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THE UNIVERSITY OF ALBERTA

ECOLOGICAL CORRELATES OF SOCIAL DOMINANCE IN WINTER FLOCKS OF BLACK-CAPPED CHICKADEES

by

ANDRE DESROCHERS

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

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Date: 23 Oct 1987

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Abstract

Black-capped chickadees (*Parus atricapillus*) live in flocks outside the breeding season. Because social dominance influences the outcome of contests between individuals, dominance status may be important to the acquisition of limiting resources in non-breeding chickadees. I conducted a two-year field study to relate dominance within (and to a lesser extent, between) flocks to access to winter resources, winter survival and territory acquisition.

Survival rates of chickadees was higher in the winter 1985-86 than in the winter 1986-87. Survival was higher in an area with feeders each year, suggesting that food abundance/distribution limited survival. Survival of males was higher than lower-ranking females in the control area in 1986-87, but not in 1985-86. Survival was also higher in birds that were dominant within their age/sex class. No consistent difference of survival was found between adults and young. In the two years of this study, a sharp decline in population size occurred at the onset of spring territoriality. Birds that disappeared were mainly subordinates of each sex. Removals of territorial birds each year suggested the existence of a non-breeding surplus in early spring.

Female flock members foraged higher in trees, further from the trunk and spent more time using their bill in search for prey than males. A male removal experiment showed that males and females competed for foraging areas and suggested that interference by males (which dominate females) caused the sexual niche separation. Payoffs to females' and males' niches are discussed.

Dominance status of an individual varied little within flocks, but interactions between members of different flocks showed that it varied considerably in inter-flock encounters: members of a flock foraging close to the center of its home range dominated members of "intruding" flocks in the same area. In the two years of this study, this site-related dominance did not lead to spacing among flocks, and home ranges overlapped broadly. However, this may have been the result of mild weather in winters 1985-86 and 1986-87.

Résumé

Les Mésanges a tête noire (Parus atricapillus) vivent en groupes hors de la saison de nidification. Puisque la dominance sociale influence l'issue des combats entre les individus, le statut social peut exercer un rôle sur l'acquisition de ressources limitantes par les mésanges dans les groupes. J'ai mené une étude de terrain de 2 ans afin de relier la dominance dans les groupes (et, dans une moindre mesure, entre les groupes) a l'accès aux ressources hivernales, la survie en hiver et l'acquisition de territoires.

Le taux de survie des mésanges était plus élevé en hiver 1985-86 qu'en hiver 1986-87. Les taux de survie étaient plus élevés dans un secteur avec mangeoires, ce qui suggère que la nourriture (dispersion et/ou abondance) limitait le taux de survie. Les mâles en conditions naturelles ont péri dans une moindre proportion que les femelles en hiver 1986-87, mais pas en 1985-86. Les individus dominants dans leur sexe/âge avaient un taux de survie plus élevé que les subordonnés. Les comparaisons entre adultes et juvéniles n'ont pas révélé de différence de taux de survie. Dans les 2 années de cette étude, la population a décliné brusquement au début de la territorialité printannière. Les oiseaux disparus durant cette période étaient principalement des subordonnés de chaque sexe. Leretrait d'oiseaux territoriaux chaque année suggérait l'existence d'un surplus de non-nicheurs tôt au printemps.

Les femelles dans les groupes cherchaient leur nourriture plus haut dans les arbres, plus loin du tronc et utilisaient leur bec plus souvent en quête de nourriture que les mâles. Le retrait de mâles a révélé que mâles et femelles compétitionnaient pour les lieux de

recherche de nourriture et suggérait que l'interférence par les mâles (lesquels dominent les femelles) était a l'origine de la séparation des niches écologiques des mâles et femelles. Le bénéfice net associé aux différentes niches est discuté.

Le statut social d'un individu variait peu a l'intérieur des groupes, mais les interactions entre membres de différents groupes ont démontré que ce statut variait considérablement dans les rencontres entre groupes: les membres d'un groupe se trouvant près du centre de son domaine vital dominaient les membres de groupes "intrus" dans le même secteur. Dans les 2 années de cette étude, cette relation entre la dominance et le site n'a pas amené de séparation des groupes dans l'espace; les domaines vitaux se chevauchaient considérablement. Cependant, ceci était peut-être dû à la température douce des hivers 1985-86 et 1986-87.

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I. INTRODUCTION

Competition exists when resources are in short supply, and is best illustrated by agonistic behaviour among individuals using similar resources. Studies of agonistic behaviour between conspecifics have described ~~two~~ main, but not mutually exclusive, types of social organization: 1) territoriality, in which the outcome of contests between individuals is determined by the location of the contest (Brown and Orians 1970, Kaufmann 1983), and 2) dominance hierarchies, in which the outcome of contests depends on the social rank of the individuals involved (Wilson 1975).

In group-living birds, social rank is usually determined by giving each group member a score for its performance in contests against group-mates, and then ordering them in a hierarchy (Schjelderup-Ebbe's (1922) "peck-order"). Descriptions of dominance hierarchies in a wide range of taxa pervade the literature (reviewed by Gauthreaux 1978), yet there are still relatively few accounts of the function or the ecological consequences of dominance, especially among animals in the wild.

Ecological studies of social dominance have led to two kinds of interpretations: 1) subordinates make the best of a bad situation, given that dominants are larger, older, or more capable fighters (Alexander 1974, West Eberhard 1975, Pulliam and Caraco 1984), and 2) subordination and dominance are two frequency-dependent, alternative strategies with equal payoffs (Rohwer and Rohwer 1978, Rohwer and Ewald 1981). In birds, nearly all available evidence shows a higher net benefit to dominants than to subordinates in mating success (Wiley 1973), survival (e.g. Fretwell 1969, Kikkawa 1981, Smith 1984, Arcese and Smith 1985, but see Scharf 1985), and territory acquisition (e.g. Knapton and Krebs 1976, Smith 1984, Arcese and Smith 1985). The only evidence in support of dominance and subordination as equally valuable survival strategies comes from Rohwer and Ewald's (1981) study of Harris' sparrows (*Zonotrichia querula*). Also, Smith's (1984, 1987) studies of black-capped chickadees (*Parus atricapillus*) suggest that winter dominance and subordination (as correlates of stability of flock membership) may act as frequency-dependent strategies equally successful in terms of territory acquisition.

Titmice (Aves: Paridae) are well-suited for ecological studies of dominance and other agonistic behaviour, as they are highly social outside the breeding season, easy to capture, band, and observe. Dominance hierarchies have been extensively described in this family, in the past decades (e.g. Hamerstrom 1942, Brian 1949, Hinde 1952, Saitou 1979, Hogstad 1987). Some studies on parids have shown that dominant flock members of both sexes are more likely to obtain a breeding territory than subordinates (Smith 1984), and that adults (which dominate young) survive better in winter than young (Ekman and Askenmo 1984). Despite the overwhelming number of studies of parids, the ecological relevance of dominance in this family is still poorly understood, even though its importance in the evolution of social behaviour of titmice and their population dynamics may be great.

The aim of this study was to relate access to resources, winter survival and territory acquisition to dominance in flocks of black-capped chickadees in a northern population. I emphasize the underlying mechanisms of resource partitioning among conspecifics, within and among flocks, under natural conditions (no feeders).

I present the results in three chapters. The first (Chapter II) deals with the ultimate effects of dominance and subordination in chickadees as estimated by two measures of short-term fitness: winter survival and territory acquisition. I also discuss factors limiting numbers of chickadees in Meanook and their relationship with dominance. The second (Chapter III) addresses mechanisms of resource partitioning among flock members of different social status using natural food sources. The third (Chapter IV) deals with dominance relationships between members of different flocks, its site-dependence, and the lack of spacing between flocks. Though not directly related to the analysis of payoffs of social status within flocks, the latter chapter is relevant to the study of competition among conspecifics for potentially limiting winter resources. Lastly (Chapter V), I integrate the findings of these chapters and of other studies to discuss the ecological consequences of dominance in titmice and other bird species.

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II. WINTER SURVIVAL AND TERRITORY ACQUISITION IN A NORTHERN POPULATION OF BLACK-CAPPED CHICKADEES

INTRODUCTION

Since the early days of avian population ecology, there has been much controversy on the importance of winter survival and territoriality in limiting numbers of temperate-zone birds. This is best exemplified by studies of European members of the family Paridae (e.g. Kluyver 1951, Krebs 1971, Perrins 1979, Jansson *et al.* 1981, Ekman 1984). In central Europe, territoriality in fall may limit numbers of breeding great tits, *Parus major* (Dhondt and Hublé 1968, Kluyver 1971). However, this does not apparently occur in willow tits (*P. montanus*) and crested tits (*P. cristatus*) in Scandinavia (Ekman *et al.* 1981), and Perrins (1979) argued that fall territoriality is not found in British tits either. Spring territoriality in tits can limit numbers of breeders in optimal habitats, but usually not in suboptimal habitats (Kluyver and Tinbergen 1953, Krebs 1971, but see Krebs 1977). In northern Europe, a removal experiment in spring failed to reveal a non-breeding surplus of parids (Cederholm and Ekman 1976).

In northern Europe, numbers of breeding parids are limited by winter mortality, because of food shortage and predation (Ekman *et al*. 1981, Jansson *et al*. 1981), and this is consistent with Lack's (1964) 'winter food limitation hypothesis'. Lack (1964) argued that variation in numbers of some European parids could be explained by the abundance of food in winter. However, winter mortality is usually unimportant compared to late-summer mortality in central Europe (Perrins 1979), even though food addition in winter corresponded to increased population levels in some cases (e.g. Dhondt 1971, Krebs 1971, van Balen 1980).

In North America, little is known about the factors limiting the numbers of breeding parids. Studies of black-capped chickadees (*P. atricapillus*) suggest that they are limited mostly by spring territorial behaviour (Smith 1967), unlike European parids. Territoriality in this species presumably results in the exclusion of subordinate birds from breeding (Glase 1973, Smith 1984), but no removal experiment has been conducted to reveal a non-breeding surplus.

A problem of major interest to behavioural ecologists is determining which individuals will breed. Individuals that obtain a territory are often dominant (Wilson 1975, Gauthreaux 1978). This has been supported in studies of parids (Glase 1973, Saitou 1979, Smith 1984) and other bird species (e.g. Wiley 1973, Arcese and Smith 1985). Some studies have also shown that dominant individuals survive the winter better (Fretwell 1969, Kikkawa 1981, Ekman and Askenmo 1984, Arcese and Smith 1985). However, dominance and subordination in wintering social birds may be frequency-dependent tactics with similar adaptive values (Rohwer and Ewald 1981, see also Smith 1984). Little field data is available to evaluate the occurrence of this.

Black-capped chickadees are the most common parids throughout most of North America, and their range extends to the treeline in Alaska and western boreal Canada. Despite their extensive range, no major study of this species has been conducted north of 50°N. Also, chickadee studies have been conducted mainly on populations that use feeders. Therefore, little is known about their ecology under natural conditions over a substantial part of their range. This study reports on survival rates and territory acquisition in black-capped chickadees in central Alberta, Canada, and the relationship of these variables to dominance, age and sex. Results of a removal experiment to test for the occurrence of a floating population in spring are also discussed.

STUDY AREA AND METHODS

This study was carri~~ed out at the~~ Meanook Biological Station (54°37'N, 113°20'W), near Athabasca, Alberta, Canada, from March 1985 to August 1987. The area of 5 km^2

was a combination of public and private land. Three houses were located in an area with feeders (see below), and the research station was in an area without feeders. The habitat was a mosaic of poplar (*Populus tremuloides* and *P. balsamifera*) woodland interspersed with fields (20% of the area), and stands of willows (*Salix spp.*) of up to 4 ha.

A woodland area of 2.6 km^2 was provided with feeders filled with sunflower seeds, and 1.9 km^2 was without feeders (Fig. II-1). Fifty nest boxes were erected with a regular distribution in each area. Ten feeding stations were scattered in the feeder area from late October 1985 to early April 1986, and 14 in the same period in 1986-87. Each feeding station contained two to four feeders, to minimize the effect of despotic behaviour by dominant individuals and other species. Each full feeder contained about 4.5 L of sunflower seeds, and feeding stations were filled about once a week. At least 300 kg of seeds were used by chickadees each winter. The feeder and control areas were in the same location in the two winters of the study and were separated by grain fields, which helped limit the number of birds visiting both control and feeder areas (such birds were known and not included in the analyses). I did not replicate feeder and control areas, but I assume vegetation structure and species composition were similar in the two areas.

In both winters, about 95% of the locally wintering birds were marked with coloured leg bands to which strips of electrician's tape (1 cm) of corresponding colours were

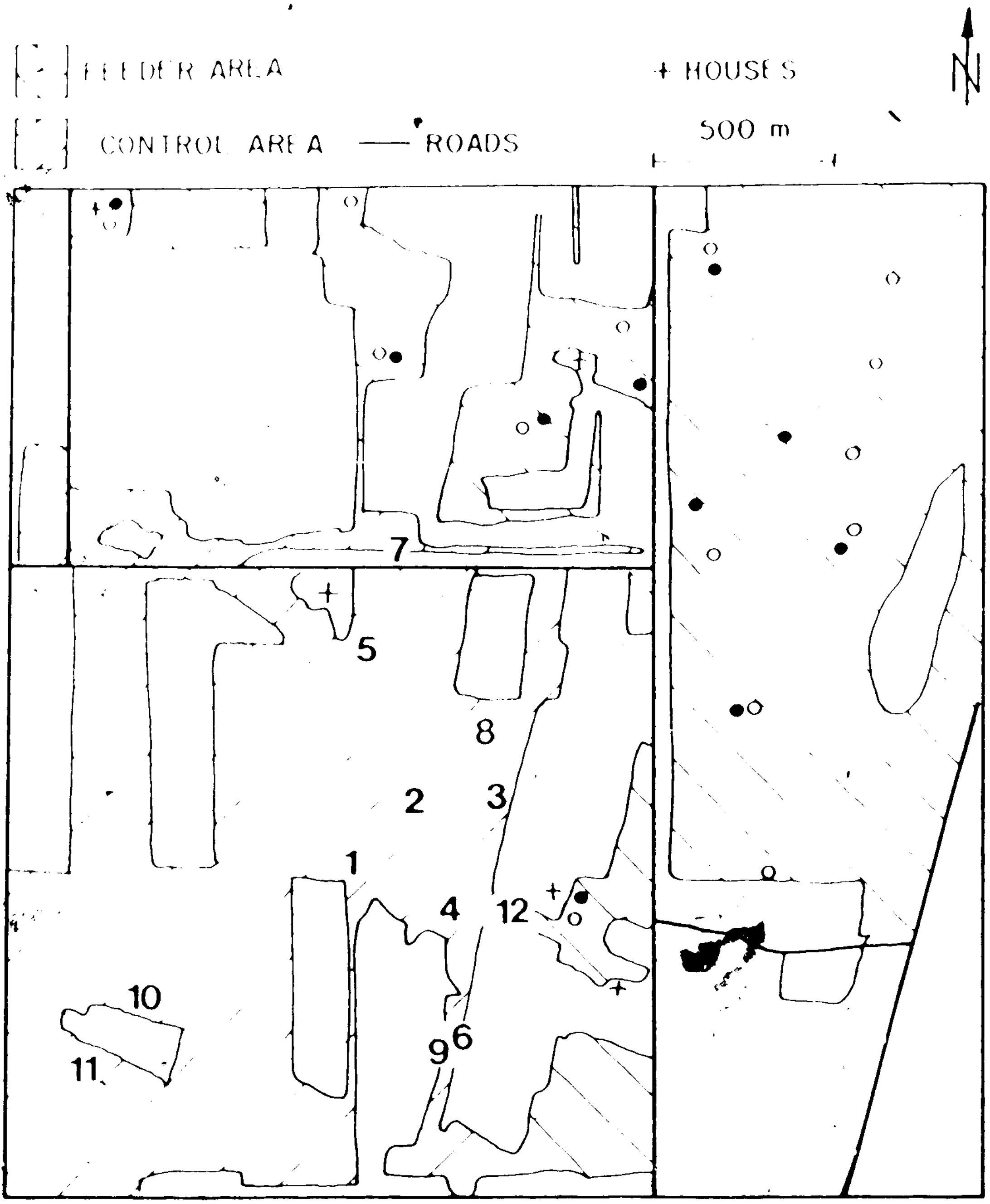

Figure II-1: The study area. Blank spaces are fields. Circles denote feeding stations (open: 1985-86, solid: 1986-87). Numbers refer to individuals removed in spring: 1-4= females (1986), 5= male (1986), 6-7= pairs (1986), 8-12= females (1987).

stuck to enhance visibility of combinations. Birds were attracted to mist nets with feeders or a recording of chickadee vocalizations. Feeders were occasionally used to capture birds in feeder and control areas and were removed after the mist-netting. However, most of the banding was conducted before birds started using feeders. Three hundred and twenty marked birds were studied between 1 November 1985 and 1 March 1986, and 363 between 1 November 1986 and 1 March 1987. Birds that were last seen on the day they were handled and birds observed on less than three separate days were considered as transients or possibly killed by handling and were not included in the analyses.

To determine sex, a discriminant analysis was performed on the combination of body mass, flattened wing length, and the length of the outer right rectrix (Appendix I). Reference samples of 143 females and 171 males (known from their behaviour in the breeding season) were used to compute the discriminant function. The function classified correctly 94% of the birds of a sample of 143 known individuals of both sexes other than the reference sample. Therefore, this discriminant analysis was used to assign a sex to 'unknown' birds. Banded individuals known to be more than 1-y old were classified as adults and unbanded immigrants in summer and fall were considered to be yearlings (less than 1-y old).

The moult of flight feathers was observed in August and September in both years, with yearlings having a different molt pattern than adults (Meigs *et al*. 1983). All the immigrants from fledging to mid-September were positively identified as "yearlings".

Flock membership and social status

Weekly censuses were made over the study area, by one to three persons. I attempted to record the identity of each member of each flock encountered and the number of unbanded flock members. Unbanded birds stopped joining flocks of banded birds in late October. Twenty control and 13 feeder flocks were observed in 1985-86, and 22 control and 18 feeder flocks in 1986-87.

Dominance hierarchies were determined in 12 control and five feeder flocks in 1985-86 and in 13 control and 13 feeder flocks in 1986-87. Kaufmann's (1983:2) definition of dominance was used ("a relationship between two individuals in which one (the subordinate) defers to the other (the dominant) in contest situations"). Four interaction types were considered: displacement of one bird by another, chase, unsuccessful supplanting attempt, and waiting by one bird until another leaves the feeder (Smith 1984). All agonistic interactions seen in free-roaming flocks were recorded and observations were carried out at the permanent feeders (in the feeder area) and at temporary feeders (control area), to increase the number of interactions observed. Temporary feeders were provided to control flocks only during dominance observations. Each of the control flocks had access to a temporary feeder for no more than 5-6 days during winter. Birds in the control area were seen hoarding seeds taken from temporary feeders, but they took no more than 5 kg of seeds each year, compared to 300 kg taken by chickadees in the feeder area. Thus, I assume that temporary feeders had little or no effect on their survival.

All the interactions recorded for each flock were pooled in a dominance matrix and rearranged by the technique of Brown (1975), to generate dominance hierarchies. I used hierarchical ranks instead of the proportion of interactions won by each individual (Fretwell 1969, Ketterson 1979, Kikkawa 1981, Arcese and Smith 1985, Arcese and Ludwig 1986) as a means of describing dominance status of chickadees. Hierarchies are easy to obtain in small social groups like chickadee flocks (e.g. Hamerstrom 1942, Glase 1973, Smith 1976, 1984), and rank estimates do not depend upon the assumption that dyads of interacting birds arise at random (as they do with estimates based on the proportion of wins).

Survival and territory acquisition

Black-capped chickadees are well-suited for analysis of survival in winter, since they exhibit a high degree of site-fidelity in that season (Weise and Meyer 1979, Loery and Nichols 1985). In this study, philopatry in winter was indicated by the virtual absence of unbanded immigrants in areas where all the chickadees were banded in fall. Thus, all the chickadees that disappeared during the period of site-tenacity (1 Nov.-1 March; see below) were classified as dead. Birds that disappeared after this period were considered as either dead or having left the study area. From March to June, all pairs of chickadees remaining on the study area were counted, and I found as many nests as possible. All tests reported are two-tailed, and P values equal to or smaller than 0.05 were considered as significant.

Removal experiment

To determine if there was a non-breeding surplus during the reproductive period, I mist-netted four females and one pair (all territorial) from 19 to 26 April 1986. In addition, one male and one pair (also territorial) were accidentally caught and killed in stored fish traps at the research station, in the first week of May 1986. Between 20 April and 3 May 1987, I removed five more females (Fig. II-1).

To document the timing of the removals in relation to the breeding of chickadees, I estimated the time of onset of territoriality and the time the first egg was laid. A convenient way to determine when territoriality started was to delimit the period of flock break-up, which is marked by an increase of territorial behaviour in males (Odum 1941, Glase 1973). In 1986 and 1987, the proportion of groups observed that were still in flocks decreased sharply between 20 February and 10 March (from 88% to 48% in 1986; from 77% to 25% in 1987; based on 20+ observations). I estimated median laying dates from 15 nests in 1986 (including two nest boxes) and 10 nests in 1987 (no nest boxes). I used only laying dates from nests on which enough data were collected to determine beginning of laying with an accuracy of about 3 d. I used observations of nest contents and parental behaviour (nest lining, incubation, feeding of young: Stokes 1979) to estimate date that laying was initiated. Removals in 1987 were made later relative to the median date of first egg laid than in 1986, but removals in the two years were at similar times relative to the onset of territoriality (Fig. II-2).

Three of the 11 birds removed in two years died before the time of release (presumably of stress). Surviving birds were released at least 65 km away, less than 24 h after capture. Daily searches were made in and around removal areas for replacement birds the week following the experiment, and about twice a week in the following 4-5 weeks.

RESULTS

Flock membership and social status

Flocks had a stable membership from late October to early March in winters 1985-86 and 1986-87. Only four individuals were known to switch from one flock to another regularly. Permanent changes of membership from one flock to

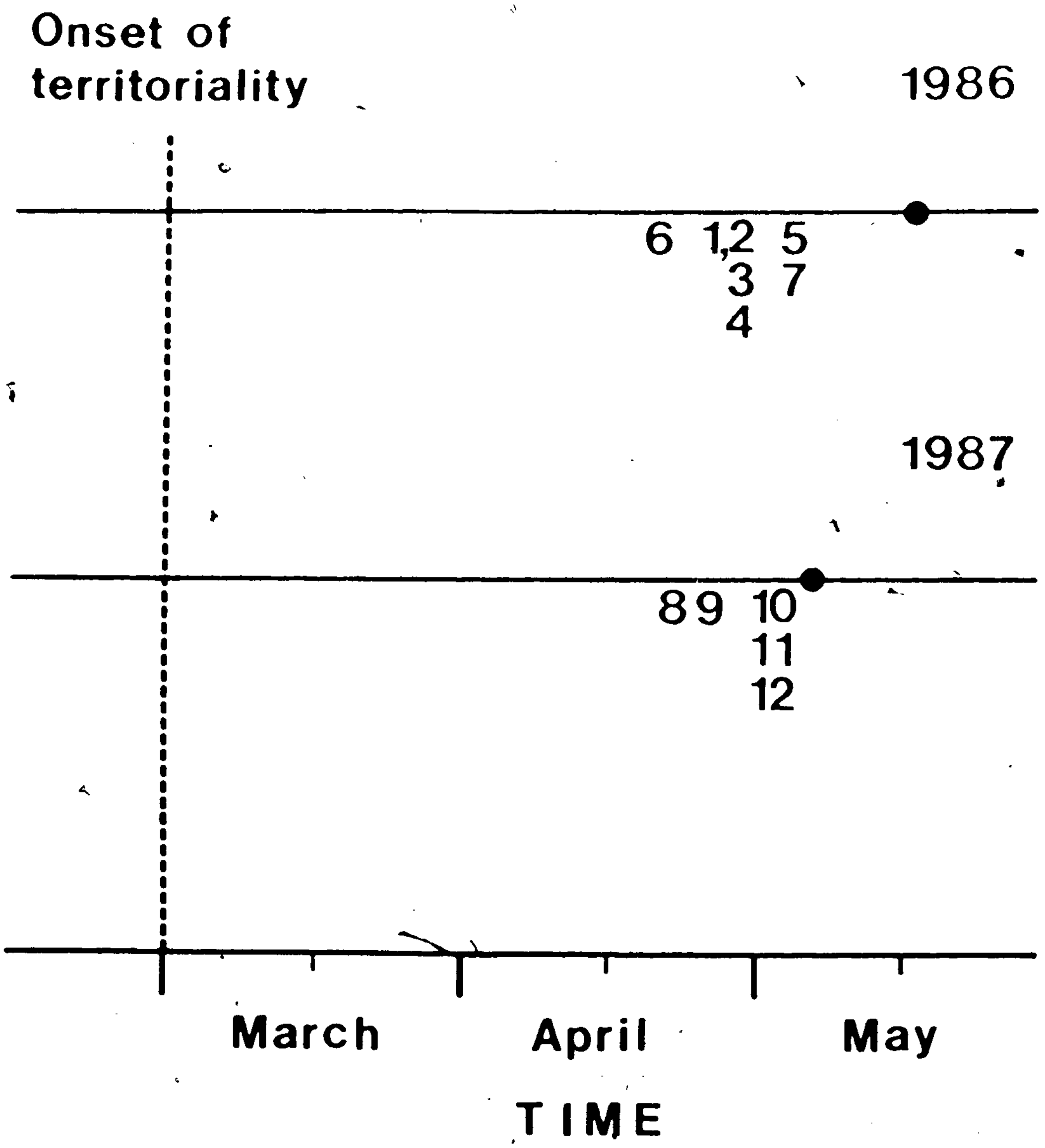

Figure II-2: Timing of removals in relation to onset of territoriality and laying. Numbers refer to individuals removed (see also Fig. II-1): 1-4=females, 5=male, 6-7=pairs, 8-12=females. Solid circles represent median dates of first egg laid (earlier in 1987 than in 1986; Mann-Whitney *U*-test, df=24, P=0.0003).

another occurred only twice. Mean flock size was 8.1 individuals in November 1985 (SE=0.55, n=26) and 8.1 in November 1986 (SE=0.41, n=38). In November and December, several chickadees from neighbouring areas discovered the feeder area and settled there for the rest of the winter. These birds were not considered as part of the "feeder" population. Nearly all the unbanded immigrants were using feeders on the perimeter of the study area (and thus were not seen deep inside the study area). It thus seems that most of the unbanded immigrants came from flocks adjacent to the study area.

All 24 flocks in which all possible pair-wise interactions were observed (i.e. any two individuals were involved in at least one interaction) showed a linear hierarchy. 158 of the 7,896 intra-flock interactions recorded at feeders were in the opposite direction as predicted by a perfectly linear hierarchy; only 2 of the 825 interactions observed in free-roaming flocks were reversals. All but one of the shifts in ranks observed throughout the winter coincided with the disappearance of one or more flock members (the rank of birds lower than the missing bird in the hierarchy automatically increased by one). Males generally dominated females: females "won" only 109 of 3,114 male-female interactions at feeders and only one of the 327 male-female interactions away from feeders. Adults always dominated young of their sex. Females ranked higher than males in only 21 of 462 male-female dyads in dominance hierarchies. Thus, adult males were generally at the top of hierarchies, followed by yearling males, then adult females, and finally, yearling females.

Survival and territory acquisition

To eliminate confounding effects of rank, sex, and age in the analysis of survival and territory acquisition, I designated as dominant each bird that ranked higher than more than half of its flock-mates of the same sex and age. Other flock members were classified as subordinates, except when they were exactly in the middle of the hierarchy of their sex/age group in which case their status was undefined. Birds that were the only flock members of their category also had an undefined dominance status.

Individuals that resided in the study area for the winter and that were sighted on or after 1 March were classified as winter survivors; others were regarded as dead.

I analysed the data with multidimensional contingency table analysis (MDCTA; Norusis 1986), using data from Table II-1. The basic advantage of using MDCTAs rather than two-way contingency tables is that it allows for the testing of three-way and higher-order interactions. As in ANOVA, several models can be created that include different combinations of main effects and interactions terms. I used the method of model selection of Norusis (1986) to obtain the "best-fit" models to explain most variation in survival

TABLE II-1: Survival rates of black-capped chickadees at the Meanook study area, 1985-1987.

	% Survivors (N)	
	Adults	Yearlings
Control 1985-86	74 (19)	79 (108)
Control 1986-87	64 (44)	48 (93)
Feeder 1985-86	50 (2)	91 (89)
Feeder 1986-87	69 (55)	62 (135)
	Males	Females
Control 1985-86	79 (75)	82 (66)
Control 1986-87	64 (70)	44 (64)
Feeder 1985-86	88 (82)	92 (75)
Feeder 1986-87	60 (97)	69 (94)
	Dominants	Subordinates
Control 1985-86	91 (46)	82 (49)
Control 1986-87	76 (38)	47 (36)
Feeder 1985-86	96 (26)	89 (18)
Feeder 1986-87	87 (38)	65 (43)

rates among years, feeding conditions, sexes, ages and dominance. Addicott (1978) provides an example of the application of MDCTA to ecological data.

I divided the original survival data into three non-exclusive subsets: 1) birds of known age, 2) birds of known sex, and 3) birds of known dominance status (Table II-1). To avoid having more than 20% of cells with expected values <5 (Sokal and Rohlf 1981), I pooled sexes and dominance status in the first subset, ages and dominance status in the second, and ages and sexes in the third subset. To facilitate the presentation of the analyses, I abbreviated particular interaction terms by joining associated variables by a star(*). For example, the interaction between year and survival rate was denoted by (YEAR*SURVIVAL).

The analyses indicate that the interaction between year and survival rate was present in the best-fit model for all three subsets of data (Table II-2). Survival rates in 1985-86 were consistently higher than in 1986-87 (Table II-1). Lower survival rates in 1986-87 were apparently not due to colder weather, since winter 1986-87 was slightly milder than the previous winter (Table II-3). Preliminary data taken at the end of the 1984-85 winter (which was colder than the average) indicated that at least 77% of 26 winter survivors remained to breed, compared to 54% in 1985-86 and 66% in 1986-87 (X^2=6.98, df=2, P=0.03). Assuming that the number of birds that cannot secure a

TABLE II-2: Analyses of the survival rates of chickadees with multidimensional contingency tables (MDCTAs). G^2 is the log-likelihood ratio.

Subset of data	Best-fit model	G^2	df	P
Known age	(YEAR*AREA[1]*AGE) (AREA*SURVIVAL) (YEAR*SURVIVAL)	7.15	5	0.21
Known sex	(AREA*SEX*SURVIVAL) (AREA*YEAR) (YEAR*SURVIVAL)	4.99	5	0.42
Known dominance status	(AREA*SURVIVAL) (YEAR*SURVIVAL) (DOMINANCE*SURVIVAL) (AREA*YEAR)	2.57	7	0.92

[1] Control or feeder area.

TABLE II-3: Mean monthly temperatures (^{o}C) and cold spells at the Athabasca meteorological station, 14 km away from Meanook. Data from Alberta Environmnent.

Month	1984-85	1985-86	1986-87	1951-80
Oct	1.4	3.3	6.1	4.6
Nov	-11.1	-15.1	-9.7	-6.1
Dec	-18.1	-8.5	-6.2	-13.8
Jan	-10.3	-8.1	-7.6	-17.9
Feb	-14.6	-12.9	-5.4	-11.9
Mar	-1.8	-0.2	-5.9	-6.4
Apr	4.2	3.1	6.5	3.4
Average	-7.2	-5.5	-3.2	-6.9
Days < -20.0^{o}C	32	21	2	--
Longest spell (d) below -20.0^{o}C	11	11	2	--

territory increases as winter survival increases, then these percentages suggest that survival reached a lower value in 1984-85 than in the two years of this study. Also, only 14 pairs of chickadees nested on an area censused in summer 1985, compared to 25 on the same area in 1986 and 26 in 1987. The much lower breeding density in 1985 may have resulted from high mortality the previous winter.

Survival was related to the area where birds spent the winter, as indicated by the association between feeding status ("AREA") and SURVIVAL in all models of Table II-2. Table II-1 shows consistently higher survival rates in the feeder area. Although this suggests that food addition helped winter survival of chickadees, I cannot conclude this indisputably, since I did not randomize the possible effect of differences between the sites (other than food addition). Although numbers of winter survivors were relatively higher in the feeder area, there was no measurable difference between the density of breeding birds in control and food-supplemented areas (Table II-4). Also, the proportion of winter survivors that acquired territories was not significantly different between the two areas (Table II-4).

No difference was found in survival rates between flock members of different ages, as the AGE factor was not associated to SURVIVAL in the interaction terms of the best-fit model with birds of known age (Table II-2).

The only significant three-way interaction involving survival rates was the interaction between SEX, SITE (feeder

TABLE II 4: Net population changes in control and food supplemented areas from November to May. P>0.45 for all comparisons.

	Control Population size Area=1.86 km^2	Feeder Population size Area=2.55 km^2	χ^2
1985-86			
1 November	143	163	
1 March (survivors)	114	144	
15 May (breeders)	64	78	
% change 1 Nov.-15 May	-55.2	-52.2	0.183
% change 1 Mar.-15 May	-43.9	-45.8	0.036
Density (Pairs/km^2)	17.2	15.3	0.028[1]
1986-87			
1 November	137	192	
1 March (survivors)	73	124	
15 May (breeders)	52	82	
% change 1 Nov.-15 May	-62.0	-57.3	0.564
% change 1 Mar.-15 May	-28.8	-33.9	0.525
Density (Pairs/km^2)	14.0	16.1	0.043[1]

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[1] Compared to expected densities calculated by dividing the total number of pairs (Feeder + Control) by the total area (Feeder + Control) each year.

or control area), and SURVIVAL (Table II-2). This interaction was probably the result of the particularly low female survival in the control area in 1986-87 (Table II-1).

Finally, the MDCTA revealed a significant interaction between dominance and survival rate (Table II-2), and dominant birds (within their sex/age class) had a consistently higher over-winter survival rate (Table II-1).

Among the survivors, dominant yearlings of each sex were far more likely than subordinates to acquire a breeding territory, in feeder and control areas, in both years (Table II-5, Fig. II-3). In a MDCTA incorporating probability of territory acquisition, dominance, year, and area (feeder or control), the partial log-likelihood ratio for the interaction between dominance and territory acquisition in juveniles was highly significant ($G^2=99$, df=1, $P<0.001$), supporting the hypothesis that dominance conferred a higher probability of territory acquisition. Sample sizes were too low to detect difference in probabilities of territory acquisition between dominant and subordinate adults. However, nearly all adults secured a territory (Table II-5). In March-April, many banded winter survivors disappeared (125 in 1986 and 76 in 1987), leaving only breeders and a few unpaired birds.

During March-April each year, transient unbanded birds were observed on nearly every censusing day, but their numbers were difficult to estimate, as they behaved secretively (very mobile, silent). There were also more than

TABLE II 5: Probability of obtaining a territory for dominant and subordinate chickadees that survived the winter. *=P<0.005, **=P<0.001.

	% Obtaining territory (N)		
	Dominants	Subordinates	χ^2
All birds			
Control 1985-86	88 (41)	15 (40)	40.1 **
Control 1986-87	93 (27)	46 (22)	11.0 **
Feeder 1985-86	100 (25)	12 (17)	30.6 **
Feeder 1986-87	91 (33)	50 (26)	10.3 *
Yearlings only			
Control 1985-86	85 (27)	13 (38)	30.5 **
Control 1986-87	100 (17)	20 (15)	18.5 **
Feeder 1985-86	100 (11)	6 (16)	19.6 **
Feeder 1986-87	88 (24)	35 (20)	10.8 *
Adults only			
Control 1985-86	100 (4)	100 (1)	---
Control 1986-87	80 (10)	100 (7)	NS[1]
Feeder 1985-86	?	?	?[2]
Feeder 1986-87	100 (9)	100 (6)	---

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[1] Fisher's exact test, 2 tailed P=0.485.
[2] No data available.

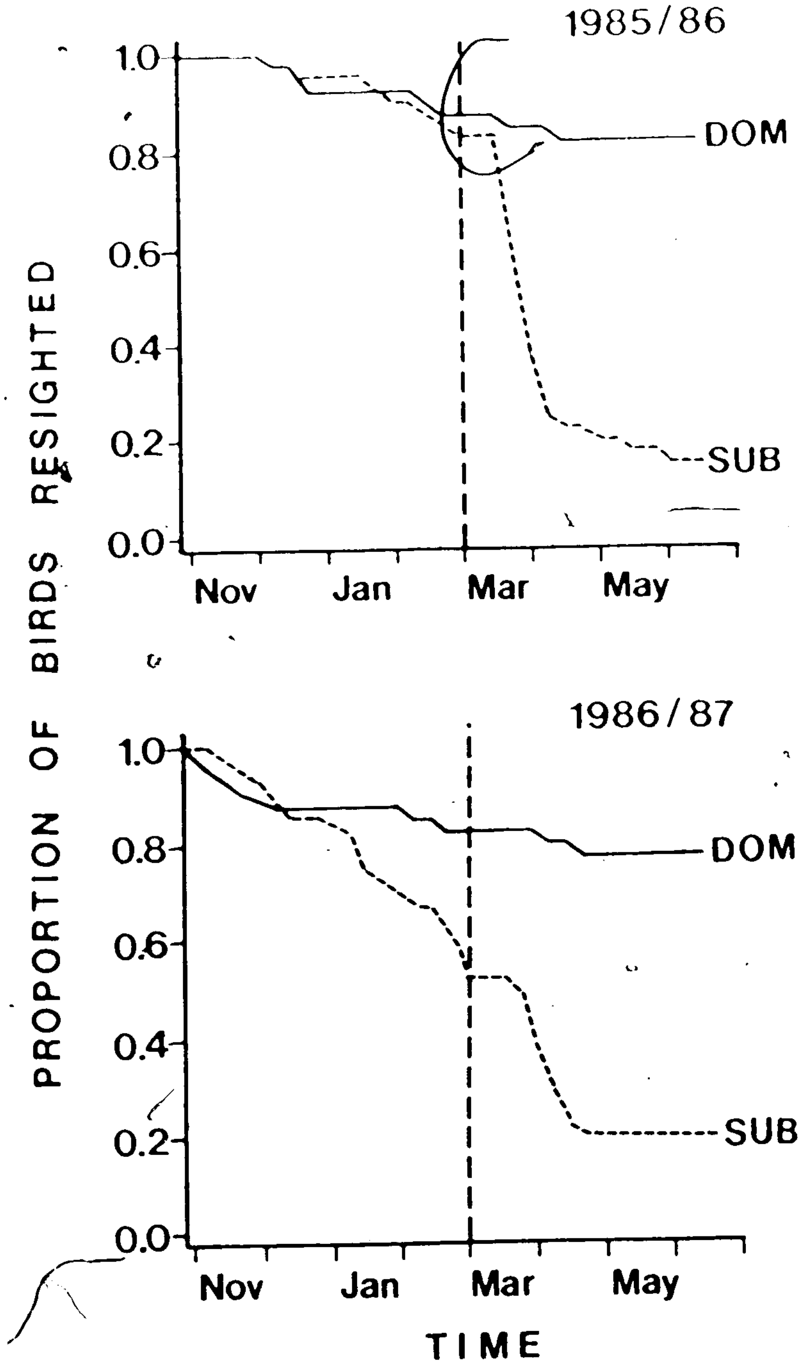

Figure II-3: Number of dominant(D) and subordinate(S) yearling black-capped chickadees that survived or stayed in the study area (feeder and control pooled). Vertical lines delimit approximately the onset of territoriality. Numbers of birds on 1 November were: 72 dominants and 68 subordinates (1985-86), 79 dominants and 95 subordinates (1986-87).

20 instances of banded birds moving to locations where they had never been seen before (all these birds failed to get a territory in the study area and disappeared). I found no positive evidence of a spring immigrant acquiring a territory on the study area. Some unbanded chickadees bred near the perimeter of the study area, but I do not know whether they were unbanded winter residents or spring immigrants (the proportion of unbanded chickadees increased rapidly near the perimeter of the study area). Finally, a subordinate yearling female, last seen at Meanook on 24 March 1987 was observed at a feeder 39 km south of Meanook, on 29 March 1987.

Removal experiment

In 1986, three females and two pairs that were removed were replaced by previously unsettled birds. The fastest replacement occurred one day after the removal, and the slowest, 16 d after the removal. Three of these seven unsettled birds were banded unpaired yearlings that remained on the study area in the spring. The others were unbanded birds of unknown origin and age. The remaining widowed birds (one female and one male) were on adjacent territories and formed a new pair, leaving one vacant area. In 1987, the outcome differed: only one of the five females removed was replaced. One widowed male disappeared after singing for several days, another paired with the female of an adjacent pair (leaving the original mate unpaired) but did not breed.

Two others stayed on their territories as solitaires. One of these two birds was seen once with an unbanded bird, but did not breed.

DISCUSSION

A central question raised in this study is, what factors influence the recruitment of birds to the breeding population? Even though winter survival is a prerequisite of territory establishment, I will consider them separately in the following discussion, in order to evaluate their individual importance.

Winter survival, weather and food

Previous studies of black-capped chickadees suggest that winter survival rates in food-supplemented populations are higher than 60% (Samson and Lewis 1979, Smith 1967, 1984). My results were consistent with this figure. Perrins (1979) noted that winter temperatures do not generally influence numbers of parids in Britain, but that in severe winters (especially in continental Europe), survival may decline. Neither winter was particularly cold, however, winter survival was higher in the colder winter of this study (1985-86). Thus, factors other than temperature *per se* must have been responsible for the differences in survival rates between the two winters.

Food availability probably influenced chickadee survival, as suggested by the feeding experiment. Higher survival in food-supplemented areas does not necessarily prove that food shortage is the proximate cause of death in wintering passerines. Instead, as Jansson *et al.* (1981) and Ekman (1987) pointed out, more efficient foraging in feeder areas may give birds more time to look for predators and avoid them. In our study, northern shrikes (*Lanius excubitor*) were seen stalking chickadees each week and remains of five individuals apparently killed by shrikes were found. Unfortunately, I could not measure the contribution of shrike predation to chickadee mortality. Food availability occasionally influences survival in parids in central Europe, as shown by studies of blue tits (*P. caeruleus*; Krebs 1971) and great tits (e.g. van Balen 1980), but its effect seems more striking and regular in Scandinavian willow tits (*P. montanus*) and crested tits (*P. cristatus*; Jansson *et al.* 1981). All feeding experiments done in Europe, except the one on great tits by Krebs (1971), produced larger breeding populations in food-supplemented areas (van Balen 1980 and references therein; Jansson *et al.* 1981), thus supporting Lack's (1964) 'winter food limitation' hypothesis.

Supplemental feeding did not influence the breeding densities in feeder and control areas. After a cold winter (1984-85), the surplus of birds at the end of the winter was apparently reduced or nonexistent and the breeding density fell to half the 1986-87 levels, suggesting that winter mortality may limit numbers of breeders, in harsh winters. However, only long-term data will establish whether winter mortality regularly affects the breeding density of chickadees at this latitude.

Differential winter survival among individuals

As in the present study, Smith (1984) found no relationship between age and survival in a food-supplemented population. This suggests that greater experience of adults *per se* did not confer greater foraging efficiency, or if it did, it was not essential to survival. This is also consistent with the study of Ekman *et al.* (1981) on willow tits *P. montanus* and crested tits *P. cristatus*, in which they showed that survival of young reached the same level as that of adults, when the latter were removed from flocks. However, the results of Ekman *et al.* (1981) may have been caused by the lower densities of tits after removals (but see Ekman and Askenmo 1984).

If survival rate is a function of social rank alone, then there should be a decrease of survivorship as rank decreases. This was found by Ekman and Askenmo (1984) in a natural population of willow tits, and in studies of other avian species (e.g. Fretwell 1969, Kikkawa 1981, Arcese and Smith 1985). In Meanook, as in other studies of black-capped chickadees (e.g. Hamerstrom 1942, Hartzler 1970, Glase 1973, Smith 1976, 1984), males dominated females, and adults dominated young of their sex. If dominance *per se* influences survival, males should, on the average, exhibit higher survival rates than females. The MDCTA showed that a difference between survival rates of males and females was present and dependent upon the feeding conditions. Since supplemental feeding apparently increased survival rates, one would predict that the difference between survival rates of males and females is lower in the feeder area, since higher resource abundance reduces competition and presumably the difference between "payoffs" (benefits/costs) to dominants and subordinates (Wittenberger 1981). The difference between males and females found in this study in 1986-87 in the control area is consistent with this hypothesis, and is perhaps attributed to the exclusion of females from possibly better foraging areas used by males (Chapter III). However, the evidence is inconclusive, since in other comparisons, males and females had similar survival rates. The higher overall winter survival in 1985-86 suggests that resources (cover against predators, food) were more available than in 1986-87. This could explain the similar survival of females and males in 1985-86.

An alternative cause of male-female differences in survival of chickadees may be related to sexual size dimorphism; large birds often have higher winter survival rates than smaller conspecifics (Hamilton 1961, Calder 1974, Wiley 1974). However, these studies dealt mostly with species that are more sexually dimorphic than black-capped chickadees in which males are only about 5% larger than females (based on wing length). The small degree of sexual size dimorphism of chickadees makes an explanation of survival differences based on body size unlikely. Nevertheless, Lehikoinen (1986) found a tendency of larger great tits to survive better than smaller ones in winter. However, as body size was somewhat related to dominance in Lehikoinen's (1986) study, no inference could be made on the effect of body size alone. Smith (1984) found no relationship between sex and survival in black-capped chickadees. As in this study, she found that intra-sex dominance status influenced survival rate (dominant chickadees survived better than subordinates of their sex).

Another factor that could explain lower female survival in winter is their reproductive effort in the previous summer. If females invest more than males, they may enter the winter in poorer condition than males, especially in years of high reproductive cost. The effect of differential reproductive costs can be controlled for by removing all adults from male-female comparisons, since young did not breed the previous year. Comparisons of yearlings yielded the same results, thus indicating that sexual differences in reproductive cost did not cause the differential winter survival of males and females.

Thus, my evidence suggests that high social rank somehow increased the probability of winter survival in this population. If survival is rank-related, then mixed foraging tactics as described by Rohwer and Ewald (1981) and Barnard and Sibly (1981) do not occur in black-capped chickadee flocks. But long-term data are needed to account for yearly variations of relative payoffs to dominants and subordinates in winter.

Territory acquisition

At the end of winter, a survivor must face the challenge of becoming part of the breeding population. Acquisition of a territory through competition will occur only if over-winter survival is high enough to produce more potential breeders than the available habitat can contain. This is true for several bird species (Wittenberger 1981, Hannon 1983), and anecdotal accounts suggest that it regularly occurs in the black-capped chickadee (Glase 1973, Smith 1967, 1984), in contrast to all European parids (Perrins 1979, Jansson *et al.* 1981). As in Glase's and Smith's studies of chickadees, the number of birds at Meanook at the end of winters 1985-86 and 1986-87 was substantially greater than the number of locally breeding birds.

Even though all the adults became territorial, only dominant yearlings had a high probability of settling in the study area. Were subordinate chickadees prevented from breeding? If most of the surplus winter survivors were looking for breeding opportunities later in spring, then all the territorial birds that were removed should have been replaced. This was nearly true in 1986, as only one territory remained unused after removals. In a similar experiment with great tits, Krebs (1971) found that replacement birds previously had territories in nearby marginal areas in which breeding success is lower that in optimal habitat. Vacated marginal areas in Krebs' (1971) study remained unoccupied after desertion by replacement birds. Thus, replacement of removed great tits did not demonstrate the existence of a non-breeding surplus, but it showed the exclusion of some individuals from the best breeding habitat. In a later experiment, Krebs (1977) established the presence of a true non-breeding surplus of great tits, suggesting that territoriality can indeed limit numbers of breeders.

That replacement chickadees came from nearby marginal areas was unlikely in Meanook in 1986, since three of the replacement birds were banded and not territorial before removals, and there was no marginal area comparable to that of Krebs' (1971) study. Although clumps of willows were present in the area, they did not contain nest boxes as did Krebs' marginal areas, and shrubs were too small to allow excavation of nests. Thus, a non-breeding surplus was apparently present in 1986, about two weeks before laying. This is the first experimental evidence for a non-breeding surplus in a North American parid.

However, surplus black-capped chickadees may remain in the area for only a few weeks: such a surplus was small or nonexistent about one week before laying in 1987, as only one of five removed females was replaced. Different replacement rates in 1986 and in 1987 were possibly due to the timing of removal in relation to breeding. The breeding season was more advanced at the time of removals in 1987 than in 1986 and surplus birds may have left or died by May 1987. Also, there were fewer subordinate birds present at the onset of territoriality in 1987 and their disappearance was more abrupt (Fig. II-3).

One important question is whether the gradual decrease of the non-breeding surplus in spring is due to migration of part of the population, mortality, or simply secretive behaviour allowing birds to escape the attention of observers. 'Secretive behaviour' is unlikely, as no adults other than the known breeders were observed in late summer flocks, when all chickadees were easy to observe.

One could argue that subordinates in winter were in fact visitors from more northern populations that subsequently returned to their breeding grounds in spring. Partial migration has been documented in European parids (Ulfstrand 1962), and subordinate individuals may have a higher tendency to migrate (Smith and Nilsson 1987 for parids; Ketterson and Nolan 1983). Also, local migration to towns in winter (where food may be more abundant) has been reported in European parids (Dhondt 1971). However, three observations provide evidence against the existence of significant numbers of migrant black-capped chickadees: 1) there is no published evidence for cyclic large-scale movements between breeding and wintering grounds in North American parids; 2) other studies of black-capped chickadees (Odum 1941, Smith 1967, 1984, Glase 1973) failed to demonstrate the arrival of breeding immigrants in spring, and 3) chickadees are winter residents as far north as Fairbanks, Alaska (Kessel 1976), near the edge of their range. Finally, temporary movements of chickadees to local marginal areas are an unlikely cause of "disappearance" in spring. I censused in a 25 ha isolated stand of willows near the study area in March-April 1986 and I counted only two to three chickadees on each of the six visits, which suggests that willow stands were not used as a "buffer area" for a large non-breeding surplus.

As Smith (1967) suggested, spring territoriality seems to be the principal factor limiting numbers of breeding chickadees, in various parts of their range. However, data from harsher winters in our study area and from more northerly latitudes might show that winter mortality, instead of territoriality, occasionally limits the number of breeders. Whether the effect of spring territoriality is density-dependent remains unknown; our data did not show density-dependence, but the size of the non-breeding surplus in the feeder and control areas were probably too similar in the two years of this study to reveal any density-dependence. Non-breeding surplus seemed to be gradually eliminated before the laying period, possibly by mortality. Birds moving out to new areas would presumably face costs such as unfamiliarity with new resources, and energetic costs (Greenwood and Harvey 1982); such costs can lead to high mortality, but are hard to document, since it is extremely rare to find dead passerines in the wild. However, regardless of the exact timing of post-winter mortality in chickadees, it was clearly influenced by the exclusive use of breeding resources by birds that were dominant in winter.

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III. SEX, DOMINANCE AND MICROHABITAT USE IN WINTERING BLACK-CAPPED CHICKADEES: A FIELD EXPERIMENT

INTRODUCTION

Intraspecific variation in foraging behaviour of birds has received much attention since the early work of Selander (1966) who outlined the mechanisms of ecological separation between males and females. Observational studies have revealed differences between foraging niches of males and females for a wide range of bird species (reviewed by Morse 1980). Age-related differences in foraging have been reported less frequently (e.g. Ekman and Askenmo 1984, Glase 1973). Also, recent work suggests that there can be a relationship between social dominance *per se* and foraging niches of conspecifics in social groups (Schneider 1984).

One hypothesis explaining intersexual differences outside the breeding season is that males and females prefer different, genetically determined niches that evolved as a mechanism to partition resources and maintain a low rate of male-female agonistic behaviour ('specialization hypothesis': e.g. Selander 1966, Jackson 1970, Glase 1973, Austin 1976, Busby and Sealy 1979, Morrison and With 1987, Morton *et al.* 1987). One prediction of the 'specialization hypothesis' is that situations where resources are limited produce exploitation competition (Park 1962) between males and females. A second hypothesis states that birds of one sex socially dominate those of the opposite sex and dominants exclude subordinates from a part of the species' niche that is preferred by both sexes ('interference hypothesis': e.g. Ligon 1968a, 1968b, 1973, Kilham 1970, Hogstad 1976, 1978, Murton *et al.* 1971, Peters and Grubb 1983, Schneider 1984).

A large number of field experiments have addressed resource partitioning between sympatric animal species at the community level (reviews by Connell 1983, Schoener 1983, but see Underwood 1986). At the species level, however, very few field experiments have attempted to determine the mechanism behind inter-sexual separation of foraging niches, especially in birds (but see Peters and Grubb 1983, Ekman and Askenmo 1984).

Black-capped chickadees (*Parus atricapillus*) are omnivorous parids found year-round in most of temperate North America. They form stable flocks of unrelated (non-sibling) individuals outside the breeding season (Odum 1942, Weise and Meyer 1979, this study). A strongly linear dominance hierarchy is observable in each flock; all males generally rank higher than all females and older birds dominate younger birds of their sex (Hamerstrom 1942, Odum

1942, Hartzler 1970, Glase 1973, Smith 1976, but see Smith 1984). Glase (1973) showed that, in an eastern deciduous forest, male and female chickadees in his study area (and adults and yearlings to a lesser extent) foraged in different locations. The present study investigated intersexual differences in foraging sites, activity budgets, and foraging efficiencies of male and female black-capped chickadees, in poplar (*Populus tremuloides* and *P. balsamifera*) woodland. Data from birds foraging in willow (*Salix* spp.) stands are also reported.

Finally, I examine with a field experiment that the presence of males influences the foraging sites, activity budgets and foraging methods of females. Costs and benefits associated with different foraging niches, and the importance of interference versus exploitation competition in chickadee flocks are discussed.

STUDY AREA AND METHODS

The study was conducted at the Meanook Biological Station (54°37'N, 113°20'W), near Athabasca, Alberta, Canada, in the winters 1985-86 and 1986-87. The study area was a 2.5 km^2 mosaic of poplar (*Populus tremuloides* and *P. balsamifera*) woodland interspersed with fields (20% of the area), and stands of willows (*Salix spp.*) of up to 4 ha. Poplar woods typically had a continuous canopy height of about 20 m, whereas willow stands were dominated by groups of trees less than 10 m high.

In both winters, virtually all the chickadees in the study area (>95% of approximately 175 birds each winter) were captured in mist nets and individually marked with coloured leg bands. Strips of electrician's tape of the corresponding colours were stuck to the bands to make 1 cm long "flags" that enhanced the visibility of colour combinations. A discriminant analysis based on body mass, flattened wing length, and length of the outer right rectrix (appendix I) was used to assign sex. Reference samples of 143 females and 171 males (known from their behaviour in the breeding season) were used to compute the discriminant function. The function classified correctly 94% of a second sample of 143 known individuals of both sexes. Banded individuals known to be more than 1-y old were classified as adults and unbanded immigrants in summer and fall were considered to be yearlings. I observed the moult of flight feathers in August and September in both years, and yearlings had a different pattern than adults (Meigs *et al*. 1983). All the immigrants were positively identified as "yearlings".

Foraging and agonistic interactions

I observed the foraging behaviour of flock members from January to February in the first winter, and from December to February in the second. Most observations were made on members of eight flocks. One of these flocks used primarily a willow stand, the others used mainly poplar. I also observed nine members of six other flocks in poplar. Observations were made only when a single flock was in an area. I described the foraging sites of the birds visually with three measures: 1) relative height of the bird in the canopy (10 classes of equal size), 2) relative horizontal distance of the bird from the tip of the used branch to the trunk (10 classes), and 3) the foraging substrate (trunk or branch). Foraging sites were sampled each minute with the instantaneous sampling method (Altmann 1974) on randomly chosen focal birds. I used an electronic metronome and recorded data onto a portable audio-cassette recorder. I tested whether the consecutive records of foraging height and distance to trunk were statistically independent with the Runs test above and below the median (Sokal and Rohlf 1981). 1-min intervals between records of distance to trunk were long enough to produce independent observations for more than 95% of the birds, whereas intervals of 2-3 min were necessary to produce independent observations of relative heights. Each day, I randomly chose the sequence that I would observe individuals before going in the field. Observations started about 30 min after the flock was found to minimize the possible effect of my initial disturbance. Each focal bird was observed with binoculars for 15 min, and once the last individual in the sequence was observed, I repeated the initial sequence until I stopped observations.

Each observation period lasted about 3 h. Similar numbers of foraging records were generated for each bird.

In the second winter, I counted the number of items probed by the bird/min and used prey-encounter rates to calculate its success (percentage of probes that uncovered prey). Chickadees generally take their prey to a new location, after capture, eat it, and wipe their bill after the prey is consumed, which makes it possible to measure feeding rates. However, I cannot exclude the possibility that chickadees took small, unnoticed prey, but the proportion of their diet represented by small prey (e.g. spider eggs, aphids, etc) is assumed to be low. The number of times the bill touched the substrate without apparently contacting prey (generally less than five times/min) seemed too low to contribute a significant proportion of items in the diet.

In the second winter, I also recorded the activity budget of focal birds. The focal bird's behaviour was recorded at 1-min intervals. I divided activities in eight classes: 1) visual search (bird moving through the environment, head movements), 2) probing (bill contacts substrate), 3) prey handling, 4) sitting, 5) flying, 6) freezing (halts all movement when predator present), 7) maintenance activities (preening, bathing), and 8) other behaviours.

In both winters, I also recorded all agonistic interactions (interference) involving focal birds, i.e.

displacements (the aggressor flies towards a conspecific and makes the latter fly to another location) and chases. This was done at the same time as the instantaneous sampling, but independently from it, since the probability of scoring fast-occuring events with instantaneous sampling is remote (Altmann 1974). This 'all occurences' sampling of agonistic interactions with focal birds enabled me to estimate the rate of agonistic encounters (encounters/h) of all the focal birds. I did not attempt to count all interactions in a flock, because of the danger of missing some interactions and thus underestimating interaction rates, especially in large flocks. Interactions not involving focal birds were also recorded (*ad libitum*) to generate dominance hierarchies based on matrices of 'pair-wise' interactions of flock members. I also observed agonistic interactions at temporary feeding stations early in the winter in each flock, to generate more dominance data (see Chapter II). I used Kaufmann's (1983) definition of dominance: "a relationship between two individuals in which one (the subordinate) defers to the other (the dominant) in contest situations". This definition emphasizes a social relationship between two individuals and does not imply priority of access to resources (Rowell 1974, Bernstein 1980, Dewsbury 1982) thus avoiding circularity in statements on rank and differential access to resources (Barrette and Vandal 1986).

Removal experiment

In 1986-87, I used six, randomly chosen flocks to test for competition between males and females: three control and three experimental flocks (Table III-1). None of the chosen flocks shared the same woodland area (except flocks Ctrl(2) and Exp(3) (Fig. III-1), which overlapped slightly during the time of the experiment). All males of the three experimental flocks were captured with a mist net near feeders which were used to attract birds, but provided for only a few hours to mini[illegible]e the effect of supplemental feeding on the females' behaviour. Three solitary chickadees were also removed from the experimental plots, in order to keep these areas free from intruding birds for as long as possible. Removed birds were immediately brought to indoor cages, weighed, and provided with *ad libitum* sunflower seeds, water, and "softbill mix" (dried arthropods). The remaining birds (females) were then observed for 2-3 d. Longer removal periods were not possible, because neighbouring chickadees began to visit the experimental plots. When observations on females were completed, males were weighed again, and released in their home range. No male died, and none lost more than 5% of initial body mass. Since it was impossible to remove the males of the three flocks at the same time, I did the removals sequentially, and as a result, I watched the three experimental flocks one at a time. To control for possible effects of weather on the birds' behaviour, I paired a control flock with each

TABLE III-1: Sex composition of the control and experimental black-capped chickadee flocks (1986-87), number of males removed, and duration of the removals.

	Females	Males	Total	temporary removals
Control:				
1	5	3	8	none
2	4	5	9	none
3	5	7	12	none
Experimental:				
1	3	3	6	3 males (19-20 Jan)
2	3	3	6	3 males (31 Jan-1 Feb)
3	2	2	4	2 males (8-9 Feb)

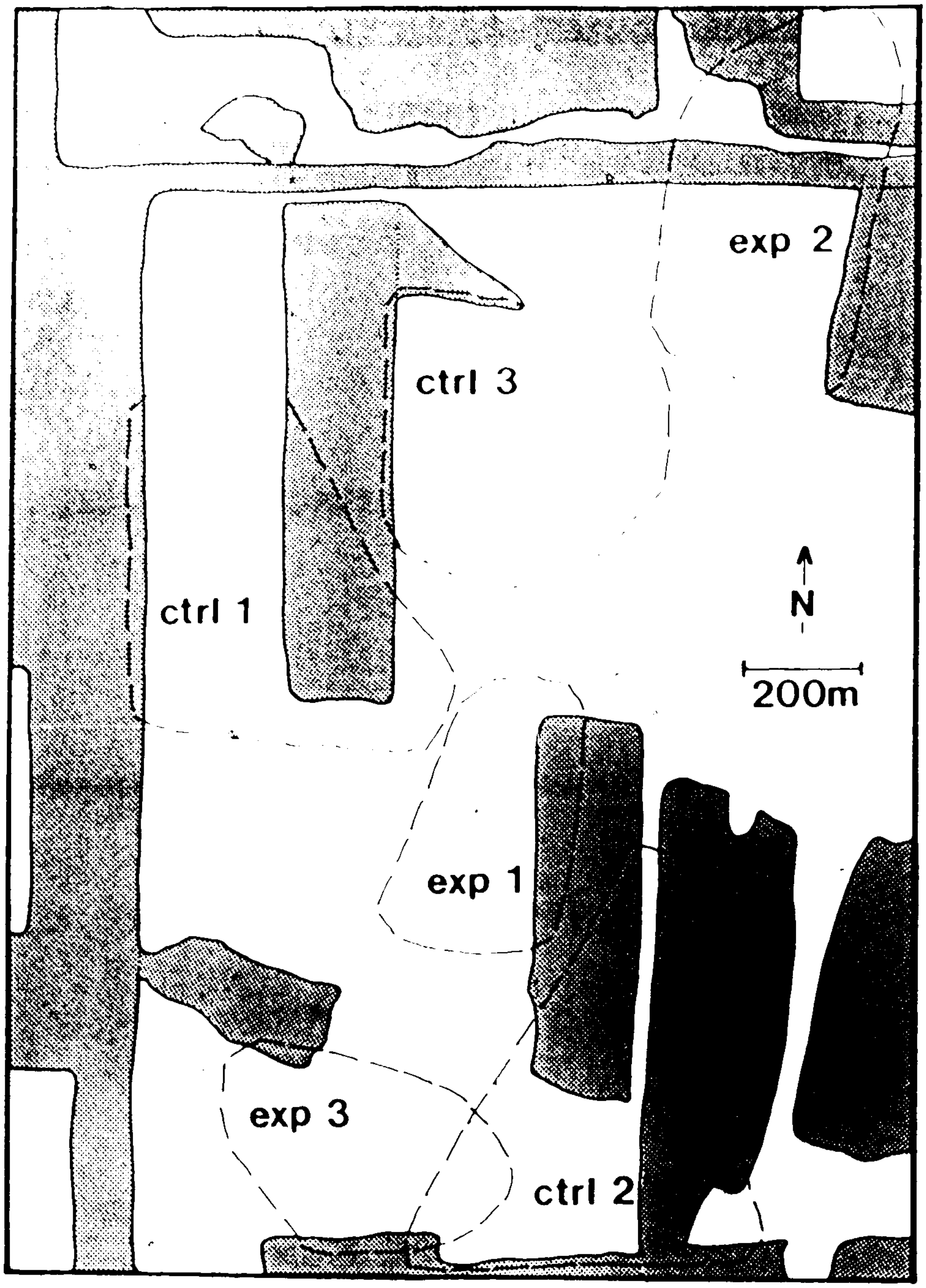

Figure III-1: Spatial distribution of the experimental (exp) and control (ctrl) flocks. Approximate home range limits: ----. Shaded areas are fields and open areas, woodland.

experimental flock, and I alternated observations of control and experimental flocks within all three phases of each removal (before, during, and after the absence of males). Three (ctrl 1,2) or two (ctrl 3) females were observed in control flocks to match the number of females observed in the corresponding experimental flocks.

All hypothesis testing was performed with nonparametric statistics; none of the frequency distributions met the assumption of normality. For comparisons of the foraging height, distance from trunk, time on trunk, time probing, and probing success between experimental and control females one-tailed tests were used, because the statistical alternative hypothesis (H_1) for each of these variables was that the foraging patterns of females would converge towards those of males in the absence of the latter (males and females differed significantly for all these variables in flocks; see below). P values equal or smaller than 0.05 were considered significant.

RESULTS

Most chickadee flocks in the study area foraged primarily in poplar, which composed about 80% of the woodland. As a result, this study will concentrate on the chickadees in poplar habitat, unless otherwise specified.

Dominance and interference

Eight hundred and twenty-five agonistic encounters were recorded in free-roaming flocks. In the first winter, individual flock members were involved in an average of 4.2 encounters/h (SE=0.57, n=24 individuals), and in the second winter, 6.2 encounters/h (SE=0.60, n=48 individuals). I found no difference between hierarchies generated with free-roaming flocks and flocks at feeders, ~~so I~~ pooled all interactions in a dominance matrix for each flock. Rearranged matrices (Brown 1975) indicated that hierarchies were linear in each of the eight flocks (see Chapter II). I noted only two reversals in free-roaming flocks (a bird won a contest against a higher ranking bird).

No change was noted in the membership and the dominance hierarchies of the study flocks during the period of foraging observations, but slight rank changes occurred over longer periods of time. These were apparently readjustments caused by the disappearance of a flock member. Only one case of rank shift did not coincide with the disappearance of a bird. Males generally dominated females (see Chapter II), and adults always dominated young of the same sex.

Agonistic interactions were not evenly distributed throughout the canopy (Fig. III-2); proportionately more interactions occurred in the lower part of the tree, in the male's niche (all interactions: $X^2=46$, $N=335$, $P<0.001$). Less than 20% of interactions observed resulted in direct gain of a food item by the aggressor, a situation very

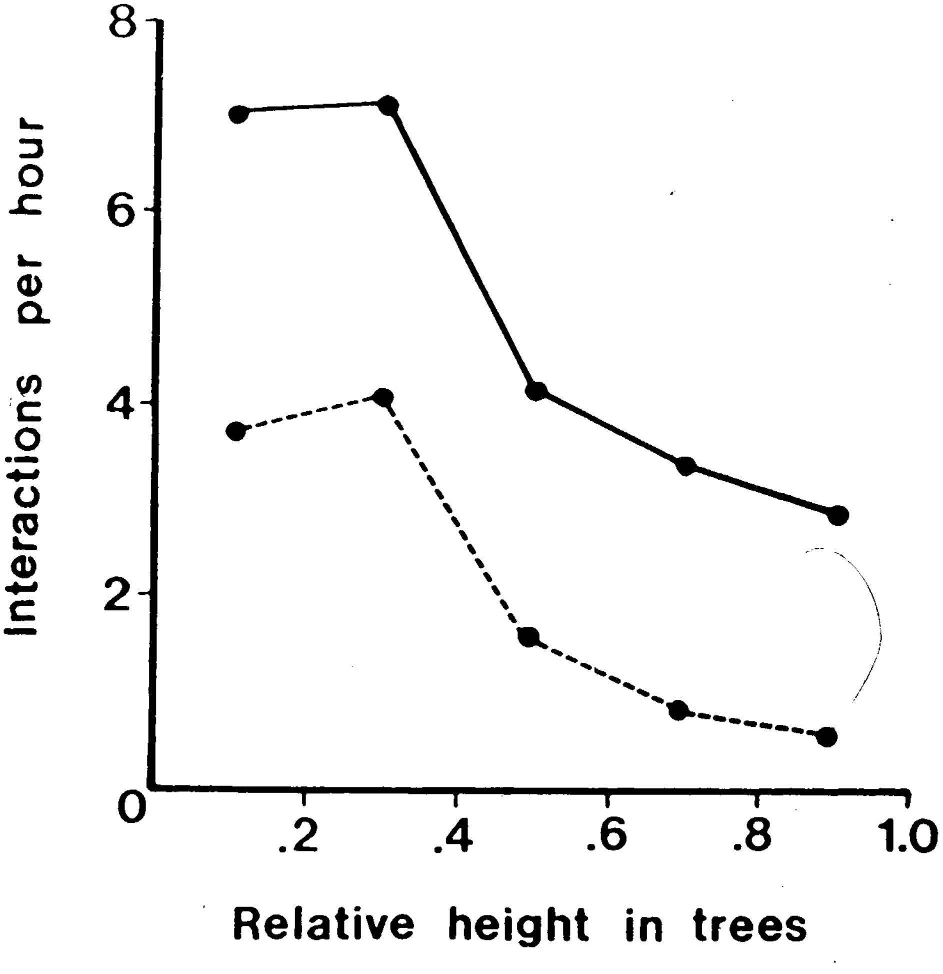

Figure III-2: Rate of agonistic interactions of black-capped chickadees at different heights in trees. Solid line: all interactions, dashed line: male-female interactions only. Data from winters 1985-86 and 1986-87 pooled.

different from interactions at artificial feeding stations, where most agonistic encounters resulted in food gain by aggressors. These observations suggest that social rank can influence access to resources other than individual prey items.

Foraging behaviour in flocks using natural resources

Inter-individual variation in foraging heights and relative distance to the trunk was high in each of the eight study flocks (including the three control and the three experimental flocks; Kruskal-Wallis tests, P<0.001 within each flock). Consequently, I analysed the observational data by taking each individual (and not each foraging observation) as an independent observation. Males clearly foraged lower and closer to the trunk than females in poplar woods in both winters and used trunks and main appendages as a foraging substrate more often than females (Table III-2). In willows, I detected no significant differences, but trends were in the same direction as in poplar habitat (Table III-2). I detected differences in the foraging heights among members of the same sex (Kruskal-Wallis tests, P<0.05) in five flocks, but no consistent pattern emerged between foraging heights and intrasexual dominance status, or age. As a result, the relationship between social rank in the flock and foraging height was not linear (Fig. III-3).

Prey-searching behaviour of the chickadees generally involved up to three steps: 1) visual search, 2) probing

TABLE III-2: Foraging sites of female and male chickadees in winter flocks using natural resources. N represents the number of foraging observations.

	Females	Males	Mann-Whitney	
	$\bar{X}$ (N)	$\bar{X}$ (N)	*U*	P
<u>1985/1986</u>				
Poplar (12 females, 12 males; df=22):				
Relative height[1]	0.66(225)	0.53(197)	9	<0.001
Distance to trunk[2]	0.49(664)	0.35(580)	15	<0.005
Prop. of time on trunk	0.04(664)	0.18(580)	19	<0.005
Willow (3 females, 4 males; df=5):				
Relative height	0.63(069)	0.44(128)	2	0.23
Distance to trunk	0.52(137)	0.39(252)	2	0.23
Prop. of time on trunk	0.12(137)	0.14(252)	4	0.63
<u>1986/1987</u>				
Aspen (24 males, 24 females; df=46):				
Relative height	0.66(1087)	0.40(522)	52	<0.001
Distance to trunk	0.61(1986)	0.31(1001)	24	<0.001
Prop. of time on trunk	0.03(1986)	0.21(1001)	26.5	<0.001

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[1] 0=on ground, 1=on top of tree,
[2] 0=on trunk or main appendage, 1=on branch tip.

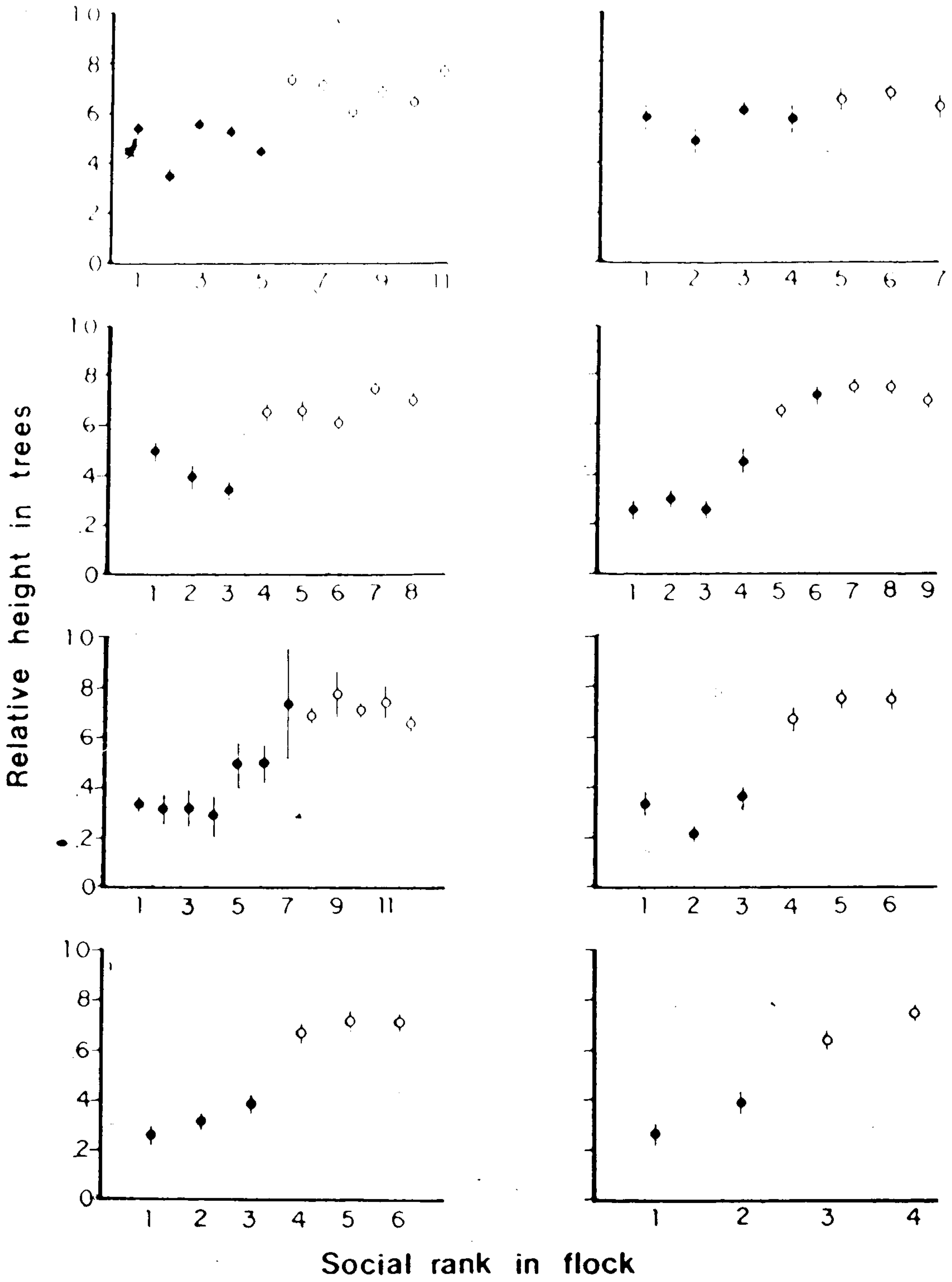

Figure III-3: Relationship between social rank (1=most dominant), sex and average foraging height of birds in 8 flocks of different sizes, in aspen woodland. o= females, •= males. Vertical bars represent standard errors.

with bill for potential prey, and 3) handling prey. The percentage of time spent probing in males and females was dependent on the location in the canopy, with highest probing rates in the upper canopy (Fig. III-4). Not surprisingly, females (which foraged higher) spent on average more time probing than males, but found prey in proportionately fewer probes (Table III-3). However, females and males found a nearly equal number of prey/h (Table III-3).

Removal experiment

None of the estimated parameters (height, distance to trunk, time on trunk, prey per hour, and probing success) varied among flocks when observations before, during, and after removals were analysed separately (Kruskal-Wallis tests, P>0.10 with all variables). Thus, data were homogeneous among flocks and observations from members of different flocks could be treated as statistically independent observations.

In experimental flocks, only the number of prey/h did not vary between the three periods of the experiment (before, during, and after the absence of males); all the other variables (see above) varied markedly. In the control flocks, no variation was found in any of the foraging variables across time periods (Table III-4, Fig. III-5). None of the variables differed between females of experimental flocks and control flocks prior to, and after

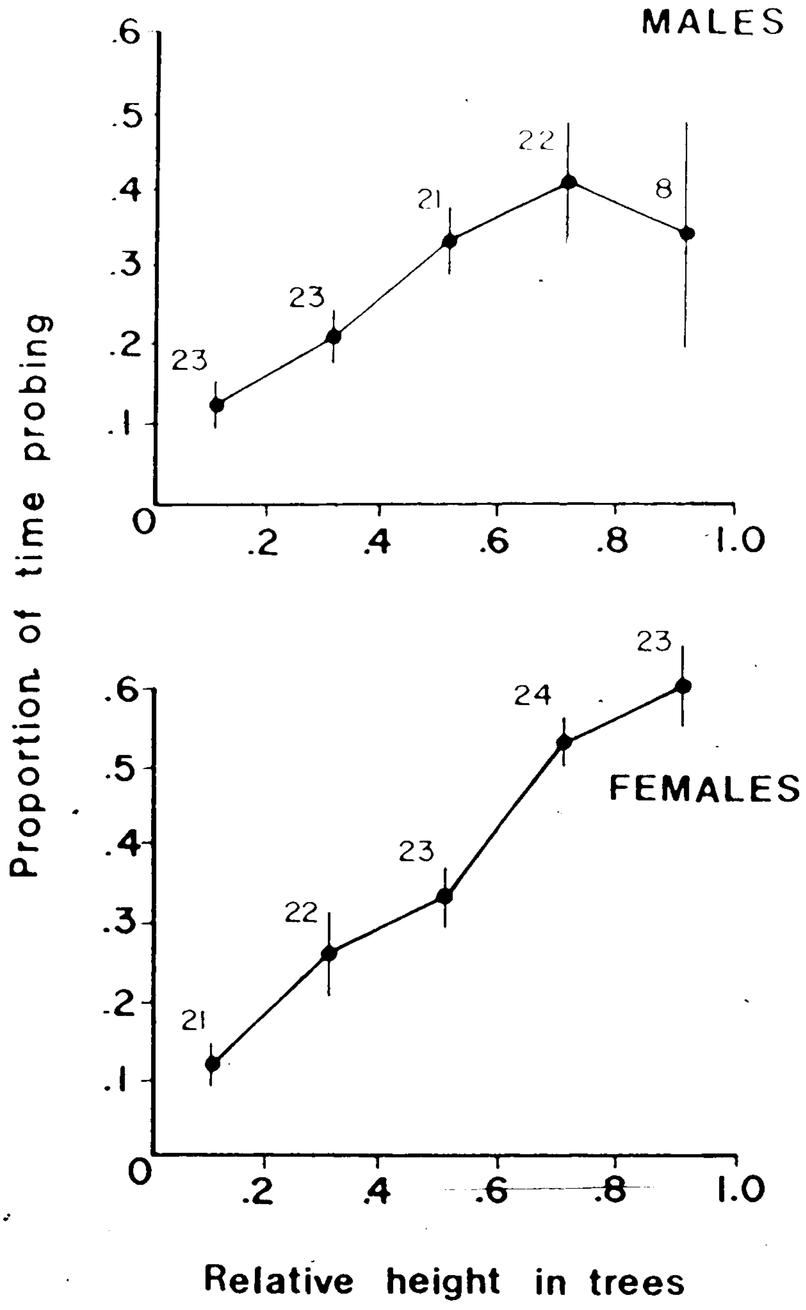

Figure III-4: Probing rates of female and male chickadees at different heights in aspen woodland. Vertical bars represent standard errors. Numbers represent numbers of individuals observed at each level.

TABLE III-3: Foraging efficiency of 24 female and 24 male chickadees in poplar woodland (1986-1987): probing rates, prey-encounter rates and proportion of successful probes. N represents the number of foraging observations.

	Females	Males	Mann-Whitney U	P
	$\bar{X}$ (N)	$\bar{X}$ (N)	df=46	
Proportion of time probing	0.44(1986)	0.21(1001)	73	<0.001
Proportion of successful probes	0.064(1986)	0.126(1001)	146	<0.005
Prey/hour	10.1(1986)	10.4(1001)	271	0.72

TABLE III-4: Foraging sites and techniques used by females of three experimental flocks, before, during, and after the temporary removal of males, and the behaviour of females in control flocks during the same time periods.

	Time relative to removal			Kruskal-Wallis test (df=2)	
	Before	During	After		
	$\bar{X}$ (N)	$\bar{X}$ (N)	$\bar{X}$ (N)	H[1]	P
Experimental flocks (8 females)					
Relative foraging height[2]	0.70(232)	0.40(297)	0.72(176)	16	0.0004
Distance to trunk[3]	0.65(445)	0.34(567)	0.69(338)	16	0.0004
Proportion of time on trunk	0.02(445)	0.13(567)	0.01(338)	15	0.0006
Proportion of time probing	0.48(445)	0.29(567)	0.53(338)	13	0.0018
Number of prey per hour	8.3(445)	7.4(567)	9.2(338)	3.4	0.18
Proportion of success. probes	0.05(373)	0.08(431)	0.06(242)	8.0	0.019
Control flocks (8 females)					
Relative foraging height	0.70(22~~7~~3)	0.70(104)	0.70(158)	0.23	0.89
Distance to trunk	0.62(432)	0.69(314)	0.69(304)	5.2	0.08
Proportion of time on trunk	0.02(432)	0.01(314)	0.01(304)	1.2	0.54
Proportion of time probing	0.49(432)	0.52(314)	0.55(304)	0.82	0.66
Number of prey per hour	9.1(432)	8.7(314)	7.3(304)	1.1	0.59
Proportion of success. probes	0.06(348)	0.05(227)	0.04(228)	1.9	0.38

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[1] Estimated with the chi-square distribution,

[2] 0=on ground, 1=on top of tree,

[3] 0=on trunk or main appendage, 1=on branch tip.

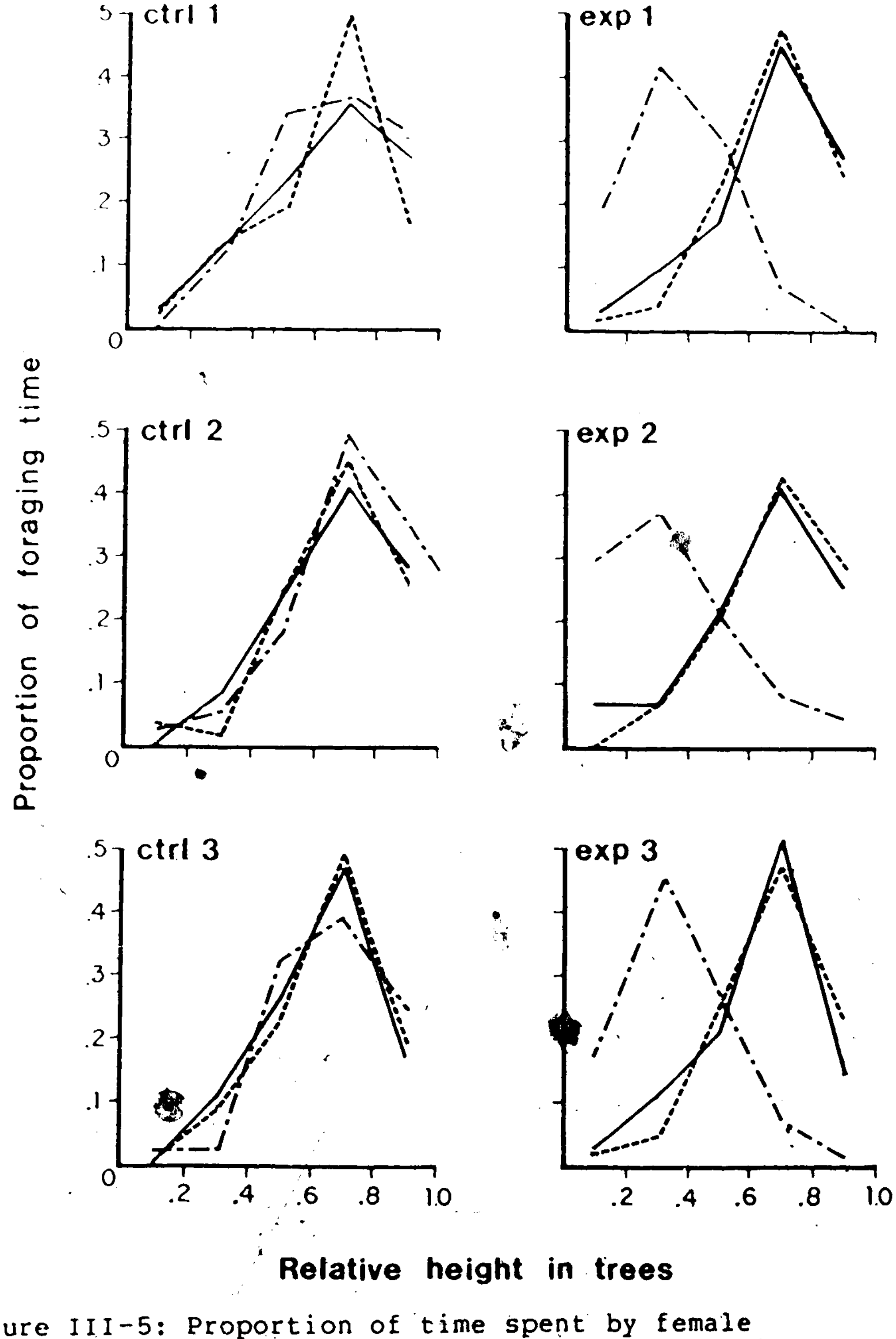

Figure III-5: Proportion of time spent by female black-capped chickadees foraging at different heights before (———), during (—·—·—), and after (------) males were removed from flocks. The total number of observations for each frequency polygon is more than 40.

the absence of males (*U*-tests, 1-tailed, *df*=15, P>0.10 in all the comparisons). However, during the absence of males, all experimental females foraged lower than controls, closer to the trunk, used trunks more often as a foraging substrate, probed less often, and increased their probing success (*U*-tests, 1-tailed, *df*=15, P<0.033 in all comparisons). No difference was found between the feeding rate of control and experimental females (*U*-test, 2-tailed, *df*=15, P=0.23). Conclusions remain the same if flocks, instead of individual females, are taken as independent observations; experimental flocks foraged lower, closer to the trunk, more often on the trunk, spent less time probing, and had a higher probing success than control flocks (*U*-tests, 1-tailed, *df*=5, P=0.05). Feeding rates did not differ between control and experimental flocks (*U*-test, 2-tailed, *df*=5, P=0.10).

All female flocks did not forage on all tree parts as did unmanipulated flocks. Instead, they concentrated on the lower parts of the trees, leaving the upper levels relatively vacant (Fig. III-6). Thus, females became more like males in their foraging during the removal period. However, they did not become identical (Table III-4, top center, compared to Table III-5, left). Females still foraged higher than males, farther from the trunk, less often on the trunk. Females spent more time probing and had lower probing success than the males of the experimental flocks (*U*-tests, two-tailed, *df*=15, P<0.003 in all

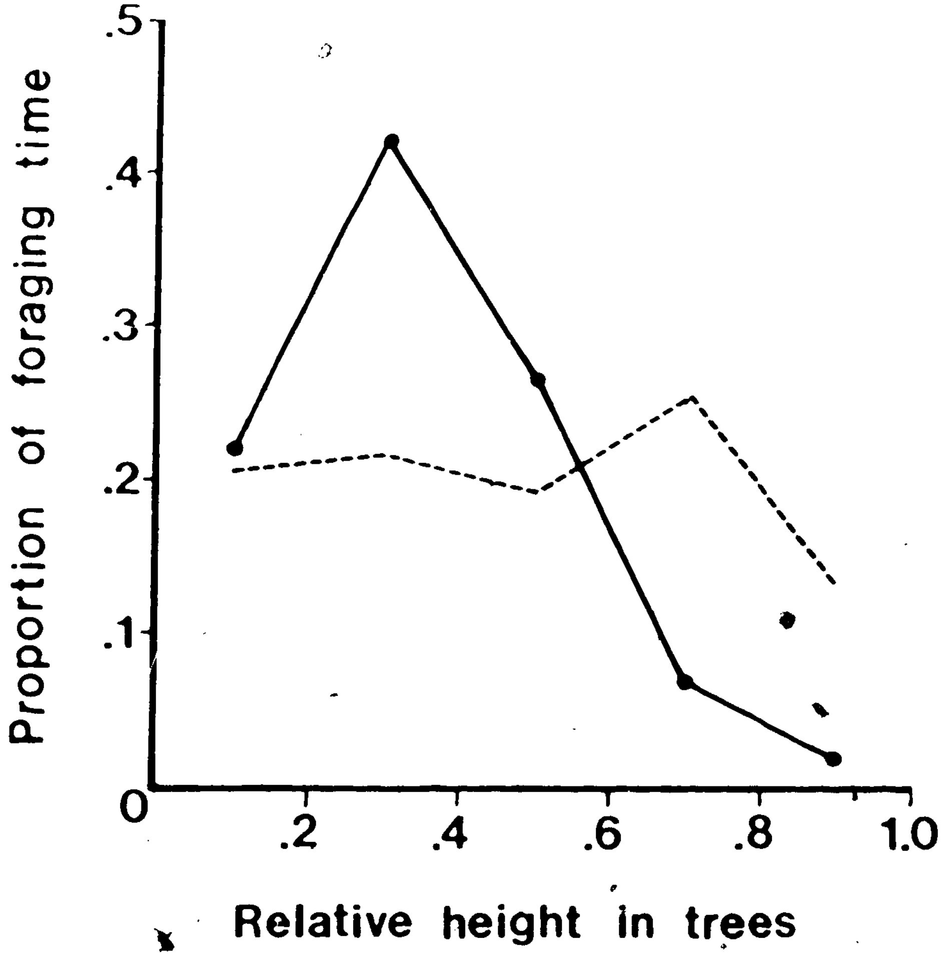

Figure III-6: Proportion of time spent by all flock members (pooled data) at different heights in undisturbed flocks (------) and in flocks without males (——). $X^2=118$, df=4, $P<0.001$. Expected frequencies generated from experimental flocks with males, observed frequencies from observations of experimental flocks without females (N=281).

TABLE III-5: Foraging sites and techniques used by the eight males of the three experimental flocks, before and after the removals. N represents the number of foraging observations.

	time relative to removal				Mann-Whitney	
	Before		After		U	P
	$\bar{X}$	(N)	$\bar{X}$	(N)	df=14	
Relative foraging height[1]	0.29	(169)	0.32	(137)	23	0.38
Distance to trunk[2]	0.23	(329)	0.27	(260)	22	0.33
Proportion of time on trunk	0.29	(329)	0.19	(260)	16	0.10
Proportion of time probing	0.13	(329)	0.16	(260)	25	0.51
Number of prey per hour	10.1	(329)	8.22	(260)	20	0.23
Proportion of success. probes	0.16	(279)	0.13	(193)	22	0.33

[1] 0=on ground, 1=on top of tree,
[2] 0=on trunk or main appendage, 1=on branch tip.

comparisons). Also, experimental females tended to have a lower feeding rate than males (*U*-test, two-tailed, *df*=15, P=0.083).

Males from the three experimental flocks joined their flocks within 1 d of release and foraged again in the lower parts of the trees, and closer to the trunk (Table III-5). Males also regained their dominance over females; all 25 male-female interactions observed in experimental flocks after the release of males were won by males.

DISCUSSION

Niche differences among populations

In aspen, male chickadees foraged differently from females. Similar patterns may have occurred in willows, but sample sizes were too small to demonstrate it unequivocally. Glase (1973) also found differences between foraging sites of male and female black-capped chickadees, and, to a lesser extent, adults and young, but he did not attempt to measure differences in their foraging methods. In Glase's (1973) study, males foraged higher than females, as opposed to birds in this study.

How to explain this difference in behaviour between sites? Several factors are probably involved (e.g. canopy structure, plant and insect species, climate, predators). It is difficult to compare the habitats adequately, but it is worth noting that the main predators differ between the two locations. In the northeastern United States, where Glase did his study, sharp-shinned hawks (*Accipiter striatus*) are the primary wintering predators on chickadees (Terres 1980). In contrast, the main chickadee predators in Alberta in winter are probably northern shrikes (*Lanius excubitor*) and perhaps hawk owls (*Surnia ulula*; Salt and Wilk 1966, personal observation). Weasels (*Mustela erminea*) possibly prey on chickadees in roosting cavities, but their effect on chickadees' foraging behaviour is probably small. Differences in the hunting behaviour of shrikes and hawk owls could influence the relative predation risk associated with foraging high or low in trees (e.g. shrikes at Meanook apparently directed most of their attacks high in trees, whereas *accipiter* hawks seem to hunt in all canopy zones). Of course, a detailed foraging study across different geographic areas would be necessary to help determining the causes of niche variation across different areas.

Intersexual competition

The foraging behaviour of individual birds following the removal of members of their flock ("competitive release": Alcock 1984) provides far more convincing evidence of intraspecific competition for foraging sites within flocks than the mere observation of consistent differences in the foraging sites of members of unmanipulated flocks or between populations (Alatalo *et al.* 1986).

Except for the work of Peters and Grubb (1983), field experiments on inter-sexual niche differences are virtually absent. These authors removed male downy woodpeckers (*Picoides pubescens*) and showed that the niche of females niche shifted towards that of males. However, the niche of males did not change in the absence of females. They concluded that males excluded females from some resources, by means of dominance. In another removal experiment, Ekman and Askenmo (1984) concluded that adult willow tits (*P. montanus*) in winter flocks excluded yearlings (subordinates) from areas best protected against predators, the yearlings shifted to the adult's niche in the absence of the latter.

What prompted female and male chickadees to forage in different ways? The removal experiment reported here showed that ~~the~~ foraging sites of females were largely a result of the presence of males, suggesting intersexual competition for winter resources. Female chickadees showed a great flexibility in their foraging behaviour, not only by moving rapidly to lower parts of the trees in the absence of males, but also by decreasing their percentage of time probing and increasing their percentage of successful probes (possibly in direct response to different resources). Despite this, the feeding rate of females did not change in the absence of males. Since the energetic content of prey from different sites was unknown, it was unfortunately not possible to determine whether male removals changed the energy intake of females. However, removals apparently lowered the cost of foraging to females (assuming that probing demands more energy than visual search for prey).

Interference or exploitation competition?

Depending on whether the niches of females and males have different "values", and on how specialized females and males are, either interference or exploitation competition will operate in chickadee flocks.

Glase (1973) did not compare the costs and benefits associated with niches of female and male chickadees. He suggested, on the basis of the slight sexual size dimorphism in chickadees, that females have become specialized in using different zones than the higher ranking males. This niche differentiation would lead to reduced intersexual interference and better foraging efficiency for the group as a whole (Glase 1973). This kind of argument has also been invoked by several authors to explain sexual niche differentiation in hawks, owls, woodpeckers, warblers, and icterids (reviewed by Morse 1980).

Another view states that interference (or dominance), rather than exploitation competition (or specialization), acts as a proximal factor causing niche separation, and has been proposed on the basis of very low size dimorphism in some species (e.g. Ligon 1968a), frequent agonistic encounters between putative competitors (Schneider 1984), or the use of apparently better areas by dominants (Schneider

1984). Peters and Grubb (1983) provided experimental evidence supporting this view (see above).

Although I have no experimental evidence to distinguish between interference and exploitation competition, two observations suggested that interference competition prevailed in my population (i.e., males excluded females from certain sites). First, females showed flexibility in their foraging behaviour; they were not restricted to their niche by specialization. Changes in behaviour were observed not only in response to the removal of males, but females also changed their probing rate when they visited portions of trees typically used by males. The relationship between foraging height and probing rate in both sexes suggests that differences in foraging method were related to a heterogenous distribution of prey types across heights, rather than morphological specialization (e.g. bill size, shape).

A second observation supporting interference competition was that during the removal period females did not use all parts of trees exploited when both sexes were present, but rather abandoned their normal areas and concentrated their search in the lower parts of the trees, where males were usually found. The latter point suggests that it was more profitable for all chickadees to forage lower in poplar woods.

Despite the flexible behaviour of females and their preference to forage in areas usually occupied by males, specialization may have played a role in their search for food, as they did not behave exactly like males in the absence of the latter. Possibly, because females spend much more time in the higher parts of trees, they may become more skilled than males in finding prey there.

Foraging site payoffs

Do male chickadees use "better" foraging sites than females? Since high social rank generally equates priority to limited resources (Wilson 1975, Gauthreaux 1978, Kaufmann 1983), it is reasonable to suspect that males may secure the best foraging sites. Potential costs possibly higher in the foraging area of females include: 1) a lower foraging efficiency, and 2) increased exposure to predators. Most published studies simply discuss whether specialization or interference leads to the niche separation of females and males; no study on sex dimorphism in foraging niches of birds has documented costs and benefits associated with the niches of females and males. However, Ekman (1987) showed a number of advantages to the foraging niche of adult willow tits compared to that of young, in terms of foraging efficiency and avoidance of the main local predator, the pygmy owl (*Glaucidium passerinum*). Ekman *et al.* (1981) also showed that young willow tits suffered a higher mortality rate than adults.

In my population, four observations suggest that males exploit better food and/or cover against predators than females. First, observations at feeding stations adjacent to the main study area showed clearly that males had priority of access to resources, as found in several other chickadee studies (Hamerstrom 1942, Odum 1942, Hartzler 1970, Glase 1973, Smith 1976, 1984). Thus, by means of overt aggressiveness, males can secure a limited, defensible resource. This is further supported by frequent intersexual agonistic encounters in foraging chickadee flocks, which occurred primarily in areas typically used by males, even though most interactions away from feeders did not directly involve a prey item. A second relevant observation is that even though females had a similar feeding rate as males, females had to make a larger number of unsuccessful probes. Therefore females invested more time and energy per prey capture, and if prey eaten by the t~~wo sexes we~~re equivalent energetically, females would experience a lower return rate while foraging than males. Moreover, assuming that probing for food and scanning for predators were mutually exclusive activities, females were more likely to be taken by surprise by predators, since they spent less time scanning.

A third factor suggesting that males exploited preferred areas is that exposure to the main local diurnal predators of wintering passerines (northern shrikes and hawk owls) was potentially higher for females, since they foraged mainly in the upper parts of the trees, where northern shrikes (Bent 1965, Cade 1962, 1967) and hawk owls (personal observation) usually hunt. A last, and perhaps most critical point is that females suffered higher mortality than males in the second year of this study (see Chapter II).

A difficulty with this experiment is that sex and social rank are confounded, i.e. 'female' and 'subordinate' being nearly equivalent categories. Similarly, age and rank were somewhat confounded in Ekman and Askenmo's study, all adults dominating all young (Barrette and Vandal 1986). However, a combination of the results from the willow tit study (Ekman and Askenmo 1984) and the present one give some insight as to whether sex, age or social rank *per se* is the main proximal factor that leads to differences in observed foraging niches of titmouse flock members. In both studies, socially subordinate birds foraged in different areas than dominants, even though the sex and age of those subordinates varied between studies. This suggests that social dominance, rather than sexual specialization or lower foraging ability of young, is the chief proximal factor leading to differences in observed foraging behaviour among members of willow tit and black-capped chickadee flocks, a premise of the interference hypothesis.

In spite of the possible short-term advantages of the male's niche in this study, it would be necessary to collect long-term data on winter survival rates of females and males to measure the ultimate adaptive value of exploiting a given niche, and to determine whether sexual niche differentiation is evolutionarily relevant.

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IV. SITE-RELATED DOMINANCE AND HABITAT USE AMONG WINTER FLOCKS OF BLACK-CAPPED CHICKADEES

INTRODUCTION

A crucial attribute of territorial behaviour in birds is that owners socially dominante intruders within a topographical area from which they exclude intruders (Brown and Orians 1970, Brown 1975, Kaufmann 1983). In contrast, social rank in hierarchical systems is typically independent of location, and members of a social group share a common home range (Wilson 1975). An intermediate situation occurs, in which birds shift social rank according to their location, but nevertheless tolerate "intruders" in their area of dominance (or "dominion": Brown 1975). This latter pattern has been described in several bird species (Odum 1941, Colquhoun 1942, Brian 1949, Michener 1951, Brown 1963, Willis 1968, Glase 1973, DeLaet 1984).

A large number of studies of agonistic behaviour in flocking birds has focussed on dominance relationships within groups (reviewed by Schein 1975, Wilson 1975 and Gauthreaux 1978). However, very little is known about the relationships between adjacent social groups, perhaps because of the infrequent encounters between groups, or the lack of recognition of individual groups within large, but temporary aggregations. Nevertheless, interactions between social groups of birds have been illustrated in some studies of communal (or "group") territoriality between flocks of Australian magpies, *Gymnorhina tibicen* (Carrick 1963), acorn woodpeckers *Melanerpes formicivorus* (Koenig 1981, Hannon *et al*. 1985), Australian noisy miners *Manorina melanocephala* (Dow 1977), antbirds (Aves:Formicariidae; Munn and Terborgh 1979), and titmice (Aves: Paridae: Odum 1942, Dixon 1963, 1965, Condee 1970, Hartzler 1970, Glase 1973, Ekman 1979, Nowicki 1983, Smith 1984). Such spacing between groups can set an upper limit on population size by restricting access to breeding resources (Carrick 1963, Dow 1977, Hannon *et al*. 1987) or resources for survival outside the breeding season (Ekman *et al*. 1981).

Despite the numerous studies that regard winter flocks of black-capped chickadee as territorial (Odum 1941, 1942, Hartzler 1970, Glase 1973, Nowicki 1983, Smith 1984), little quantitative data has accumulated on the relationships between flocks, and most of the information comes from populations using artificial bird feeders. Here, I report on the relationship between the use of home range in winter and agonistic behaviour between members of contiguous flocks of black-capped chickadees in food-supplemented and control populations. I also discuss the economics of flock-spacing and allocation of resources for survival among winter flocks.

STUDY AREA AND METHODS

This study was conducted at the Meanook Biological Station ($54^{\circ}37'$N, $113^{\circ}20'$W), near Athabasca, Alberta, Canada, in the winters 1985-86 and 1986-87. The study area was a 5 km^2 mosaic of poplar (*Populus tremuloides* and *P. balsamifera*) woodland interspersed with fields (20% of the area), and stands of willows (*Salix spp.*) of up to 4 ha. A woodland area of 2.6 km^2 (private and Crown land) was provided with feeders filled with sunflower seeds, and 1.9 km^2 (wildlife area) was not disturbed by feeders. Nine feeding stations were scattered in the feeder area in 1985-86, and 14 in 1986-87. The feeder and control areas were separated by grain fields to limit the movement of birds, especially from the control area to the feeder area.

In both winters, virtually all the chickadees on the study area (>95% of approximatively 350 each winter) were captured in mist-nets and individually marked with coloured leg bands. Strips of electrician's tape were stuck to the bands to make "flags" that enhanced the visibility of the colour combinations.

Flock home ranges

In the two winters, I determined the membership of each flock from August to November when flock membership stabilized). When at least three birds were consistently seen together, they were considered a flock. Also, I did not record a sighting of a flock unless I positively identified at least three known members.

I mapped sightings of each flock at least once a week (four to five times a week during most of the winter). Sightings were recorded daily on maps of the study area (scale 1:7500) that were based on aerial photos. The accuracy of the sightings was about ±25 m, depending on the distance of known landmarks. A transparency with a 50 m grid (on scale) was put on each daily field map to code the locations of the sightings. When I was observing a flock, I recorded its location once every 5 min, sometimes for up to 3 h, but most often for less than 15 min. Such a short interval between observations probably resulted in autocorrelated sightings (Swihart and Slade 1985, Ford and Myers 1981), but I assume this is not critical here, since I used minimum convex polygons instead of a probabilistic home range model in this study.

I determined the home range of 20 flocks in the control area in 1985-86, from October to March, and 22 in 1986-87. I also determined the home range of "feeder" flocks in the two years, but only before they started to use supplemental food. I mapped the home ranges of 13 "feeder" flocks in

1985-86, and 18 in 1986-87. I used the flock home ranges primarily to determine the location of encounters between flocks relative to the center of their home ranges. The latter information was used to examine site-related dominance among flocks (see below).

Site-related dominance

When two or more flocks were found together (either in the control or feeder area), I recorded the winner and the loser of all agonistic interactions between members of different flocks. I classified the interactions into four types: displacement, chase, unsuccessful attempt to displace a bird, and waiting by one bird until another has left the food location (see Dixon 1965, Smith 1984). When a sequence of several consecutive chases or displacements involving the same two birds occurred, only one interaction was recorded. Thus, I considered all interactions as independent.

I observed dominance interactions primarily in the feeder area, where several flocks were often using feeding stations at the same time. I also recorded all interactions between members of neighbouring flocks on the control area, whenever two or more flocks were found together. In three cases, I induced grouping of two flocks in the control area by attracting a flock to a feeder, then carrying the feeder, followed by the flock, to the neighbouring flock's range, to attract the second flock. These artificially induced encounters lasted between 30-60 min. The location of all encounters between flocks was recorded on daily field maps.

Finally, I recorded all agonistic interactions between members of flocks (at and away from feeders) to obtain dominance hierarchies within each flock (see Chapter II).

Agonistic defence of space between flocks

If flocks agonistically defend a communal territory, one would predict that when two or more meet, individuals will direct relatively more aggressiveness interactions towards members of "intruding" flocks than towards members of their own flock. To determine whether members of the study flocks behaved this way, I noted all individuals that were displaced or chased by the most dominant bird of the flock closest to the geometric center of its range (resident flock). This was done only in 1985-86 with flocks from the control area, away from feeders. Observations at feeders were not included, because ~~the~~ frequency of interactions of all birds with the most dominant bird was presumably dependent of the frequency of use of the feeder. Use of feeders was highly variable among individuals.

This method generated frequencies of attacks on "residents" and "intruders" that could be compared to the null hypothesis that target birds were selected independently with respect to flock membership. I concentrated on the most dominant resident bird so as to standardize the focal bird's rank for all observations, and because the most dominant flock member is the only individual that initiates all its interactions.

RESULTS

Flock composition and social organization

Members of each flock foraged together throughout most of the winter in the control area (see Chapter II). However, flocks did not always forage as single units in their home range; in 1985-86, 22% of the 578 social groups encountered were composed of more than one flock, and 20% of the 526 groups in 1986-87. I did not consider these large groups as "flocks" because they never lasted for more than a few hours, in contrast to true flocks. In the feeder area, chickadees were nearly always in large groups in the vicinity of feeding stations. These groups generally included resident flocks and birds from adjacent woodland that were drawn in the feeder area. The composition of large groups of chickadees in the feeder area was unstable and dependent on the arrival and the departure of flocks at feeding stations.

Habitat use and overlap between flocks

Supplemental food resources were not exclusively used by one flock, but shared by all flocks that discovered feeding stations (Fig. IV-1). In the control area, a mean number of 162 sightings per flock was made in 1985-86

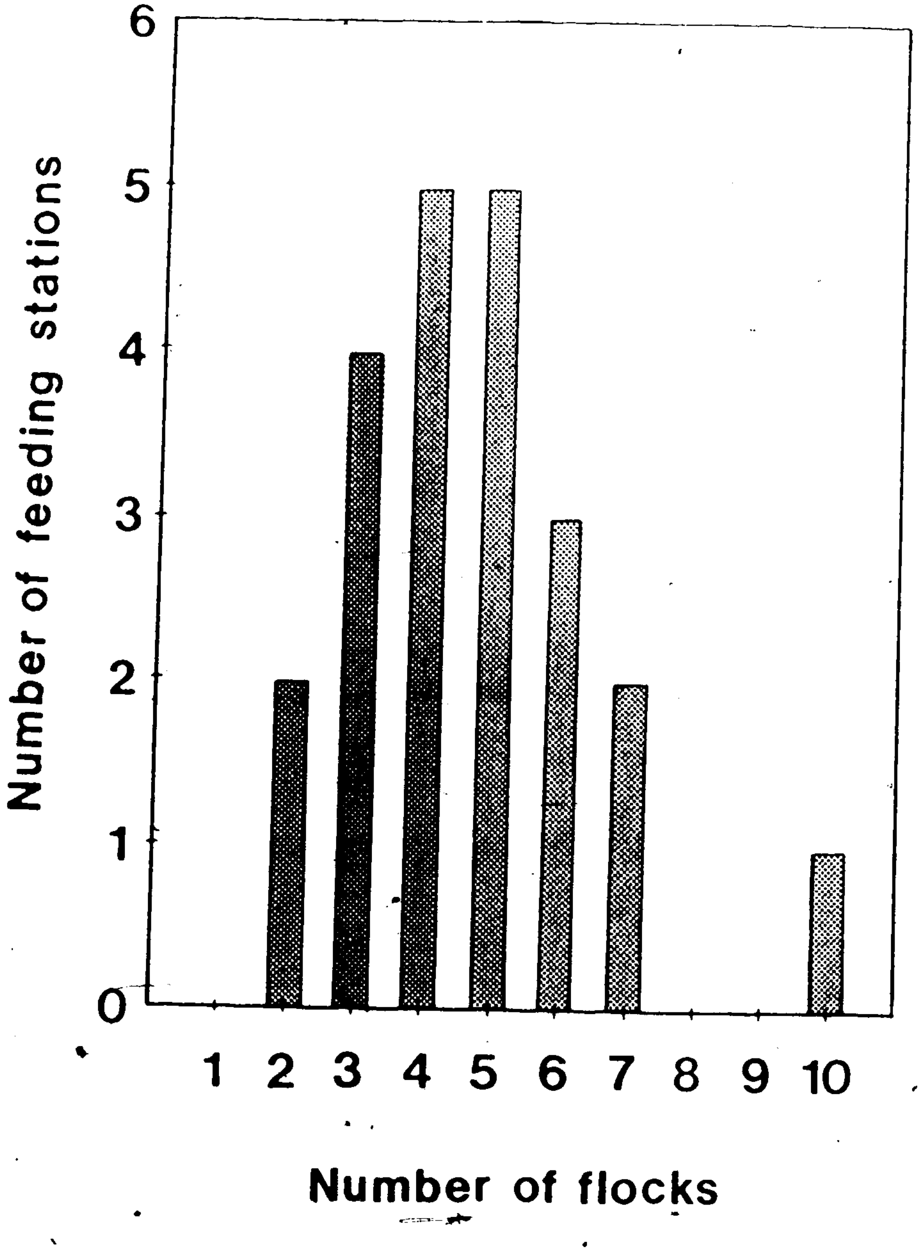

Figure IV-1: Numbers of flocks seen at each feeding station, throughout the winter. All the ~~feed~~ing stations represented were used by birds for at least one week. Data pooled from 1985-86 and 1986-87 feeders.

(SE=30, n=20) and 94 sightings per flock in 1986-87 (SE=23, n=25). Also, at least 50% (1985-86) and 33% (1986-87) of 0.25 ha grid squares in woodland were used by two or more flocks over the winter (Fig. IV-2). Since members of free-roaming flocks usually occupied an area 3-4 times larger than a grid square (personal obs.), one can rule out the possibility of undetected "core areas" within grid squares.

Estimates of overlap between winter home ranges do not contain information on the dispersion pattern between actual flocks at any time: despite their overlapping ranges, flocks may have avoided each other ("group space": Brown and Orians 1970). Mutual avoidance was unlikely in this population, as foraging groups of up to five different flocks were regularly observed. The maximum size of these large temporary groups reached 50 individuals in 1985-86, and 31 individuals in 1986-87.

The number of flocks seen on a particular 1.0 ha block (four grid squares) was positively correlated with the number of chickadee sightings on this block (Spearman's $r=0.56$, $n=200$, $P<0.001$ (1985-86) and $r=0.54$, $n=194$, $P<0.001$ (1986-87)). The number of flocks seen at a given location (without feeders) presumably increased logarithmically as a function of the number of sightings on this area, because the estimated size of each home range increases logarithmically as a function of the number of sightings (Odum and Kuenzler 1955). As a result, I made the following

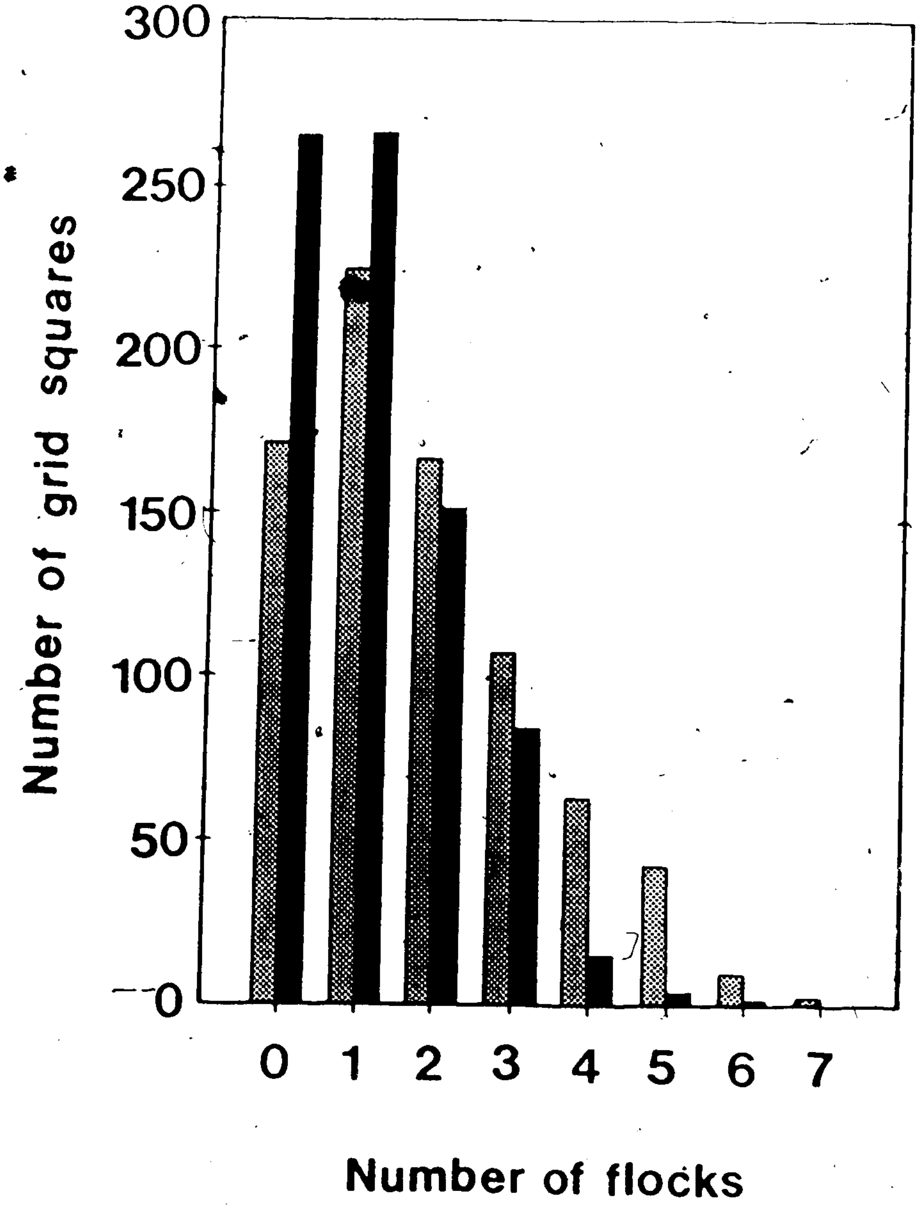

Figure IV-2: Frequency distribution of the number of flocks observed on 0.25 ha grid squares in the undisturbed area, in winters 1985-86 (hatched bars) and 1986-87 (solid bars). Only squares containing woodland were included.

transformation to correct the data for the frequency of sightings on each grid square where I observed chickadees:

$$\text{Overlap Index} = \frac{2 \times \text{Number of flocks}}{\ln(\text{Number of sightings} + 1)}$$

A factor of 2 was introduced to make index values on Figure IV-3 easier to read. The "overlap index" obtained was uniform over the control area in the two winters (Fig. IV-3), and normally distributed (Kolmogorov-Smirnov one-sample tests, two-tailed, $P > 0.05$ in the two winters). The mean overlap index in the first winter was higher than in the second winter (12.7 *vs.* 10.6 respectively, paired t-test, two-tailed, $df = 188$, $P = 0.001$), suggesting that annual variation in spacing can occur among chickadee flocks.

<u>Site-related dominance</u>

In the feeder and control areas, the rank of chickadees within their flock remained constant, regardless of the location of the flock. However, in groups of two or more flocks at a feeding station (either on control or feeder area), agonistic interactions between birds of different flocks were won more frequently by members of the flock closest to the center of its home range ("resident" flock; Table IV-1). This was true for all flock members, and most dominant birds of flocks farther from the center of their

1985-86

3	[illegible]	1	2	2					0	0		0
3	1	1	4	2	3	3	3	2	2	1	3	3
2	2	2	3	5	4	3	2	4	2	3	3	
3	1	2			3	3	3	2	3	4	3	
3	[illegible]	1		2	3	3	2	2	3	4	3	
2	2	1		3	4	4	2	2	3	3	2	
4	2	[illegible]		2	4	4	3	3	3	3	3	
2	[illegible]	[illegible]		3	5	3	3	4	3	3	3	
2	2	[illegible]		4	3	2	3	3	3	3	2	
2	4	4		5	4	2	4	5	3	3	2	
3	3	3	5	4	4	2	3	5	4	2	3	1
3	4	4	6	3	3	3	1		2	2	2	2
3	4	2	1	2	3	2	1		1		3	2
4	3	1	2	3	3	1	2		2		3	2
4	3	2		2	3	1	3		1		3	3
	3	2	2	3	2	2	3	1	1		1	
	2	1	3	3	4	3	2	1	2	1		2
1	1	2	0	4	3	1	1	1	1			3

1986-87

3	3	4	1	2					2	1	2	2
4	3	3	2	1	1	1		1	1	1	2	3
3	2	1			2	1	2	3	2	1	2	
6	1	3				3	3	3	2	2	2	
3	2	2		1	1	2	2	2	2	3	1	
3	2	2		1	2	2	2	4	4	2	1	
4	2	2		2	1	3	3	4	2	3	2	
2	2	2		1	3	2	3	5	0	2	2	
2	2	3		1	3	3	4	3	1	2	3	
5	1	3	2	3	2	3	3	3	3	4	0	
6	3	2	2	2	3	4	4	6	2	3	3	1
4	1	4	0	3	4	3	1		2	0		1
		2	2	2	2	1	2					2
2	2	0	1	3	2	1	1		1			0
0	2	0	0	4	3	3	1		1		0	0
3	4	1	4	1	2	3	2	3	2		0	
1	4	3	2	1	1	2	2	1	2		0	
1	1	4	2	1	2	1	2	2	1	2	2	0

Figure IV-3: Index of overlap between flocks in different locations in the control area. Each value represents a corrected estimate of overlap on a grid square of 1.0 ha (2 X number of flocks / ln(number of sightings + 1). Values have been reduced to one significant digit for readability. Blank areas correspond to grid squares that did not contain woodland or that were not visited by the observer.

TABLE IV-1: Site-related dominance between flocks of black-capped chickadees at feeding stations. The resident flocks were the ones closer to the center of their home range at the time of the observations. Binomial tests are two-tailed and the null hypothesis is that the birds of intruding and resident flocks are equally likely to win agonistic interactions (binomial p=0.5). Numbers of birds in each flock are in parentheses.

Date	Resident flock	Intruding flock	No. of victories		Binomial test
			Residents	Intruders	
860126	J(7)	W(7)	57	2	P <0.001
860126	J(7)	K(8)	28	4	P <0.001
860202	E(9)	A(5)	32	10	P =0.001
860202	E(9)	G(12)	43	16	P <0.001
860205	G(12)	F(10)	122	44	P <0.001
861030	F6B(6)	F5(8)	12	4	P =0.077
861104	G(13)	A(5)	19	12	P =0.281
861106	F1B(6)	O(6)	46	7	P <0.001
861120	F3(8)	F3B(?)	31	8	P <0.001
861121	F8A(5)	F6A(4)	15	3	P =0.008
861202	M(6)	F(6)	10	2	P =0.039
861203	K(11)	L(12)	86	69	P =0.199
861208	F8B(6)	C(7)	5	0	P =0.063
861215	K(10)	J(8)	16	14	P =0.855
861216	F8A(4)	F6A(4)	3	2	P =1.000
861218	F4A(7)	F5(5)	9	1	P =0.025
861228	F5(5)	F6C(7)	11	9	P =0.824
861228	F6B(6)	F5(5)	10	3	P =0.092
870101	F4B(5)	F4A(7)	13	6	P =0.167
870101	F4B(5)	F5(5)	18	3	P =0.002
870101	F4A(7)	F5(5)	9	0	P =0.004
870103	F8A(4)	F6A(4)	3	3	P =1.000

ranges ("intruder" flocks) were often displaced by lowest ranking birds of the resident flock.
However, because of the large number of birds in 'composite flocks' and the temporary nature of these groups, it was not possible to observe enough interactions to generate a "pooled" dominance hierarchy of all birds of 'composite flocks'.

Site-related dominance was apparently not an artifact of the use of feeders. In the control area in "natural" encounters away from feeders, birds of resident flocks also won agonistic interactions against birds of intruding flocks more frequently than expected (50 wins *vs.* 12 losses by birds of resident flocks in 1985-86, binomial test, two-tailed: $P<0.0001$; 61 wins *vs.* 10 losses in 1986-87, $P<0.0001$).

Agonistic defence of space between flocks

Even though birds of a resident flock were socially dominant to members of intruding flocks and thus were theoretically able to displace or chase intruders, they did not direct more agonistic interactions towards members of intruding flocks than towards the members of their own flock, at least in 1985-86 (Table IV-2). All interactions in Table IV-2 were displacements; no chases were observed. Surprisingly, data from the 1985-86 winter shows a trend opposite to the one expected if flock members communally defend a territory; the most dominant males were more

TABLE IV-2: *Individuals displaced by the most dominant bird in encounters between flocks of chickadees in the control area, 1985-86.*

Case	No. of flocks	No. of birds	Flock mates	Members of other flocks	Interactions with Flock mates	Interactions with Members of other flocks	Binomial test (2-tailed)[1]
1	3	35	12	22	12 (7.1)[2]	8 (13)	P=0.032
2	3	30	12	17	11 (6.2)	4 (8.8)	P=0.016
3	2	20	10	9	4 (3.2)	2 (2.8)	P=0.69
4	2	18	9	8	15 (11)	5 (9.4)	P=0.07
5	3	31	12	18	6 (2.8)	1 (4.2)	P=0.046
6	4	42	10	31	3 (1.7)	4 (5.3)	P=0.37

[1] Probability that the null hypothesis (that interactions initiated by the most dominant bird are directed randomly towards its neighbours) is true:

[2] Expected frequency

aggressive towards members of their own flock than predicted by chance or by the hypothesis of agonistic spacing between flocks. Whether this was because the members of the same flock were closer to each other, and consequently more likely to interact, than members of different flocks is unknown. Overall, members of different flocks tolerated each other, at least away from feeders. Although control flocks showed site-related dominance (see above), they did not seem to use their status to completely exclude intruders.

DISCUSSION

Home range overlap

Pitelka (1959) and Schoener (1968) suggested that territoriality is an ecological rather than behavioural concept and that consequently, only animals with non-overlapping home-ranges should be called territorial. If one agrees with this definition, then chickadee flocks during the two years of this study, were not territorial, in either food supplemented or control areas. The uniform degree of overlap between flocks, the apparent absence of well-defined areas of concentrated use in their home ranges, and the high frequency of foraging groups consisting of several flocks suggested that chickadees were using the woodland rather uniformly.

This is the first study that documents broad spatial overlap between winter home ranges for North American parids. Authors of previous studies on Carolina chickadees, *Parus carolinus* (Dixon 1963), mountain chickadees, *Parus gambeli* (Dixon 1965), tufted titmice, *Parus bicolor* (Condee 1970), and black-capped chickadees (e.g. Hartzler 1970, Glase 1973, Smith 1984) have all stated that parids of their studies were using exclusive ranges. The situation is similar in Scandinavia, where willow tits (*Parus montanus*) and crested tits (*Parus cristatus*) use exclusive feeding territories (Ekman 1979, Ekman *et al*. 1981). In contrast to North American and Scandinavian parids, great tits (*Parus major*) in Japan have been described as non-territorial (Saitou 1979), as their home ranges overlapped considerably and they often united in large, but temporary groups of several flocks.

How does one explain the differences in spacing among flocks between this study and others on black-capped chickadees? One possibility is simply that habitat structure, food abundance, weather, and other factors may differ between areas and among years. It is also possible that this difference is simply an artifact of the method by which home ranges were calculated. For example, the data here showed a positive correlation between the likelihood of observation (estimated by the number of chickadee sightings on a given area) and the number of flocks observed in an area. Thus the fewer observations made in an area, the more "territorial" a flock would appear if no correction is made for the number of observations. Since quantitative data on flock home ranges in previous studies of black-capped chickadees were few or even lacking, this may have contributed to the conclusion of other researchers.

Ranges of control chickadee flocks may overlap to give each flock access to more resources (e.g. food, shelter). However, this would be counterbalanced by the depletion of resources by other flocks foraging on one flock's range. Since there is an additional energetic cost to defending a territory (e.g. Brown 1964, Gill and Wolf 1975), the net "payoff" (costs/benefits) to flocks not defending a territory would probably be higher than the alternative tactic of defence, when resources are uniformly distributed. If resources are limited and distributed heterogenously, territoriality could be advantageous to birds that have a "high quality" resource near the center of their home range (Davies and Houston 1984). In this case, intrusion by other flocks could deplete these non-renewable resources more than could be compensated by the use of other flock ranges. If so, the cost of defence could be offset by the resources gained.

Resources in the control area were presumably more uniformly distributed than in the feeder area, so one would expect flocks to be more territorial in the feeder than in the control area. This was clearly not the case, since broad overlap occurred in both areas. One possible explanation is that "intruder pressure" varied in parallel to resource abundance and patchiness, which was highest in the feeder area. Clumped resources of high quality can attract considerable numbers of competitors, and the cost of excluding intruders may become higher than the value of the resource defended (Myers *et al*. 1979). This is especially true for wintering black-capped chickadees, because of their high densities. Thus, in the feeder area, flocks may have overlapped for different reasons than under natural conditions. Also, concentrated sources of sunflower seeds at feeding stations were practically unlimited, which presumably lowered competition for food among chickadee flocks, and in turn lowered the need for exclusive foraging areas. Unfortunately, the effects of food abundance and intruder pressure are hard to separate, as these two factors are often positively correlated (Davies and Houston 1984, but see Myers *et al*. 1979, and Mares *et al*. 1982). A cost-benefit model is further complicated by the effect of temperature: the relative cost of defence possibly increases when temperature decreases, since birds have to feed more and thus have less time for other activities. However, the "value" of food resources may also be higher at lower temperatures, making predictions about the relationship between weather and territorial behaviour difficult. Clearly, the qualitative model discussed above needs to be substantiated by quantitative data.

Site-related dominance

The site-related dominance observed here between chickadees of different flocks at feeding stations agrees with previous qualitative accounts of chickadee dominance at feeders (Odum 1941, Dixon 1965, Glase 1973). It also agrees partly with more recent and quantitative work on great tits in Belgium (DeLaet 1984), that showed that adult male's dominance status was dependent on the location of the feeders. However, she found that males less than one year old followed an "absolute hierarchical system" (i.e. social status independent on location).

Since other studies of site-related dominance in parids were made exclusively at feeding stations, one could argue that this phenomenon was a by-product of food supplementation. This was not the case in this study, since site-related dominance occurred at and away from feeding stations. Site-related dominance was not an early manifestation of spring territorial behaviour, as it was observed as early as October. Also, a large number of female and male flock members that did not stay to secure a breeding territory exhibited site-related dominance.

DeLaet (1984) argued that site-related dominance, and perhaps spacing, is influenced by climate, as it was most obvious in the mildest winters of her study. The present study was too short, and the two winters too similar in weather to produce enough data on yearly variation of spacing behaviour of chickadee flocks.

There is a possible interaction between food availability, temperature, and spacing behaviour. When food is not limiting, black-capped chickadees are perhaps less aggressive towards intruders in a colder winter, since they presumably have to spend more time foraging, and less time interacting socially. However, when food is scarce, flocks may need to defend the resources in their home range, in order to survive (Ekman *et al.* 1981), especially in colder years, when metabolic demand is higher (Perrins 1979). Chickadees survived more poorly in 1986-87 (see Chapter II), suggesting higher food limitation then. The apparently lower food availability in 1986-87 was accompanied by a narrower overlap between flock ranges, which is consistent with the model above. Temperature itself probably did not affect strongly spacing between flocks in this study, since it was similar in the two years (Chapter II). If flock territoriality occurs at all in this population, colder temperatures and/or food limitation seem necessary to induce it.

Agonistic defence of space between flocks

To have a complete picture of the territorial behaviour of a species, one has to document not only the degree of overlap between social units (Pitelka 1959), but also spacing behaviour *per se* (Kaufmann 1983). Even though members of a flock near the center of its home range socially dominated intruders in this study, it does not follow that flocks were defending territories.

Black-capped chickadee flocks have been described as hostile toward each other, based on the nature and intensity of vocalizations in encounters between flocks (Glase 1973, Nowicki 1983), or agonistic behaviour by the most dominant males of resident flocks towards intruders (Hartzler 1970). In the present study, however, I found no evidence for increased frequency of agonistic behaviour between members of different flocks, despite site-related dominance. One observation that failed to support active defence between flocks was that dominant males in 'composite' groups did not direct more aggressiveness towards intruders than towards members of their own flock (often, the reverse was true). Second, if flocks were mutually avoiding each other, one would expect large groups to be highly ephemeral. This was not the case, as 'composite flocks' sometimes lasted for several hours. Thus, besides overlapping broadly spatially, flocks of chickadees showed a high degree of mutual tolerance.

A growing number of accounts of the spacing behaviour of groups of non-breeding birds shows that there is a wide range of spatial organization across species, and perhaps even among populations of the same species. However, little is known about factors that influence the "decision" of non-breeding groups to defend a feeding territory. Predictions of cost/benefit models of territoriality should be tested in future studies of communal territoriality, to determine factors shaping the spatial organization of social animals and to examine the general concept of territoriality.

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V. CONCLUDING DISCUSSION

Numbers of black-capped chickadees do not continuously increase, despite their high fecundity (clutch size usually 6 8; Bent 1946). Perrins (1979) emphasized the potential importance of mortality of young in the first months of their lives, presumably because of food shortage and predation (Perrins 1979). This source of mortality, as well as fall mortality, is poorly documented for black-capped chickadees. However, summer and fall mortality of chickadees seem to contribute little to year-round mortality, especially in young, since the number of chickadees in early winter was still substantially larger than the number of breeders in the two years of my study, and in all year-round studies of chickadees published so far (Odum 1942, Glase 1973, Smith 1967, 1976, 1984). The sharp decline of the number of individuals in spring (mostly winter subordinates), combined with the results of the spring removal experiment, suggested that competition for territory acquisition led to the disappearance (and presumably death) of large numbers of young.

While territoriality was probably the process that limited the number of breeders, winter social dominance was clearly involved in determining which individuals bred. Adults, which dominated young, nearly always secured territories; as a result, the only breeding opportunities left to yearlings were vacancies created by death of adults. This is where social status in yearlings had a most obvious effect: having a high social status in winter considerably increased the probability of acquiring a breeding territory. This observation is by no means new, as Glase's (1973) work on black-capped chickadees led to the same conclusion. However, Smith (1984) reported a somewhat different system, in which unmated low ranking individuals acted as "floaters" that rapidly mated with dominant birds that lost their mate, thus gaining a higher status than already-mated birds of intermediate rank. Floating behaviour of these subordinates was regarded as a frequency-dependent, evolutionary stable strategy. Since only four chickadees behaved as "winter floaters" in Meanook, this pattern may be of limited occurrence. Contrary to a "mixed strategy" explanation, results of this study suggest that subordinates behave as "hopeful dominants" (West Eberhard 1975), i.e. they expect to become dominant later in life, a status that they automatically acquire relative to new young, as soon as they pass their first breeding season.

In this study, I dichotomized the observations on the outcome of dominance in spring: birds established a territory or failed to do so. One could argue that to get a finer-grained analysis of correlates of dominance, I should follow breeders well into summer, to get another measure of fitness such as fledging success. Although intuitively appealing, this idea poses at least one major problem: one would have to control for age effects and thus separate the analysis into pairs of yearlings and pairs of adults. It is very rare that two or more pairs of the same age from the same flock breed, thus opportunities for comparisons would be rare.

Even though territory acquisition best reflects the effects of social dominance in chickadees, it is by no means the only way in which dominance can affect fitness in parids. In Europe, spring territoriality is of little or indirect importance in limiting breeding populations of titmice (Krebs 1971, Perrins 1979, Cederholm and Ekman 1981, but see Krebs 1977). Social dominance in spring is presumably also unimportant in territory acquisition for European parids, since nearly all individuals obtain a territory. However, Ekman and Askenmo (1986) reported the existence of several unmated male willow tits in the breeding season; dominance among males may be potentially important to the acquisition of a mate, but this is not fully documented.

Besides territory acquisition, another correlate of social dominance that has received much attention is winter mortality. This factor is best documented in Scandinavian studies, where the climate is most similar to Alberta's. In their study of willow tits, Ekman and Askenmo (1984) showed that dominant individuals survived better than subordinates, and suggested that this was because they used better foraging zones in the trees. Ekman (1987) later showed that willow tits foraging in the dominants' zone were less exposed to predators than birds foraging elsewhere. Thus, dominance in these willow tit studies operated rather differently than in published studies of black-capped chickadees, even though these species are closely related.

In this study, winter survival was substantially higher than in Scandinavia but, as in several European studies of parids (e.g. Krebs 1971, van Balen 1980, Dhondt 1971) winter food apparently limited survival to some extent (but far less than in the study of Jansson *et al.* (1981)). The relatively warm temperature in the two winters of this study may explain in part why survival was higher than in Scandinavian studies, but other factors potentially contribute to such a difference. Scandinavian titmouse studies have been conducted in coniferous habitat, which probably has different resources (quality/quantity) than the poplar woodland of my study. Also, Scandinavian forests contain an avian predator unknown to central Albertan woodland: the pygmy owl (*Glaucidium passerinum*), which frequently kills willow tits (Ekman 1987).

Even though it varies among studies, the limiting effect of food or some related resource points to the existence of competition in winter flocks. In contrast to competition for territories, which is primarily intrasexual, winter competition in chickadees presumably involves contests between all individuals, regardless of their sex. If this is true, then the subordination of females to males, as shown in this study, should be detrimental to the females in contests over winter resources. Competition between flock members often took the form of contests for specific food items, most often at artificial bird feeders, but occasionally also in more natural conditions. Unfortunately, I could not estimate the importance of kleptoparasitism to survival in the Meanook population. In my study, competition in winter was best illustrated by the removal of males, which led to a marked "niche shift" by females. Exclusion of females from presumably better foraging areas by males may have led to higher female mortality in one of the two years of this study, but evidently, only long term data can determine whether higher female mortality in winter is real. Data for harsh winters might reveal a much greater mortality than in the two winters of this study, which were relatively mild.

Winter resource limitation may not only influence within-flock interactions, but also interactions between flocks, since different flocks use similar resources. Interactions between non-kin groups are poorly understood, and most literature on the relationships between such groups is descriptive (e.g. Carrick 1963, Condee 1970, Glase 1973). However, a study of willow tits in Sweden (Ekman *et al.* 1981) has experimentally shown that flocks defend territories, which results in a floating population that eventually disappears in winter. In contrast to the latter study and numerous accounts of flock territoriality in chickadees (e.g. Odum 1942, Hartzler 1970, Glase 1973, Smith 1984), I found no evidence of flock territoriality in this population, but again, this may be subject to yearly variation. Ecological factors that could lead to flock territoriality (or the absence thereof) are not well understood, but presumably involve a combination of food abundance, dispersion (Davies and Houston 1984), and weather (DeLaet 1984), as in other bird species (reviewed by Carpenter 1987).

Short-term studies like the present one cannot lead to strong inferences about the function of a particular type of behaviour; because patterns are subject to yearly variation. Only long-term data can account for a possible "year effect" on *patterns* described. However, short-term studies are adequate for the detailed analysis of *processes* that may lead to general patterns. Foraging observations in this study revealed potential costs to subordination in winter that were not previously documented in black-capped chickadees. There is a need for long-term data on winter survival to substantiate ideas developed in the two years of this study.

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VI. Appendix I.

SEX DETERMINATION OF BLACK-CAPPED CHICKADEES WITH A DISCRIMINANT FUNCTION

INTRODUCTION

As there are no marked differences in the plumage of female and male black-capped chickadees, early chickadee studies (e.g. Odum 1942, Hamerstrom 1942) have used breeding behaviour as the only criterion for sex determination. Males sing, feed the female during incubation, and only females incubate. However, the sex of only a small proportion of wintering birds can be known with such a method. Glase (1973) used a combination of the slight sexual size dimorphism, cranial pneumatization and breeding behaviour to determine the sex of more birds, but he used only wing length as a body size characteristic. No published study has used a multivariate approach to help increase the number of birds classified as males or females. Here, I summarize the results of a discriminant analysis conducted on three morphometric variables.

METHODS

Chickadees were usually captured with mist nets, and most of the banding occurred in fall, in the morning. Besides colour banding each bird captured, we usually measured the flattened wing length to the nearest 1.0 mm and body mass to the nearest 0.1 g. The outer right rectrix was plucked and measured later, to the nearest 1.0 mm. Birds with extensive tail wear were removed from the analysis. Tarsus length was also measured on most birds, but the method varied between observers. Thus, I did not include tarsus length in this analysis.

The discriminant function was computed from the measurements of the first capture of all birds whose sex was determined by breeding behaviour (143 females and 171 males). I did not use the sample that generated the discriminant function to estimate the percentage of cases correctly classified, since this method tends to overestimate the true performance of the function in the population (Norusis 1986). Instead, I used measurements from recaptures of 52 known females and 91 known males to estimate the percentage of cases classified correctly.

RESULTS

Males were larger than females in the three variables (Table VI-1) and mean discriminant scores were different for males and females (Figure VI-1). Differences between adults and juveniles were inconsistent for the three variables, and mean scores of adults and young were not different in males (Wilks' Lambda=0.987, P=0.77) and females (Wilks' Lambda=0.976, P=0.63). Thus, adults and young were pooled in the analysis. The overall rate of correct classification was 93.7% from the measurements alone (Table VI-2).

TABLE VI 1: Morphological measurements of female and male samples (first captures only). All F's are significant at the P=0.001 level.

Variable	Females (n=143)	Males (n=171)	F	Unstandardized discriminant function coefficients
Body mass (g)	11.5	12.4	135	0.4611
Tail length (mm)	62.1	64.6	133	0.0991
Wing length (mm)	64.7	68.0	352	0.4885
Mean discriminant score	-1.2583	1.0522	*	

* Wilks' Lambda=0.43, df=3, P<0.001

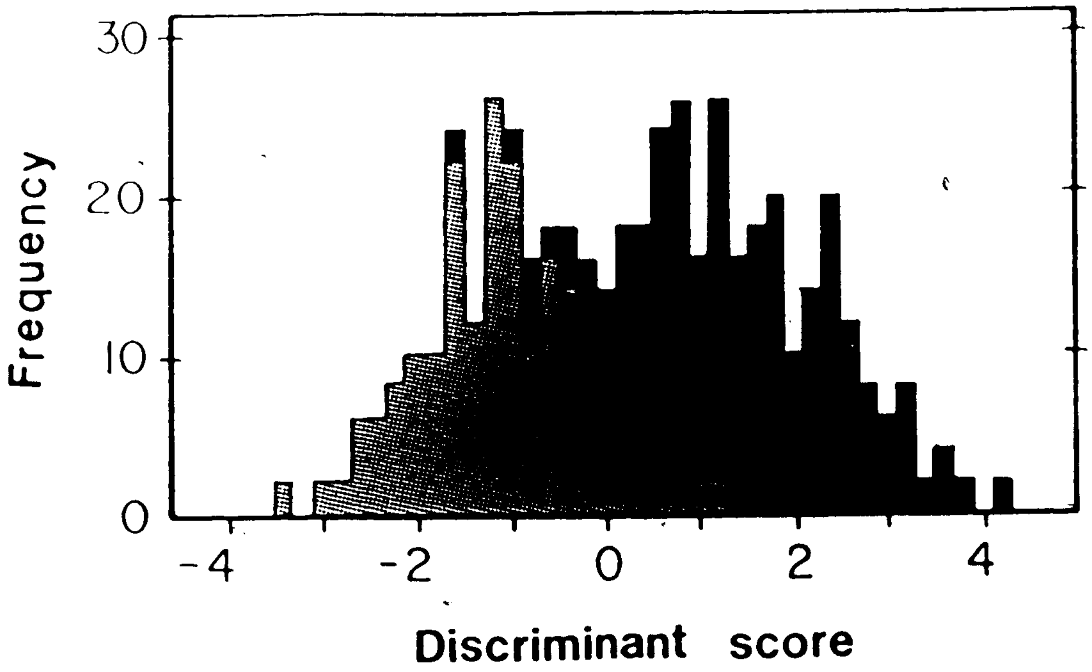

Figure VI-1: Frequency distribution of canonical discriminant scores for males (solid bars) and females (hatched bars).

TABLE VI 2: Classification results for cases not selected for use in the calculation of the discriminant function.

Actual sex	N	Predicted sex	
		Female	Male
Female	52	47 (90%)	5 (9.6%)
Male	91	4 (4.4%)	87 (96%)

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