also Balph 1976, Lago 1979), and because adults are larger-bodied than immature individuals of the same sex (Chapter 5), sex or age differences in social rank could arise simply because of body-size differences between classes. Thus, I tested the null hypothesis (3) that there is no relationship between body size and social rank. Finally, I used observations of foraging behavior and calculations of energy expenditure by different individuals to test the prediction (4) that socially-dominant individuals are at an energetic advantage relative to lower-ranking individuals. I also used time-budget analysis to help to explain variations in energy expenditures among individuals.

2. Methods

All birds used in the social-dominance experiments

were captured, color marked, housed and measured as described previously (Chapter 2). The body size of each individual was determined from principal components analysis (Tabachnick and Fidell 1983) performed on five univariate measures (wing length, bill length, bill width, bill depth and tail length) where the score on the first principal component was considered to be a measure of overall body size (see Chapter 2).

2.1 Patterns and Determinants of Dominance Among Age and Sex Groups

I used two captive flocks to determine the influence of age, sex and body size on relative social rank of Evening Grosbeaks. In the first flock ("Flock 1"), 23 individuals (four immature and eight adult females; seven immature and four adult males) were captured between 9 and 13 December 1989, and initially housed indoors in individual cages. At the end of the capture period, all individuals were introduced simultaneously into the aviary. This was done to eliminate the possibility that prior residence could influence dominance status (Cristol et al. 1990, Holberton et al. 1990, Wiley 1990). Food and water were available at all times in the aviary, but the feeding platform was constructed so that no more than four birds could forage simultaneously. I allowed the social hierarchy to develop

for seven days before starting observations on this flock.

All individuals in Flock 1 were released into the aviary in healthy condition, but several other individuals captured during the first winter of study sustained minor injuries when placed in small cages immediately after capture from the wild. Therefore, a different procedure was followed in assembling the second flock ("Flock 2"). I captured 24 birds (five immature and nine adult females; five adult and five immature males) from the wild between 11 November and 4 December 1990. Each individual was placed into the aviary within several hours of capture. Thus, the dominance rank attained by each individual could have been influenced by its period of residency. To test whether the order of introduction influenced the dominance rank in Flock 2, I classified birds according to their date of introduction into the aviary ("early", < 22 November; "late", ≥ 22 November), and used a one-tailed Mann-Whitney U-test to test the hypothesis that individuals captured during the early period should have a higher dominance rank (see below for methodology) than those introduced during the later period. Because the proportions of males and females introduced during the two time periods were unequal, a separate analysis was performed for each sex. Food and water were provided as for Flock 1, but a longer period (11 days from the addition of the last flock member)

was allowed for the formation of a stable dominance hierarchy.

I observed dyadic interactions between individuals at the feeder and water dish from a darkened room adjacent to the aviary, and determined the winner (the bird that displaced a conspecific by threat or attack) and loser in each interaction. Observations on each group of birds continued until at least five encounters were recorded between most pairs of individuals (seven to 10 days). I attempted initially to record interactions in a more-or-less random fashion (with regard to the individuals involved). However, certain members of both flocks interacted infrequently with conspecifics. During the later stages of the observation periods, I therefore focused attention on these individuals to assure that their position in the hierarchy could be assessed accurately.

I determined the dominance hierarchy in each flock by constructing a diagonal matrix of wins and losses for each pair of birds, such that the number of dominance "reversals" appearing below the diagonal was minimized (Weatherhead and Teather 1987, Komers 1989, Ficken et al. 1990). I then tested for linearity (transitivity) of the hierarchy using the method described by Appleby (1983). In this procedure, I considered a bird to be dominant over a conspecific if a binomial test (Conover 1980) indicated

that the number of wins, relative to the total number of interactions observed for that pair, was significant at $p < 0.1$. If the binomial test was not significant, the order of dominance in that pair was considered to be inconclusive, and a tie was assigned. If the overall hierarchy was significantly linear, each bird was assigned a rank, with a value of 1 being designated the most dominant individual in the flock.

I used analysis of covariance (Neter et al. 1985) with backward elimination of insignificant terms to test the hypotheses that males should be dominant over females, and that social rank should be independent of age and body size in each flock. Because the dependent variable in this analysis (rank) is an ordinal measure, I suspected that critical values of the test statistic obtained from the standard F-distribution could be misleading. To generate the appropriate critical values of F, I performed a randomization test (Sokal and Rohlf 1981) by randomly assigning combinations of rank and body size to birds of different age and sex classes. Such combinations were generated 1000 times for each flock, and the 95th percentiles of the cumulative distributions for each variable and interaction term were used to determine the critical values for each test. However, these values were virtually identical to those derived from the standard F-

distribution. I therefore used the latter values in analyses of covariance used to evaluate the relationships of age, sex and body size with social rank.

Several authors have speculated that dominance relationships observed in captivity might not be representative of those of free-living birds (Baker and Fox 1978, Wiedenmann and Rabenold 1987, Perry et al. 1988, Komers 1989). To examine this possibility, I recorded interactions opportunistically among Evening Grosbeaks of different age and sex classes at feeding stations during the winters of 1989-90 and 1990-91. Patterns of dominance between age groups were determined only for males, because females can not accurately be aged unless captured (Chapter 2). The designation of winners and losers in pairwise interactions was identical to that used for captive birds (see above). Chi-squared tests (Conover 1980) were used to compare the frequency of wins and losses among age and sex classes.

2.2 Energetic Consequences of Dominance Rank

To investigate the energetic costs and benefits to birds of different dominance rank, I assembled a flock of 11 male Evening Grosbeaks (six adults and five immatures). Eight of these males were previously used in observations of interactions between age and sex groups (Flock 2, above), while three additional individuals (birds # 68, 70

and 71) were captured from the wild on 19 January 1991. Seventeen days (from the addition of the new birds) elapsed before observations began on this flock. To facilitate identification of individuals in the aviary, all birds were marked with unique combinations of stripes (using Liquid Paper) on the nape, back or tail.

I was interested in examining the energetic consequences of dominance rank for birds subjected to conditions where intraspecific competition is intense (a condition necessary for the social dominance hypothesis to operate). Such a condition could be achieved by restricting the availability of food to flock members. However, it was difficult to determine a priori the level of food availability at which competition would be sufficiently strong for the costs and benefits of dominance to differ among individuals (if such differences actually exist). To circumvent this problem, I performed two trials in which the availability of food differed. In the "low competition" trial (6 to 7 February 1991), sunflower seed was provided from a feeder which allowed up to five individuals to feed at one time. In the "high competition" trial (23 to 24 February 1991), the feeder was modified to allow only a single bird to feed at any given time. Differences in the level of competition between trials were also promoted by selecting experimental periods when

environmental temperatures (and therefore energetic requirements) were substantially different. Specifically, temperatures during the high competition trial were colder (mean of maximum and minimum temperatures over two days = -8.4°C) than during the low competition trial (mean = 7°C). I then compared the strength of any relationship between social status and energy balance in the two trials, and predicted that patterns suggesting an energetic advantage to birds of particular social status should be most pronounced when competition is high.

During both trials, pairwise interactions between flock members were recorded with a videocamera (Sony model HVC-2800) which operated continuously (except during hours of darkness when no birds were active). To assure that a sufficient number of interactions were recorded for the construction of hierarchies, I made opportunistic observations of interactions for several days following each trial and attempted to observe at least 500 interactions among flock members at each level of food availability. The designation of winners and losers, and methods used for the construction of hierarchies, followed the procedures described above. To confirm that aggressive encounters were most frequent when access to food was restricted, I compared the frequency of interactions recorded on the videotape during each trial, as well as the

proportion of visits to and departures from the feeder in which agonistic behavior was observed.

2.2.1 *Determination of Energy Expenditures and Consumption*

The doubly-labelled water (DLW) technique (Lifson et al. 1955, Lifson and McIntock 1966, Nagy 1983, Tatner and Bryant 1989), which uses washout rates of labelled hydrogen and oxygen atoms from the body to calculate carbon dioxide (CO_2) production, was used to determine the energy expenditure of flock members in each trial. To minimize the stress on birds from excessive handling during the injection procedure (see below), all birds were captured from the aviary at dusk on the evening before trials began and housed indoors in individual cages at 2°C with water but no food. At 0700 the following morning, birds were removed from their cages in random order, weighed, and injected intramuscularly with 200 μl of water containing tritium (H-3 , 1 mCi/kg body mass) and heavy oxygen (O-18 , 3 ml/kg body mass). These dosages were based on recommendations by Nagy (1983) and assumed an average body mass of 65 g/bird. After injection, birds were returned to their cages and maintained in the dark for one hour, to allow the isotopes to equilibrate with body water (Nagy 1983, Williams 1985). A blood sample (100 to 150 μl) was then collected from the brachial vein of each bird using

heparinized hematocrit tubes. The time of sampling was recorded. After all samples were collected, birds were released into the aviary, and allowed to resume "normal" social interactions without disturbance for approximately 32 ± 0.1 h (two days and one night). At this time, all individuals were captured from the aviary as simultaneously as possible (over a period of two to three minutes) using hand nets (after restricting the birds to one end of the cage with a movable partition). Birds were weighed and resampled for blood in the order in which they were initially injected, and the time recorded. Individuals were housed indoors in individual cages before being returned to the aviary the following morning.

The difference in isotope activities between the initial and final blood samples was used to calculate the CO_2 production of each bird over each experimental period. All analyses were performed by D. W. Thomas, at the Université de Sherbrooke, Québec, following the techniques described by Nagy (1983) for H-3, and Tatner and Bryant (1989) for O-18. To convert metabolic rates from units of CO_2 production to an energy equivalent, I used a conversion factor of 0.0248 kJ/ml CO_2 . This value is based on a nutritional composition of 28% lipid, 14% protein, and 15% carbohydrate found for sunflower seeds by Kear (1962) and Willson (1971), and energy equivalents of 0.0277, 0.0231

and 0.0208 kJ/ml CO₂ for these components, respectively (Schmidt-Nielsen 1979).

To determine the energy consumption of each individual, I videotaped activity at the feeder throughout each trial, and later counted the number of seeds consumed by each bird. Only sunflower seeds were available during these trials. Seeds were presorted so that a relatively homogeneous size (and therefore energy content) of seed was provided. I used only seeds that passed through a 9.53 mm mesh, but not through a 6.35 mm mesh. A random sample of 100 seeds was then husked, and the kernels weighed (± 0.001 g). I then calculated a mean kernel mass, and then converted this value to an energy equivalent assuming an energy content of 25.9 kJ/g of sunflower seed (mean of five sources provided by Karasov 1990). I also assumed that Evening Grosbeaks assimilate 83.9% of the energy contained in sunflower seeds (West and Hart 1966).

During both trials, the feeder was placed on a large mesh-topped box, so that seed which spilled from the feeder could not be consumed by birds. In addition, the floor of the aviary was covered before each trial with a 15-cm layer of fresh snow gathered from an adjacent area. This prevented birds from finding seeds which had previously fallen onto the aviary floor. Seeds were sometimes carried away from the feeder by birds, particularly when an

individual was displaced by a conspecific. I assumed that these seeds were eventually consumed by that individual.

To determine whether energy consumption (CONSUME) or expenditures (EXPEND) varied with social rank, and to test the null hypothesis of no difference in net energy budget ($NET = CONSUME - EXPEND$) with rank, I used Spearman's rank correlation analysis (Conover 1980). Theoretically, all three of these variables could be influenced by body size, because larger-bodied individuals should require more food to sustain their greater expenditures (Calder 1974). Thus, I used partial correlation analysis to control for the influence of body size (PC1, see above).

2.2.2 *Calculation of Time Budgets*

I assessed the time spent by individuals in various activities in two ways. First, I analyzed videotapes of feeding activity during each trial, and estimated the following parameters for each bird: total length of time on feeder (TFEED), mean length of time feeding per visit (MEANTIME), total number of visits to the feeder (NVIS), percentage of arrivals on feeder where a subordinate bird was displaced (ARRDISP), and percentage of departures from the feeder where the bird was displaced by a more dominant individual (DEPDISP).

Because variations in energy budgets may result from

activities which occur away from the feeding platform, I supplemented the video analysis with a separate analysis of time budgets for each bird. Before each trial, 100 random sequences of 11 numbers (corresponding to the number of birds used in the trials) were generated by computer. I visually located birds in the aviary according to this predetermined order, and repeated observations on individuals throughout each day (approximately 0830 to 1630). Each bird was observed for exactly one minute, and the following information was recorded: time resting (TREST, including preening), time spent in aggression (TAGGR), time spent in avoidance (TAVOID), and time spent in non-agonistic locomotion (NONAGGR). Aggressive and avoidance movements were identified based on whether the individual was a winner or loser in a particular pairwise interaction (see Section 2.1, above). For calculating TAGGR, TAVOID and NONAGGR, I considered three types of movements: hopping (movements < two body-lengths in distance), short flights (flights $\leq$ half the length of the aviary), and long flights (flights > half the length of the aviary; see Chapter 2 for aviary dimensions). I converted these movements to time values by measuring the duration of 50 short and long flights (mean duration = 0.58 ± 0.02 (SE), and 1.12 ± 0.03 seconds, respectively), and assuming that hops took 0.40 seconds each. Occasionally, a bird

displaced a conspecific with a "threat" (aggressive posturing without locomotion). These actions were included in TAGGR, assuming a duration of 0.75 seconds. I also recorded the time spent on the feeder by birds. However, many observations of feeding were censored (birds were on the feeder either at the beginning or end of the one-minute observation period). Because censored observations may be inaccurate (Bressers et al. 1991), and because an unbiased estimate of feeding time was obtained from the video analysis (TFEED), estimates of feeding time derived from the time budget analysis were omitted.

I calculated mean values (s/h) of each activity for each individual during a trial. I then used Spearman rank correlation analysis (Conover 1980) to determine the relationship of each time budget component with energy expenditure, energy consumption, net energy budget, and social rank in each trial.

3. Results

3.1 Patterns of Dominance Among Age and Sex Groups

A total of 3768 and 3028 pairwise interactions were used to construct the dominance hierarchies for Flocks 1 and 2, respectively (Tables 10 and 11). Both hierarchies were significantly linear (Flock 1: coefficient of linearity $[K] = 0.97$, chi-square = 210.2, d. f. = 29, $p <$

Table 10. Matrix of dominance interactions observed in Flock 1 during December 1989. Circled numbers indicate that members of a particular pair of birds could not be identified as dominant or subordinate (binomial test, $p > 0.1$). For age groups, I = immature (first-winter) and A = adult.

Sex:	Males												Females											
Age:	I	I	I	I	I	I	I	A	A	A	A	I	I	A	A	A	A	I	A	I	A	A		
Bird #:	13	12	14	7	10	3	18	5	9	22	8	2	4	15	11	16	20	1	6	23	19	21	17	
13		23	15	25	15	16	30	27	17	7	16	13	19	9	7	8	14	7	5	15	7	1	8	
12			26	29	20	10	15	40	16	13	11	14	23	12	11	13	17	11	18	20	8	3	9	
14				19	26	14	7	31	7	22	13	13	19	5	9	8	13	20	19	10	8	18	8	
7					9	16	11	31	24	9	19	13	13	16	13	13	4	13	16	6	4	9	6	
10			1	1		19	10	38	8	20	11	17	26	9	9	14	16	12	10	9	6	10	11	
3						1		9	18	6	4	6	9	16	8	4	5	7	7	4	8	4	5	6
18			11					31	29	15	5	30	22	14	16	23	13	9	24	15	7	13	18	
5			1				2		24	9	8	32	44	26	15	34	30	20	27	26	7	19	21	
9					1					5	11	27	17	14	8	11	11	11	19	11	5	8	17	
22					1	1	3				7	9	10	8	5	7	5	6	17	8	7	5	14	
8												12	25	3	14	12	11	9	11	12	2	7	13	
2													31	15	13	18	8	11	14	18	15	18	14	
4														34	26	20	28	20	40	50	13	15	22	
15												1			10	8	14	9	17	16	11	13	22	
11												1				11	4	10	18	11	5	5	11	
16										1						2	16	17	22	19	12	10	14	
20															1	1		21	15	21	5	8	19	
1														1					37	25	19	25	27	
6														1				2		29	9	8	4	
23																				1		12	19	25
19													2								1		6	23
21																				1			11	
17																				19		1		

Table 11. Matrix of dominance interactions observed in Flock 2 during December 1990. Circled numbers indicate that members of a particular pair of birds could not be identified as dominant or subordinate (binomial test, $p > 0.1$). For age groups, I = immature (first-winter) and A = adult.

Sex:	Males										Females													
Age:	I	I	I	A	I	I	A	A	A	A	I	I	I	I	A	A	A	A	A	A	I	A	A	A
Bird #:	42	47	43	53	58	59	41	48	40	49	50	45	44	55	51	52	54	39	60	56	62	63	57	46
42		21	(11)	16	26	24	(10)	17	(7)	9	8	11	9	16	13	8	8	7	7	8	6	10	9	9
47			17	11	18	26	9	12	10	12	8	9	4	4	8	7	9	9	16	13	11	15	9	8
43	7	1		17	11	20	26	12	10	5	19	20	7	13	7	10	11	20	8	19	9	9	6	4
53			3		24	19	19	17	17	15	13	19	7	13	3	9	7	7	6	12	11	10	9	6
58			2	1		16	19	16	(10)	16	6	8	13	14	13	12	17	16	6	3	4	7	18	6
59	2		1				25	22	15	40	8	6	11	9	8	5	3	7	8	10	9	6	6	3
41	8							14	4	21	6	16	9	13	12	12	7	9	8	8	18	7	6	9
48									4	11	10	8	19	7	9	8	16	12	8	17	10	15	7	4
40	6				3		4				13	11	18	14	17	8	12	6	7	6	10	12	4	11
49								5	3			6	23	8	11	9	11	10	7	12	4	4	3	13
50												11	8	12	13	8	8	10	5	4	4	3	12	8
45													17	10	11	12	7	7	16	6	10	12	21	9
44														8	7	6	6	4	7	4	3	5	8	6
55											1		1		13	18	16	7	5	4	9	9	10	7
51																13	5	8	18	11	9	5	10	9
52												1					5	27	12	7	18	9	25	13
54														1	1			4	15	19	7	4	23	13
39																			13	6	11	4	(12)	12
60												1	1				5	1		7	6	6	8	16
56												1									9	4	8	3
62																		1				7	9	8
63																1	1	1					8	5
57																		6		1				11
46																		1			2			

0.0001; Flock 2: $K = 0.92$, chi-square = 214.7, d. f. = 30, $p < 0.0001$). There was no difference in dominance rank between birds in Flock 2 introduced "early" or "late" into the aviary for either sex (males: $T = -0.2$, $p > 0.8$; females: $T = -0.4$, $p > 0.7$), and therefore no evidence that prior residence affected dominance.

In both flocks, males were socially dominant over females (Flock 1: $F = 64.7$, d. f. = 1, 19, $p < 0.0001$; Flock 2: $F = 78.8$, d. f. = 1, 19, $p < 0.0001$). There was also a significant effect of age on social rank in both flocks (Flock 1: $F = 8.1$, d. f. = 1, 19, $p < 0.01$; Flock 2: $F = 13.5$, d. f. = 1, 20, $p < 0.01$), but no interaction effect of age and sex (both $p > 0.2$). Within each sex, immatures tended to be socially dominant over adults (Tables 10 and 11). There was no significant main or interaction effect which included body size in either flock (both $p > 0.2$).

I recorded 467 intersexual interactions among free-living Evening Grosbeak at feeders. Males were identified as winners in all but one encounter (99.8%), and were clearly dominant over females (chi-square = 925.1, d. f. = 1, $p < 0.0001$). Among males, immatures won 114 of 161 (70.8%) interactions (chi-square = 55.8, d. f. = 1, $p < 0.0001$). This frequency is lower than was observed among captive males (92.1% of 913 encounters were won by immature

males over adults in Flocks 1 and 2 combined; chi-square = 1295.4, d. f. = 1, $p < 0.0001$).

3.2 Energetic Consequences of Dominance Rank

Dominance hierarchies were constructed from 682 and 509 interactions observed under conditions of low and high competition, respectively. In both trials, hierarchies were significantly linear (high: $K = 0.76$, chi-square = 52.9, d. f. = 20, $p < 0.0001$; low: $K = 0.75$, d. f. = 20, chi-square = 52.1, $p < 0.0001$). The order of individuals in the two hierarchies was identical, so the observations were combined ($K = 0.76$, chi-square = 52.6, d. f. = 20, $p < 0.0001$, Table 12). Interactions recorded on videotape were more numerous in the high competition trial (28.7/h, versus 16.1/h in the low competition trial). In addition, a significantly higher proportion of arrivals on the feeder resulted in the displacement of a conspecific in the high competition trial (430 of 1215 visits [35.5%]) than in the low competition trial (192 of 1038 visits [18.5%], chi-square = 46.0, d. f. = 1, $p < 0.0001$). The number of departures that resulted from displacement was also greater in the high competition trial (469 of 1215 visits [38.6%] versus 237 of 1038 visits [22.8%], chi-square = 34.3, $p < 0.0001$). Thus, aggression was almost twice as frequent when access to food was highly restricted.

Table 12. Matrix of dominance interactions observed in a flock of 11 males used to assess the costs and benefits of dominance to birds of different social rank. Values are the combined number of interactions observed in the low and high competition treatments, because the rank order of the hierarchy was identical for both treatments (see text). Circled numbers indicate that members of a particular pair of birds could not be identified as dominant or subordinate (binomial test, $p > 0.1$).

Bird #:	42	47	43	53	58	59	41	68	71	70	48
42		30	(4)	15	21	39	(3)	19	17	15	7
47			22	16	18	45	13	22	22	5	2
43	5	1		22	16	51	(8)	7	16	8	9
53					27	56	14	22	22	19	10
58						60	19	21	28	25	9
59			5	1	1		22	33	38	47	22
41	2		5			1		16	22	6	9
68	1						1		34	22	10
71	6			1				2		45	16
70			1					1			17
48							1		1		

3.2.1 *Energy Expenditures and Consumption*

The average mass of sunflower kernels was 0.069 ± 0.002 g, and the average amount of assimilable energy obtained was therefore estimated to be 1.50 kJ/seed. Individuals expended more energy in the high competition trial than in the low competition trial (Table 13, Mann-Whitney U-test, $T = 2.1$, $p < 0.05$), but there was no difference in average consumption ($T = 1.6$, $p > 0.1$) or net energy ($T = 0.1$, $p > 0.9$) between trials. In neither trial did energy expenditure correlate with dominance rank (both $r < 0.22$, $p > 0.5$). However, dominant birds (i.e., birds with a low numerical value for rank) consumed more energy when competition was high ($r = -0.63$, $p < 0.05$), and had a greater net energy gain than subordinates at both levels of competition (low: $r = -0.63$, $p < 0.05$; high: $r = -0.75$, $p < 0.01$).

3.2.2 *Time Budgets*

Time budget data for individuals in each trial are provided in Tables 14 and 15. Dominance rank was inversely correlated with ARRDISP and TAGGR in the low competition trial (both $p < 0.001$), and positively correlated with DEPDISP ($p < 0.05$) and TAVOID ($p < 0.001$, Table 16). Thus, dominant birds spent more time in aggressive manoeuvres than subordinates, and less time avoiding conspecifics. The same pattern for ARRDISP, DEPDISP and TAVOID was found in

Table 13. Energy consumption (CONSUME), energy expenditure (EXPEND) and net energy (NET) of individual Evening Grosbeaks during high and low competition trials.

RANK	Low Competition			High Competition		
	CONSUME (kJ)	EXPEND (kJ)	NET (kJ)	CONSUME (kJ)	EXPEND (kJ)	NET (kJ)
1	240.0	201.7	38.3	361.5	229.4	132.1
2	270.0	209.5	60.5	319.5	319.5	139.0
3	316.5	155.0	161.5	246.0	200.6	45.4
4	189.0	137.4	51.6	310.5	220.7	89.8
5	318.0	230.1	87.9	373.5	305.5	68.0
6	258.0	188.7	69.3	390.0	218.5	171.5
7	262.5	221.9	40.6	274.5	249.0	25.5
8	232.5	181.3	51.2	268.5	248.1	20.4
9	204.0	200.7	3.3	255.0	217.8	37.2
10	262.5	229.3	33.2	244.5	212.4	32.1
11	151.5	198.5	-47.0	109.5	244.1	-134.6
Mean	245.9	195.8	50.0	286.6	229.7	57.0
SE	15.3	8.8	15.5	23.7	9.8	24.7

Table 14. Time budgets of individual Evening Grosbeaks during the low competition trial. See text for definitions of acronyms.

RANK	NVIS	TFEED (s)	MEANTIME (s)	ARRDISP (%)	DEPDISP (%)	TREST ^a (s/h)	TAGGR ^a (s/h)	TAVOID ^a (s/h)	NONAGGR ^a (s/h)
1	86	550	6.4 ± 0.6	34.9	3.5	3439.8 ± 23.5	10.4 ± 2.8	1.6 ± 1.0	103.7 ± 17.0
2	72	2330	32.4 ± 4.1	34.7	15.3	3220.8 ± 85.0	17.3 ± 4.2	4.4 ± 1.7	103.9 ± 15.3
3	102	2229	22.1 ± 2.4	19.8	4.0	3288.3 ± 73.0	13.7 ± 4.1	1.5 ± 0.9	121.1 ± 14.3
4	79	1036	13.1 ± 1.3	39.2	8.9	3375.5 ± 38.2	12.8 ± 2.9	2.5 ± 1.2	123.7 ± 19.3
5	108	2350	21.8 ± 2.5	27.8	16.7	3083.4 ± 92.9	12.2 ± 4.2	7.6 ± 2.8	152.1 ± 22.2
6	119	2431	20.4 ± 2.2	16.8	31.9	3369.3 ± 37.2	9.6 ± 2.2	7.5 ± 2.5	128.6 ± 20.8
7	98	1223	12.7 ± 1.2	7.2	17.5	3264.6 ± 58.8	4.2 ± 1.4	4.7 ± 1.6	158.5 ± 20.4
8	120	968	8.1 ± 0.6	9.2	21.0	3375.5 ± 44.4	6.8 ± 2.9	11.7 ± 3.2	91.1 ± 13.1
9	74	1022	14.0 ± 1.6	12.2	56.8	3247.2 ± 50.9	7.1 ± 2.3	21.2 ± 4.8	189.1 ± 22.6
10	102	1523	15.1 ± 1.7	6.9	40.6	3296.4 ± 44.0	3.6 ± 1.5	24.5 ± 4.7	163.2 ± 16.1
11	78	431	5.5 ± 0.5	1.3	38.5	3443.0 ± 34.6	2.0 ± 1.2	13.8 ± 3.7	103.5 ± 21.9

^a Values (mean ± SE) of TREST, TAGGR, TAVOID and NONAGGR are based on 79, one-minute observation periods for each individual

Table 15. Time budgets of individual Evening Grosbeaks during the high competition trial. See text for definitions of acronyms.

RANK	NVIS	TFEED (s)	MEANTIME (s)	ARRDISP (%)	DEPDISP (%)	TREST ^a (s/h)	TAGGR ^a (s/h)	TAVOID ^a (s/h)	NONAGGR ^a (s/h)
1	117	823	7.0 ± 0.7	62.9	1.7	3432.5 ± 27.5	10.1 ± 4.6	1.6 ± 0.8	95.7 ± 15.5
2	81	2666	32.9 ± 4.2	65.0	13.8	3372.7 ± 72.2	4.8 ± 1.5	1.5 ± 0.7	60.8 ± 11.8
3	79	2463	31.2 ± 3.2	55.1	34.6	3260.7 ± 92.3	5.9 ± 2.3	1.1 ± 0.6	72.0 ± 11.8
4	111	1603	14.4 ± 1.0	44.5	17.3	3273.6 ± 62.1	11.2 ± 2.8	2.7 ± 1.2	162.0 ± 30.2
5	107	3810	35.6 ± 4.3	44.9	28.0	3120.5 ± 102.3	5.6 ± 2.7	5.8 ± 2.0	101.8 ± 14.5
6	230	7795	33.9 ± 2.5	33.6	54.6	2793.0 ± 114.5	17.5 ± 3.8	11.7 ± 2.5	142.4 ± 18.8
7	98	1354	13.8 ± 1.3	21.4	31.6	3239.3 ± 69.7	11.9 ± 3.0	12.6 ± 4.9	156.1 ± 18.9
8	134	1171	8.7 ± 0.5	26.1	43.3	3395.1 ± 37.7	1.9 ± 0.8	16.1 ± 4.9	90.2 ± 13.4
9	98	1352	13.8 ± 2.6	16.3	69.4	3345.5 ± 52.5	9.3 ± 2.2	15.4 ± 3.3	121.3 ± 20.9
10	111	1595	14.4 ± 2.0	7.2	50.5	3277.5 ± 58.2	0.3 ± 0.3	24.6 ± 4.9	121.3 ± 14.5
11	49	435	8.9 ± 1.4	12.2	81.6	3472.1 ± 26.4	0.0 ± 0.0	15.9 ± 3.2	90.6 ± 21.0

^a Values (mean ± SE) of TREST, TAGGR, TAVOID and NONAGGR are based on 80, one-minute observation periods for each individual

Table 16. Rank correlations of social rank and energetic variables with time budget components for Evening Grosbeaks during low and high competition trials. See text for explanation of acronyms.

Time Budget Variable	Low Competition				High Competition			
	RANK	EXPEND	CONSUME	NET	RANK	EXPEND	CONSUME	NET
NVIS	0.10	-0.05	0.31	0.44	-0.10	0.22	0.54	0.34
TFEED	-0.30	0.25	0.76 ^a	0.76 ^a	-0.38	-0.28	0.56	0.66 ^a
MEANTIME	-0.38	0.16	0.76 ^a	0.72 ^a	-0.24	-0.27	0.42	0.54
ARRDISP	-0.89 ^b	-0.21	0.19	0.55	-0.96 ^b	-0.19	0.63 ^a	0.72 ^a
DEPDISP	0.91 ^a	0.21	-0.33	-0.56	0.86 ^b	-0.03	-0.55	-0.53
TREST	0.16	-0.53	-0.72 ^a	-0.42	0.14	-0.07	-0.45	-0.36
TAGGR	-0.87 ^b	-0.22	0.45	0.75 ^a	-0.43	0.08	0.62 ^a	0.55
TAVOID	0.89 ^b	0.36	-0.27	-0.59	0.92 ^b	0.32	-0.46	-0.69 ^a
NONAGGR	0.26	0.45	0.26	-0.06	0.23	0.30	0.21	0.07

^a $p < 0.05$

^b $p < 0.001$

the high competition trial (all $p < 0.001$), but there was no relationship between dominance rank and TAGGR ($p > 0.1$). In neither trial was there a significant relationship between energy expenditure (EXPEND) and any time budget variable (all $p > 0.1$). Consumption was positively related to feeding time (TFEED and MEANTIME, both $p < 0.05$) and inversely proportional to the time spent resting (TREST, $p < 0.05$) in the low competition trial. However, in the high competition trial, consumption was positively correlated with measures of aggression (ARRDISP and TAGGR, both $p < 0.05$). Finally, NET was positively correlated with TFEED, MEANTIME and TAGGR (all $p < 0.05$) in the low competition trial, and with TFEED and ARRDISP in the high competition trial (both $p < 0.05$). In the latter trial, there was also an inverse correlation between NET and TAVOID ($p < 0.05$).

4. Discussion

I predicted that if the social dominance hypothesis can account for the winter distribution of age and sex classes in the Evening Grosbeak, then males should be socially dominant over females, but there should be no difference in social rank between age groups for either sex. The first prediction was supported: males invariably displaced females from food. The second prediction was not supported. Surprisingly, immature birds were socially dominant over adults within each sex. For this trend to be

consistent with the social dominance hypothesis, immatures should have a more northerly distribution during winter than adults. This pattern does not occur (Chapter 3). Furthermore, the null hypothesis of no relationship between body size and social rank could not be rejected. Even though age and sex groups differ in dominance status, these differences are independent of group differences in overall body size (see Chapter 5).

The observation that immature Evening Grosbeaks are socially dominant over adults of the same sex is contrary to the pattern observed in most other birds (Ketterson 1979, Ekman and Askenmo 1984, Desrochers et al. 1988, Hogstad 1988, Piper and Wiley 1989). However, similar results have been noted in captive Black-billed Magpies, Pica pica (Komers 1989) and in free-living Mexican Jays, Aphelocoma ultramarina (Barkan et al. 1986), Pinon Jays, Gymnorhinus cyanocephalus (Balda and Balda 1978), and Semipalmated Sandpipers, Calidris pusilla (Harrington and Groves 1977). In none of these species is there a clear explanation for why birds attain a high social rank early in life. Barkan et al. (1986) suggested that, in species in which family associations persist through the nonbreeding season, adults may tolerate aggression from their offspring so that young birds gain access to territories which enhance breeding success later in life.

There are several reasons why "parental facilitation" (Barkan et al. 1986) should not apply to dominance relationships in Evening Grosbeaks. Unlike most other species in which immatures attain high social status, Evening Grosbeaks are migratory (Chapter 3), and therefore occupy areas during the winter that are far removed from breeding sites. Social relationships during winter should therefore have little bearing on the acquisition of a breeding territory. There might be other benefits from parental facilitation that could occur in migratory species during the nonbreeding season (e.g., increased survival of offspring). However, the tendency for individual grosbeaks to mix freely among flocks during winter (Parks 1945, Fast 1962) suggests that family groups do not remain intact for extended periods. The possibility that individuals in the captive flocks that I observed were genetically related is even more remote, because individuals were collected from several widely-spaced locations. In short, parental facilitation probably does not play an important role in determining the patterns of dominance I observed between adult and immature Evening Grosbeaks.

Barkan et al. (1986) and Komers (1989) proposed that immatures may dominate adults because the advantages of high dominance status ("pay-off asymmetry", Maynard Smith and Parker 1976) could differ between age groups. For

example, immature birds could be less efficient foragers, such that access to food through aggressive behavior could be of greater importance to immatures than to older, more experienced individuals (Barken et al. 1986). Similarly, immatures might benefit from aggressive behavior if they are more gregarious than adults, or if dominance is more important to immatures in obtaining future reproductive resources (Komers 1989). For most birds, including Evening Grosbeaks, any differences in pay-off asymmetries are difficult to identify (Komers 1989). Thus, reasons for social dominance of immatures over adults remain elusive.

Although patterns of dominance among age groups are inconsistent with the social dominance hypothesis, it is premature to reject the hypothesis as a factor in the evolution of differential migration in Evening Grosbeaks. Males invariably dominate females in both free-living and captive flocks, which is consistent with the tendency for males to winter farthest north. However, there was much more overlap in dominance status between age groups in both sexes. Among males, at least, the tendency for immatures to be dominant was lower in wild flocks than it was in captivity. This probably occurred because free-living birds encounter fewer individuals with which they have prior experience, so dominance hierarchies are probably less transitive than those observed in captivity (see also

Balphy 1979). Thus, age differences in dominance status may be less pronounced than in the captive flocks that I observed, and may not be sufficiently large to result in differential migration by age groups.

I observed no rank-associated differences in energy expenditure. There is therefore no evidence that increased energy expenditures are required to maintain a high social status in Evening Grosbeaks, as previously suspected for other species (Farr and Andrews 1978, Rohwer and Ewald 1981, Roskaft et al. 1986, Hogstad 1987). However, dominant Evening Grosbeaks have a higher net energy budget than subordinates (particularly when food is in short supply), because they gain priority of access to food resources. In short, dominants accrue an energetic benefit from their high status, but without a higher metabolic cost. At least in terms of an energetic currency, dominance and subordination are therefore not equally viable strategies. Although the costs and benefits of social dominance have not previously been measured in a common currency, other authors have reached similar conclusions (e.g., Ekman and Askenmo 1984, Wiley 1991). Typically, such conclusions have been taken as evidence that subordinate birds are "hopeful dominants" that will increase their social rank later in life (Ekman and Askenmo 1984, Ekman 1987, 1988). Although the net benefits to

individual grosbeaks clearly vary with social rank, the "hopeful dominants" view does not apply to Evening Grosbeaks because social rank decreases with age in this species.

The relationship between energy budgets and social rank provides further evidence that the social dominance hypothesis might account for differential migration by Evening Grosbeaks. If subordinates are at an energetic disadvantage relative to dominants, then their survivorship might be lower (e.g., Fretwell 1969, Baker and Fox 1978, Kikkawa 1980, Smith 1984, Arcese and Smith 1985) unless they move to areas where conditions are less severe. Because snowfall (which might reduce food availability) and cold temperatures (which increase energy expenditures) are most pronounced in the northern parts of the winter range of the Evening Grosbeak (Bryson and Hare 1974), then low-ranking birds should benefit from extending their fall migration to more southerly latitudes where their energy budgets might more easily be balanced. However, this view predicts that the winter ranges of age or sex classes which differ in dominance rank should be allopatric (Ketterson 1979). This should be especially true of the sexes in Evening Grosbeaks, where males are invariably of higher social rank than females. This does not occur. Rather, sex ratios show clinal variation during winter

(Chapter 3).

Perhaps the anticipated effects of social dominance are moderated by other factors. Females may be prevented from migrating to areas where males are absent if, as proposed by some researchers (e.g., Tucker 1971, Ketterson and Nolan 1976, Blem 1980), the costs of migration are high. If so, females should coexist with males, but they might be forced to occupy peripheral habitats (Kluyver 1957, Gauthreaux 1978, Nichols and Haramis 1980). Even if longer migrations could be completed at low cost, there may be benefits to subordinates remaining in the company of more dominant birds. For example, subordinates might learn the location of food sources from dominants (Baker et al. 1981, Rohwer and Ewald 1981). Furthermore, aggressive interactions are often most frequent among high-ranking birds than between high- and low-ranking individuals (Fretwell 1969, Ketterson 1979, Ficken et al. 1990). Birds with low social status may therefore gain access to high-quality habitats with little interference from dominant birds (Rohwer and Ewald 1981).

Finally, the costs and benefits associated with dominance rank observed in captivity may be unrealistic. In my experiments, seeds were concentrated in a single location, and subordinates were forced to interact frequently with dominants. Food is likely to be more

dispersed in the wild, so that subordinate grosbeaks might typically feed with less interference from dominants than I observed in captivity (see also Theimer 1987, Wiedenmann and Rabenold 1987). Also, it has been proposed that subordinates might be better food-finders than dominants when food is distributed in patches, because they spend less time interacting with conspecifics (Rohwer and Ewald 1981). Although this possibility has been questioned (Wiley 1991), it suggests that captive subordinates may sometimes be unable to realize advantages over dominants that would be experienced by free-living birds (Baker and Fox 1978).

CHAPTER 8

SYNTHESIS

The process of testing various predictions of the arrival time, body size and social dominance hypotheses has involved a variety of approaches and analytical methods. Before completing the evaluation of these hypotheses, a summary of experimental results is warranted.

1. Summary of Results**1.1 Patterns of Distribution of Age and Sex Classes**

Based on patterns of winter distribution observed in other temperate-zone migrants, I predicted that male Evening Grosbeaks should winter farther north than females. I made no specific prediction concerning age differences in winter distribution (Chapter 1).

An analysis of bird-banding data indicated a strong tendency for males to winter farther north than females (Chapter 3). This trend was more pronounced in regions east of 85°W longitude (28 of 31 winters), than in central regions between 85°W and the continental divide (12 of 31 winters). Overall, the percentage of males in eastern regions declined from 65% at the northernmost latitudes, to 18% at the southern edge of the winter range. In central regions, the proportion of males declined from 53% in the north to 27% in the south.

There was no tendency in either sex for first-winter and adult individuals to winter at different latitudes.

1.2 Arrival Time Hypothesis

This hypothesis states that males winter farther north than females in order to gain early access to resources on the breeding grounds in spring (Chapters 1 and 4). I used banding and band-recovery data to examine whether the chronology of northward migration by males and females in different parts of the winter range was consistent with this idea (Chapter 4).

In none of the five years examined was there a sexual difference in the rate of northward movement during spring. Males could therefore achieve early arrival on the breeding grounds because of their more northerly distribution during winter. However, males in the southern part of the winter range started migrating earlier than females from the same area, and earlier than males wintering at more northerly sites. This suggests that males that winter closer to the breeding grounds need not arrive at breeding sites any earlier than males which extend their migration farther south.

1.3 Body Size Hypothesis

The body size hypothesis argues that individuals of larger-bodied age or sex classes should winter farthest

north because they are better able to endure cold temperatures or periods of food shortage (Chapters 1, 5 and 6). I used measurements of free-living birds wintering in southern Alberta, and of study skins of birds collected throughout the winter range, to test the hypothesis that males should be larger-bodied than females, and that there should be no difference in body size between age classes of males or females. I also used study-skin measurements to test whether the body size of individuals within each age and sex class increases with wintering latitude (Chapter 5). Finally, I subjected wild-caught birds to severe cold stress and food deprivation to test the assumption that larger-bodied individuals (or age and sex classes) should be better able to survive harsh winter conditions (Chapter 6).

As predicted, males were significantly larger-bodied than females. However, adult males were larger than immatures in the sample obtained from study skins (age classes could not be assigned to study skins of females), but there was no body size difference between age classes of live-caught birds in either sex. I observed a weak tendency for larger-bodied females to be found farthest north during winter, but no such pattern was found in either age class of males.

Males maintained homeothermy longer than females under

conditions of severe cold stress, but this ability was unrelated to sexual differences in body size. There were no sex, age, or body size differences in the ability to withstand food deprivation.

1.4 Social Dominance Hypothesis

The social dominance hypothesis states that socially-subordinate individuals (or age and sex classes) must make longer migrations from breeding areas in order to escape competition from more dominant individuals (Chapters 1 and 7). Based on the known distribution of age and sex classes during winter, I predicted that male Evening Grosbeaks should be socially-dominant over females, but that there should be no difference in social rank between age classes of either sex. I also tested the assumption that socially-subordinate individuals are at an energetic disadvantage relative to more dominant conspecifics (Chapter 7).

Males were decisively dominant over females in both captive and wild flocks. However, immatures tended to be dominant over adults of the same sex.

There was no relationship between energy expenditures and social rank, but dominant individuals had preferential access to food, and consumed more energy than subordinates. As a result, there was a positive relationship between net energy and social rank. This trend was most pronounced

when access to food was restricted.

2. Evaluation of Hypotheses

I now ask which of the three "major" hypotheses comes closest to explaining the evolution of differential migration in the Evening Grosbeak. In so doing, it is important to reiterate that it is unlikely that the evolution of migration patterns in any species is entirely a result of a single factor (Ketterson and Nolan 1983, 1985). However, it is likely that some factors are more influential than others.

My results suggest that the arrival time hypothesis should not be an important determinant of sexual differences in winter distribution by Evening Grosbeaks. This conclusion is based on the observation that males from the southern part of the winter range start migrating earlier than females from the same area, and earlier than males wintering at more northerly sites (Chapter 4). Southern-wintering males can therefore compensate for their greater distance from breeding sites by initiating migration at an earlier date. The lack of territoriality in this species (Scott and Bekoff 1991) is also inconsistent with the arrival time hypothesis, as is the observation that pair bonding may occur before arrival at breeding sites (Shaub 1956, Scott and Bekoff 1991). However, it must be emphasized that our knowledge of the

biology of Evening Grosbeaks during spring and early summer is scant, and a more complete understanding of the timing and location of pair bonding is required before a complete evaluation of the arrival time hypothesis can be made.

Unfortunately, the erratic movements and secretive behavior of this species during breeding may make such information almost impossible to obtain.

My results also question the importance of the body size hypothesis. Male Evening Grosbeaks tend to be larger than females (Chapter 5), and the ability of males to endure cold temperatures longer than females (Chapter 6) is consistent with the observed winter distribution of the sexes. However, the lack of a relationship between body size and latitudinal distribution (except in females, Chapter 5), cold tolerance or fasting endurance (Chapter 6) suggests that the body size hypothesis, in its original form, is probably not an important determinant of differential migration in the Evening Grosbeak. Because sexual differences in the ability to tolerate cold temperatures are independent of body size in this species, it might be appropriate to decouple the "cold tolerance hypothesis" from the body size hypothesis. However, I have argued previously that temperatures that are normally encountered during the winter are probably not sufficiently cold to influence survival of either males or females

(Chapter 6). This idea clearly needs to be tested under field conditions before the "cold tolerance hypothesis" can be adequately evaluated. Furthermore, a physiological basis for sexual differences in cold tolerance should be established so that the ecological ramifications of these differences can be fully explored. Until such time, I conclude that cold tolerance is potentially a determinant of differential migration in Evening Grosbeaks, but that body size differences are not.

Of the three major hypotheses I tested in this study, the social dominance hypothesis comes closest to explaining the observed patterns of differential migration in the Evening Grosbeak. Not only is the rank order of dominance between the sexes consistent with the observed winter distribution, but the assumption of an energetic advantage to individuals of high social rank was also supported (Chapter 7). The only prediction of the social dominance hypothesis that was unsupported was that there should be no age-related differences in dominance. However, I have argued that because the tendency for immature birds to be socially dominant over adults is weaker in free-living flocks than it is in captivity, differences in overall rank between age classes may be insufficient to influence the choice of wintering latitude.

3. The Dominance-Dispersal Model and Differential Migration in the Evening Grosbeak

The social dominance hypothesis is based on the dominance-dispersal model proposed by Gauthreaux (1978). This model states that when resources (in particular, food) are in short supply, subordinate birds must move away from areas occupied during the breeding season in order to secure adequate resources to survive the winter. Conversely, individuals of high social-rank can gain access to resources on, or closer to, the breeding grounds and need not undertake seasonal migrations which are as lengthy as those observed in lower-ranking individuals. Although the model is superficially consistent with the latitudinal distribution of male and female Evening Grosbeaks during winter, Ketterson and Nolan (1983) have suggested that several assumptions which underlie the model may not always be valid. The authors pointed out that birds must experience food limitation during the winter, and that access of subordinates to this food must be restricted by the presence of more dominant individuals. Low-ranking individuals must then migrate to escape competition from dominant birds.

It is difficult to determine the extent to which post-breeding movements of Evening Grosbeaks are influenced by the local abundance of food. However, studies that show

strong relationships between food abundance and population densities of other finch species provide evidence that food limitation may be a widespread event in small, granivorous passerines (Dunning and Brown 1982, Schluter and Repasky 1991). The inverse relationship between the size of seed crops in the boreal forest and the magnitude of annual irruptions in Evening Grosbeaks (Bock and Lepthien 1976) suggests that migratory movements in this species could also result from food shortages on the breeding grounds. Socially-dominant Evening Grosbeaks clearly gain priority of access to food, and experience a more favorable energy budget than subordinate individuals when food is limiting (Chapter 7). These conditions provide the necessary prerequisites for the departure of subordinate individuals from areas occupied by dominants. Whether such movements actually occur, and whether they result in the occupancy of adjacent (but lower quality) habitats, or more southerly latitudes (i.e., differential migration) remains to be seen. However, Ketterson and Nolan (1983) point out that if differential migration of dominance (i.e., sex) classes is to occur, then habitat quality and distance from the breeding grounds must covary. The difficulties of defining and assessing the relative "quality" of habitats which change (in terms of their structure and species composition) with latitude would make the assessment of

such a relationship virtually impossible.

4. Future Directions

My goal in this study was to take some initial steps toward an understanding the factors responsible for the evolution of differential migration in the Evening Grosbeak. By necessity, my approach has been relatively coarse-grained. Nevertheless, it is apparent that social interactions, and perhaps the ability to endure cold temperatures, should play a more important role in the choice of wintering latitude than should the benefits of early arrival on the breeding grounds. I have already outlined suggestions for closer examination of the arrival time hypothesis (i.e., determination of the timing and location of pair bonding, and the reproductive consequences of arrival chronology) and cold tolerance hypothesis (i.e., establishment of a physiological basis for sexual differences in cold tolerance, and whether normally-encountered temperatures can induce differences in cold endurance). I now focus on how we might refine our understanding of the role of social dominance in the evolution of differential migration in the Evening Grosbeak and other birds.

Gauthreaux's (1978) model concentrates on how differential migration (and other animal movements) might be a proximate result of direct interactions between

individuals of differing social status. I have suggested that the conditions necessary to promote longer movements by subordinates might exist in Evening Grosbeaks, but it is important to determine whether such movements actually occur in the wild. The nomadic movements of this species would make such information difficult to obtain. However, three alternative approaches, which have been used in studies of differential migration the Dark-eyed Junco, could be useful in future studies of this behavior in Evening Grosbeaks. Terrill (1987) asked whether facultative extensions of fall migration could occur in subordinate birds when their access to food was restricted by the presence of dominant individuals. In captive experiments which simulated these conditions, he found that subordinate birds could be induced to exhibit migratory restlessness in January, when "normal" migratory behavior had ceased. This suggested that these free-living subordinates would have extended their southward migrations because of dominance behavior. Rogers et al. (1989) and Cristol and Evers (1992) reasoned that if dominance was a proximate cause of differential migration in juncos, then individuals captured from northern parts of the winter range should be socially-dominant to individuals captured from more southerly locations (when matched for age, sex and body size). This prediction was not supported.

Finally, Nolan and Ketterson (1990) asked whether the timing of arrival of age and sex classes at different latitudes on the wintering grounds was consistent with predictions of the social dominance hypothesis (i.e., that the winter range should fill from north to south). They found little support for this prediction.

Although these studies offer conflicting evidence for an important proximate role of social interactions in the winter distribution of dominance classes, they illustrate the diversity of approaches that might be used in future studies which seek to clarify the proximate role of dominance in differential migration by Evening Grosbeaks. From an evolutionary standpoint, however, it is perhaps most salient to ask whether social dominance can be an important selective (ultimate) factor in the evolution of differential migration. That is, does dominance status influence individual fitness, either through reproductive advantages, or the probability of surviving the winter? Socially-dominant males in some species of birds are thought to gain priority of access to mates (e.g., Lightbody and Weatherhead 1987, Johnson 1988, Komers and Dhindsa 1989), but the complex relationships among dominance status, wintering latitude and mate choice have not been investigated previously. Numerous studies have established a relationship between dominance status and

winter survival (Fretwell 1969, Baker and Fox 1978, Kikkawa 1980, Arcese and Smith 1985, Koivula and Orell 1988), although it is not always clear whether the "disappearance" of subordinate individuals from a population is the result of their death or emigration (Ketterson and Nolan 1982, Terrill 1991). Only Ketterson and Nolan (1982) have attempted to determine whether annual or seasonal survivorship varies among age and sex (and therefore, dominance) classes of a differential migrant wintering at different latitudes. Although migration mortality was higher for southern-wintering Dark-eyed Juncos (i.e., subordinates, if the social dominance hypothesis is true) and overwinter mortality was higher for individuals in the north, the authors calculated that annual survivorship was not dependent on wintering latitude, age or sex. Thus, dominance behavior had no obvious influence on survival in this species, and the authors downplayed social interactions as an important selective factor in the evolution of differential migration (Ketterson and Nolan 1983, 1985, Nolan and Ketterson 1990). In short, the fitness consequences of dominance behavior clearly need to be elucidated before social dominance can be recognized as an ultimate cause of differential migration in Evening Grosbeaks.

5. Conclusions

Migrating birds must balance the costs and benefits of numerous endogenous and exogenous factors when selecting a wintering site (Ketterson and Nolan 1983). Although these factors are rarely easy to identify, they are particularly difficult to isolate in differential (and partial) migrants, because the costs and benefits associated with wintering in different areas undoubtedly vary among age and sex classes. The task of identifying each selective factor is usually simplified by testing predictions of single-factor hypotheses (Myers 1981). Unfortunately, this approach precludes an accurate assessment of the relative importance of each potential influence in the evolution of differential migration. Nevertheless, my single-factor approach suggests that sexual differences in the winter distribution of Evening Grosbeaks most likely results from sexual differences in dominance status (and therefore, the ability to acquire sufficient resources when energetic requirements are high), and possibly the differential ability of males and females to tolerate cold temperatures.

These conclusions are made with some caution, because our knowledge of the fitness consequences of these factors is scant. Furthermore, it is difficult to generalize these findings to other species, because quantitative assessments of competing hypotheses for the evolution of differential

migration have been attempted in only one other species, the Dark-eyed Junco (see Ketterson and Nolan 1983, 1985 for overviews). Despite these shortcomings, I suggest that future research into the proximate and ultimate roles of behavioral dominance and cold tolerance may be fertile ground for understanding the evolution of differential migration in the Evening Grosbeak, and perhaps in other bird species which occupy north-temperate regions as well.

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APPENDIX 1

SOURCES OF STUDY SKINS USED FOR MORPHOLOGICAL MEASUREMENTS

Study skins of Evening Grosbeaks contained in the following museum collections were examined (sample sizes in parentheses):

Academy of Natural Sciences, Philadelphia, PA (21); Alberta Provincial Museum, Edmonton, AB (28); American Museum of Natural History, New York, NY (83); Boston Museum of Science, Boston, MA (2); British Columbia Provincial Museum, Victoria, BC (4); Buffalo Museum of Science, Buffalo, NY (5); California Academy of Sciences, San Francisco, CA (35); Carnegie Museum of Natural History, Pittsburgh, PA (137); Charleston Museum, Charleston, SC (6); Chicago Academy of Sciences, Chicago, IL (13); Cincinnati Museum of Natural History, Cincinnati, OH (20); Clemson University, Clemson, SC (7); Cleveland Museum of Natural History, Cleveland, OH (15); Coe College, Cedar Rapids, IA (2); Cornell University, Ithaca, NY (34); Delaware Museum of Natural History, Wilmington, DE (23); Denver Museum of Natural History, Denver, CO (4); Field Museum of Natural History, Chicago, IL (51); Florida Museum of Natural History, Gainesville, FL (5); Fort Hays State University, Fort Hays, KS (18); Illinois State Museum, Springfield, IL (12); Iowa State University, Ames, IA (3);

James Ford Bell Museum of Natural History, Minneapolis, MN (76); Joseph Moore Museum of Natural History, Richmond, IN (7); Los Angeles County Museum, Los Angeles, CA (6); Louisiana State University, Baton Rouge, LA (22); Manitoba Museum of Man and Nature, Winnipeg, MB (14); Miami University, Oxford, OH (2); Museum of Comparative Zoology, Cambridge, MA (112); National Museum of Natural History (Smithsonian Institute), Washington, DC (172); National Museum of Natural Sciences, Ottawa, ON (363); New Brunswick Museum, Fredericton, NB (50); North Carolina State Museum of Natural Sciences, Raleigh, NC (27); Nova Scotia Museum, Halifax, NS (9); Oklahoma Museum of Natural History, Norman, OK (19); Peabody Museum of Natural History, New Haven, CT (13); Peabody Museum, Salem, MA (10); Putnam Museum, Davenport, IA (2); Reading Public Museum and Art Gallery, Reading, PA (16); Redpath Museum, Montreal, QB (5); Richter Museum of Natural History, Green Bay, WI (11); Royal Ontario Museum, Toronto, ON (199); San Diego Natural History Museum, San Diego, CA (3); Santa Barbara Museum of Natural History, Santa Barbara, CA (4); Saskatchewan Museum of Natural History, Regina, SK (9); Southwestern College, Winfield, KS (3); Springfield Science Museum, Springfield, MA (3); University of Arizona, Tucson, AZ (1); University of Arkansas, Fayetteville, AR (10); University of British Columbia, Vancouver, BC (3); University of Connecticut,

Storrs, CT (13); University of Georgia, Athens, GA (10); University of Guelph, Guelph, ON (4); University of Illinois, Urbana, IL (3); University of Iowa, Iowa City, IA (8); University of Kansas, Lawrence, KS (6); University of Michigan, Ann Arbor, MI (146); Welder Wildlife Foundation, Sinton, TX (4); Western Foundation of Vertebrate Zoology, Los Angeles, CA (14).