THE UNIVERSITY OF MANITOBA

BEHAVIOURAL ECOLOGY OF THE CLAY-COLORED SPARROW

Spizella pallida

BY

RICHARD W. KNAPTON

A THESIS

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ABSTRACT

In this study, I investigated the adaptive nature of behavioural and ecological aspects of the social system in two populations of Clay-colored Sparrows (Spizella pallida) in southwestern Manitoba.

The spacing system during the breeding seasons of 1974 through 1976 was one of territorial dispersion over the nesting habitat. Territories were established quickly by the males, no agonistic encounters being recorded after 20 May in 1976. Males showed a high rate of return both to the study areas and to their territories of the previous year. Returning males participated in relatively few aggressive encounters among themselves. The mechanism by which returning males recognize each other may be the retention of at least one song type from one year to the next.

Territories were small, averaging about 700 m² on one study area and about 900 m² on the other. Experimental removals of territorial males in mid-May revealed not only the existence of a surplus of non-territorial birds but also no apparent change in the territorial boundaries of those males holding territories adjacent to the vacated areas.

The mating system was monogamous. Each territorial male atracted a female, and no male attracted two females at the

same time, no matter how small or large the territory.

I examined two major forces influencing spacing systems: food and predation. Adults brought a wide variety of prey items to their young, and were probably exploiting whatever suitable foods were seasonally available to them. There was no major difference between members of a pair either in the direction of foraging flights or in food items delivered to the young. However, males foraged at slightly greater distances from the nest, suggesting spatial partitioning of foraging areas and reduced intersexual competition for food between members of a pair.

Predation was the major cause of nest losses, accounting for 60% of egg loss and 95% of loss of young. Nests that offered a high degree of nest concealment had the highest nesting success. Pairs appeared to minimize the chance of having their nests detected by predators hunting by sight by constructing their nests primarily in Symphoricarpos occidentalis, which allowed less light penetration than other potentially available shrubs. Pairs that nested close to the ground suffered less predation than those nesting higher in the vegetation. The visual outline of the nest might be difficult to detect if the nest was close to the ground as light penetration was lower there than higher in the vegetation. Returning birds were also found to have a higher rate of nesting success than new birds, possibly related to the age of the birds.

Territoriality in this sparrow has most likely evolved,

or is at least maintained, as a predator-buffer mechanism. Territory could have a selective advantage in spacing out nests as a defense against predators, as nests closer together were less successful than those farther apart. Furthermore, birds were not locating their nests randomly around the margins of the territory, but appeared to be influenced by the position of their neighbour's nest(s), such that internest distances were greater than random.

Food did not appear to be an economically defendable resource. Food for the young was collected off territory and away from the nesting habitat, thus food _per se_ did not directly affect the size of territories.

The upper limit to the size of the territory is probably determined ultimately by the amount of time and energy expended in defending a large territory. Of several proximate factors investigated, relative amounts of 'dense' _Symphoricarpos_ and numbers of adjacent territory holders were found to influence territory size. Most sparrows apparently maximized their reproductive fitness by preferentially defending territories within a particular size range. This optimal size of territory can be largely predicted by a simple model using nesting cover and nest spacing in response to predation.

Analyses of songs from four populations of Clay-colored Sparrows revealed no evidence for the existence of dialects, although some conditions exist for their establishment. I argue that dialects would not develop

across a broad homogeneous area such as the prairies in central North America if dialects function to enhance the adaptation of populations to local environmental conditions. The lack of evidence for the existence of dialects correlates with a large amount of variation in songs between individuals both within and between populations.

Most individual Clay-colored Sparrows examined had more than one song type in their repertoire. Although there is some evidence for matched counter-singing and the conveyance of different information to specific targets, the data are most consistent with Krebs' 'Beau Geste' hypothesis as an explanation of the significance of song repertoire in this sparrow.

ACKOWLEDGEMENTS

I am most grateful to my supervisor, Dr. R. M. Evans, for his advice, constructive criticisms and helpful suggestions during all stages of the thesis. Sincere thanks are extended to all other members of my advisory committee, including Drs. S. G. Sealy, J. H. Gee and D. Punter.

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The research was supported by National Research Grants to Dr. R. Evans, and by University of Manitoba fellowships to myself. My work in Mexico was funded by a Frank M. Chapman grant.

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TABLE OF CONTENTS

LIST OF TABLES

Part C

Table

LIST OF FIGURES

LIST OF APPENDICES

GENERAL INTRODUCTION

A productive field of research in recent years has been the investigation of the adaptive relationships of social systems to the environment (e.g. Crook 1965, Lack 1968, Orians 1971, Brown 1975, Wilson 1975). The spacing system of a breeding population of animals is a compromise resulting from many competing selective pressures, and is a result of the response of individuals to one another and to their common environment (e.g. Smith 1968, Brown and Orians 1970, McKinney 1973, Pitelka et al. 1974). Two major determinants of natural selection which shape the spacing system are food and predation, but it has often proved difficult to assess the relative effects of these two factors within a particular spacing system. In this study, I look at the spacing system during the breeding season in two populations of a territorial species of bird, the Clay-colored Sparrow (Spizella pallida). I ask why it is adaptive for this species to have this particular spacing system, and I attempt to determine the relative effects of food and predation on this spacing system. I further investigate singing behaviour as song is probably the main mechanism for the maintenance of stability of the territorial system in this sparrow.

The thesis is divided into the following parts. Part A presents detailed information on aspects of the natural

history of the species, as such information is necessary for a full understanding of a species' social system. In Part B, I discuss aspects of the singing behaviour in the Clay-colored Sparrow, and I attempt to relate these aspects to the sparrow's social system. In Part C, I investigate the territorial spacing system, and I attempt to answer the questions:

(a) What factors influence territory size?

(b) Why are the territories the size they are?

(c) How did they become this size?

(d) Is there an optimal territory size, and, if so, can this size be explained?

Finally, in Appendix 1, I present new criteria which can be used to determine sex and age in this sparrow.

PART A

BREEDING ECOLOGY OF THE CLAY-COLORED SPARROW

(Spizella pallida)

INTRODUCTION

The Clay-colored Sparrow _Spizella pallida_ is a common and widespread breeding bird of dry uncultivated brush regions of the great plains (Bent 1968), and Breeding Bird Surveys (Erskine 1974, 1975, 1976) indicate that it is probably the most numerous breeding passerine of low shrub communities of the southern parts of the Canadian prairie provinces. Despite its abundance, however, it has received very little study. Aspects of its nesting biology have been looked at in Michigan (Walkinshaw 1939, 1944), in Saskatchewan (Fox 1961), and in Alberta (Salt 1966), but much of this work has been based on casual observations and is anecdotal. Many basic aspects of the breeding ecology of the Clay-colored Sparrow remain essentially undescribed, such as the occurrence and degree of site tenacity, factors which influence nesting success and nest site selection, and foraging behavior including foraging locations and type of prey delivered by parents to their young. The species further provides an opportunity to study an essentially monomorphic species which reduces intersexual competition for food through spatial partitioning of the foraging areas. Finally, there appears to be some confusion

concerning the response of Clay-colored Sparrows to brood parasitism by the Brown-headed Cowbird (<u>Molothrus</u> <u>ater</u>), ranging from intolerance (Salt 1966) to acceptance (Bent 1968, Fox 1961) of the parasite's egg. This paper attempts to fill these gaps.

METHODS

The Study Areas

The study was carried out in Edward Municipality in extreme southwestern Manitoba, near the towns of Lyleton and Pierson (Figure 1). The topography of this region is gently rolling, at an average elevation of 490m above sea level. Originally, the area was mixed-grass prairie (Weir 1960), but modification of the vegetation through human settlement and containment of prairie fires has resulted in the proliferation of aspen (Populus tremuloides) bluffs and extensive stands of low shrubs, particularly Symphoricarpos occidentalis and Elaeagnus commutata. It is in these low shrub communities that Clay-colored Sparrows reach their highest densities.

Two study plots were chosen, both incorporating large expanses of shrub communities along with aspen bluffs and areas of grass. Study Area #1 was a 5.86ha plot located about 2km west of Lyleton. It included part of an unused and overgrown road right-of-way and part of a large pasture which was lightly grazed in the first summer and the first half of the second summer of the study. On 14 August 1975, about 4200m² of shrubbery were cut down on the southern boundary of the area, thereby reducing the amount of

Figure 1. Map of southern Manitoba, showing location of study sites.

51°

50°

● Delta

● Winnipeg

49°

● Pierson
● Lyleton

N

0   50   100

Scale (km)

hb

101°   100°   99°   98°   97°   96°   95°
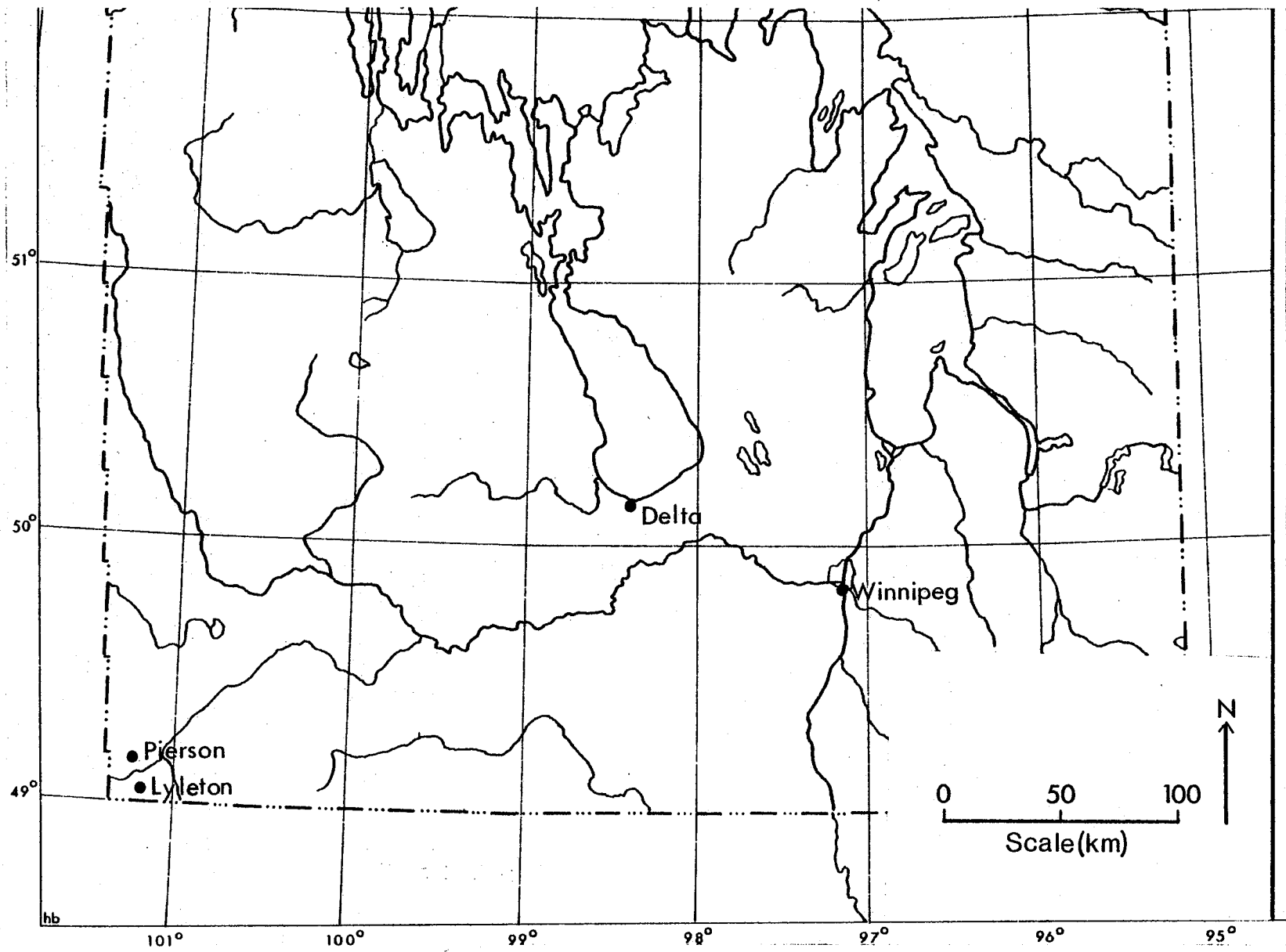
nesting habitat available to the sparrows in 1976 by about 15 percent. Study Area #2 was 5.67ha in size, and was located on the Pierson Wildlife Management Area, some 7km southwest of Pierson and about 12km northwest of Study Area #1. The areas covered by various types of vegetation on each study area were determined by compensating polar planimeter from aerial photographs.

I spent the following periods on the study areas: 15 May to 15 September 1974; 27 April to 3 September 1975; 30 April to 31 August 1976. These dates coincide with the approximate arrival and departure dates of the Clay-colored Sparrows in southwestern Manitoba. Daily observations were made during the height of each breeding season, each study area being visited on alternate days. A final visit to the areas was also made on 28 and 29 May 1977.

Capturing and Sexing Techniques

Adult and immature Clay-colored Sparrows were captured in mist nets, and nestlings were banded at about 5 days of age. Each bird received an aluminium band plus two colored plastic bands in different permutations, for individual recognition. In total, 834 birds were banded.

Male and female Clay-colored Sparrows are morphologically quite similar. Hand-held birds in reproductive condition could usually be sexed by the presence of a cloacal protuberance in the male and a brood

patch in the female. In both the field and in museum skins of birds of known sex, males had, on average, longer wings and whiter superciliary stripes than females (Appendix 1). These criteria were supplemented in the field by behavioral differences between the sexes (Appendix 1).

Nesting Data

Nests proved to be fairly easy to locate. Observations on individuals constructing nests or feeding nestlings gave a general indication of the nest site, and a short search usually produced the nest. Nests containing eggs were found by flushing the incubating bird. Two hundred and thirty-two nests were located, 41 in 1974, 84 in 1975 and 107 in 1976. Once located, each nest was visited every second day, and a log of the state of each nest was compiled.

During the study, I measured (a) the substrate of the nest, including the proportion and identity of the vegetation supporting the nest, (b) the height from the base of the nest to the ground, and (c) the distance from the surface of the vegetation to the nest rim. I measured the substrate in 1976 by counting the number of branches and/or stems supporting the nest. I divided the nest substrate into three vegetation types (Symphoricarpos, Elaeagnus/Rosa, and grasses and forbs), and expressed the amount of each vegetation type as a percentage of the

substrate of each nest. I determined the surface of the vegetation as that level at which a ruler held vertically from the nest rim was about 90% obscured by the vegetation.

In 1976, each nest was further measured for the degree of concealment afforded it by the nesting substrate. I measured each nest as soon as possible after I had found it, usually on the same day or on my next visit to the study area. Each nest measured contained either eggs or young. Measurements were taken by holding upright a Gossen Lunasix 3 light meter by the nest bowl, and taking a reading of the amount of penetration of incident light. For consistency, the readings were all taken between 0800 and 1000 hours, at the east side of the nest. A logarithmic scale of incident light, provided on the light meter and corresponding to an exponential increase in foot candles, was used in the analysis.

I determined the start of nest initiation from my own data and from that of Walkinshaw (1944), Fox (1961) and Salt (1966). I allowed four days between the start of nest construction and the onset of egg laying. I determined this value from the following information: I located six nests in the first stages of construction and on the fifth day after its discovery each nest contained one or two eggs. Also Fox (1961) found that nest construction required two to four days in four pairs observed. I allowed four days for the laying of the eggs (one egg per

day as the usual clutch size was four), and eleven days for
the incubation period. The incubation period has been
determined as ten days (Salt 1966) and eleven days
(Walkinshaw 1944, Fox 1961). I found the incubation period
between the laying of the last egg and the hatching of the
last egg to be about 11 days for 13 nests (range
approximately 10 to 12 days). Thus, I used a total of 19
days between the day the nest was initiated and the day the
last young hatched.

Cowbird Parasitism

I treated cowbird parasitism in the following manner.
Once I had located a nest containing a cowbird egg, I left
that egg in the nest for a minimum of 4 days, in order to
determine the response of the host to the parasite's egg.
On Study Area #1 in 1974, I left the eggs in the nest and
followed the eventual outcome of the nest. In all other
cases, I removed the egg on or after the fourth day, as I
intended to collect future information on the Clay-colored
Sparrow young.

Light Penetration Analysis of the Shrubbery

As there appeared to be a consistent tendency to use
Symphoricarpos occidentalis as a nest site over other
available shrubs in 1974 and 1975, I objectively measured
light penetration in 1976 within the shrub communities in

the following way. Aerial photographs of each study area were divided into 10m² sections, and the rows and columns numbered. A section of shrubbery was determined by random sampling of a pair of numbers, one from the rows and the other from the columns. This selection process was continued until there were ten samples of Symphoricarpos and ten of other shrubs, usually Elaeagnus commutata, for each study area. Then, on the study areas, a 3m stick was tossed into each of the chosen sections of shrubbery by my field assistant, the stick held upright, and penetration of incident light, using the Gossen Lunasix 3 light meter, was recorded at 10cm intervals to the top of the vegetation.

Food and Foraging Behavior

I observed individual sparrows during May and early June in 1975 and 1976 in areas around the nesting habitat. I noted the the identity of each bird, where it was foraging, and whether it was foraging alone or close (within approximately 5m) to another bird.

From 15 June to 17 July 1976, some 65 hours were spent in observing seven pairs of Clay-colored Sparrows that were feeding young in the nest. Observation periods were usually of about 2hr duration, and were carried out between 0600 and 1200 hours from blinds located within 10m of the nest. Pairs appeared to accept the presence of blinds quite readily: no nest under observation was deserted or

was lost to predation.

I collected information, by direct observation, on the number and identity of prey items brought by the parents to their young, the parent's line of flight on leaving the nest, and where possible the distance of the location of food gathering from the nest. Information was recorded on portable tape recorders and later transcribed.

To obtain a more precise identification of prey items brought to the young, I used a portable Sony Videocorder equipped with a 230mm lens and made a permanent record of food items carried by adults in their beaks. The video tapes were then analyzed on close-circuit television, a still switch on the videocorder allowing close analysis of individual frames. Thirty-five mm photographs were taken of selected stills. It was possible to identify most prey items at least to order.

I also used the neck-band method (Orians 1966, Horn 1968) of placing a structure around a nestling's neck to obtain actual samples of food brought to the nestlings by the parents. I used thin wire wrapped in cottonwool formed into bands, placed around the necks of young Brown-headed Cowbirds (one cowbird to one nest) in Clay-colored Sparrow nests in which the sparrows' own young were no longer present. Prey items were identified down to family where possible. The neck bands were left on the young cowbirds for approximately one hour. Young Clay-colored Sparrows

were not neck-banded because concurrent information was being collected on survival rates of these young, and repeated visits to their nests might have influenced predation rates. Also young Clay-colored Sparrows cannot be easily returned to the nest bowl from the sixth day after hatching, and will leave the nest prematurely by jumping out of the nest if attempts to handle them are made after that time. Clay-colored Sparrows younger than six days of age were deemed too small to support a neck band.

The neck-band method is not without potential error, as small prey items can slip through the neck-band, or else food can be coughed up and eaten by the parents (Orians 1966). The similarity in results obtained by the two methods suggests, however, that errors were not large.

Locations to which adults flew to forage for their nestlings were recorded, and the distances determined by plotting the foraging location on aerial photographs and measuring the distances to the nest. The birds were not visible when foraging, but they characteristically returned to the nest from the foraging site in which they originally alighted. It was relatively easy to observe how far individual birds flew before alighting, as the low height of the vegetation permitted an extensive panoramic view of the surrounding areas.

RESULTS

SITE TENACITY AND TERRITORIAL 'SHUFFLES'

No study to date has shown that Clay-colored Sparrows
exhibit site tenacity. Analysis of returns to the study
areas revealed that males showed a high rate of return to
the vicinity where they had nested the previous year (Table
1). On Study Area #2, the number of returning banded males
was consistently high, between 62% and 85%. Male return on
Study Area #1 ranged between 45% and 60%, and this range
was significantly lower than that on Study Area #2
(X^2 = 5.14, P < 0.05; two by two contingency table for all
years combined). The return rates of male Clay-colored
Sparrows on Study Area #2 compare favorably with those of
other grassland or shrub inhabiting species, the return
rates of males on Study Area #1 rather less so (Table 2).

Not only do the males return to the same general area
but most often (76% in 1976) to the same territory, and
they often reoccupy the same song perches. Occasionally
'shuffles' occurred, in which territories were exchanged in
successive years between adjacent males. Usually only two
territorial males were involved in such a shuffle. Five
shuffles (three on Study Area #1, two on Study Area #2)

Table 1. Return rates of male and female Clay-colored Sparrows to the study areas.

| | | Number of territorial pairs | Number (%) returning the following year | |
			Males	Females
STUDY AREA #1	1974	(17)*	9 (52.9)	5 (29.4)
	1975	27	16 (59.3)	4 (14.8)
	1976	22**	10 (45.6)	3 (13.6)
STUDY AREA #2	1974	(36)*	24 (66.7)	5 (13.8)
	1975	39	33 (84.6)	8 (20.5)
	1976	45	28 (62.2)	7 (15.6)

* Not all territorial pairs present on the study areas were banded in this year.

** The decline in numbers of territories from 1975 to 1976 was partially due to the loss of shrubbery (see text), which eliminated four 1975 territories.

Table 2. Return rates to breeding areas of some open country species
of passerines.

| Species | Average return rates (%) | | Reference |
	Male	Female	
Skylark (Alauda arvensis)	70	62	Delius 1965
Bobolink (Dolichonyx oryzivorus)	62.8	39.9	Martin 1974
Seaside Sparrow (Ammospiza maritima)	55	28	Post 1974
Field Sparrow (Spizella pusilla)	44	12	Best 1977a
Song Sparrow (Melospiza melodia)	62	42	Nice 1937
Clay-colored Sparrow (S. pallida)			
Study Area #1	52.6	19.3	This study
Study Area #2	71.2	16.6	

were recorded between 1975 and 1976, and of the 10 males involved seven had not raised any young in 1975. This raises the possibility of a connection between changing territory and nesting success between years. In 1976, however, on Study Area #2, three males holding adjacent territories exchanged their 1975 territories with each other, male A taking male B's territory, male B taking male C's territory, and male C taking male A's territory. All three males had bred successfully in 1975, suggesting that not all 'shuffling' between years was a result of nesting failure; the reasons behind this triple shuffle remain obscure. In 1976, two of these three males fledged young.

Return rates of female Clay-colored Sparrows on both study areas were significantly lower than those of males ($X^2 = 84.2$, $P < 0.001$ for all years combined), being about 13% to 30% (Table 1). The return rates of females were also appreciably smaller than those of females of most species in Table 2. In general, a female did not return to the same territory as the year before, even if she had fledged young there the previous year. Hence, of 32 females that returned to the general area, 29 (90.6%) did not mate with the previous year's male.

There was one exception to this trend; one pair occupied the same territory and stayed together for three consecutive summers on Study Area #2, an event most unlikely to have occurred by chance. The fact that flocks

of Clay-colored Sparrows on the wintering grounds in Mexico appear to be comprised of both males and females (Appendix 1), and not unisex flocks, suggests that males and females could conceivably stay together all year round. This seems somewhat unlikely under normal circumstances, however, as males arrive on their breeding grounds several days before the females, indicating a temporal separation of the sexes at least during spring migration.

During the course of the three summers, 146 nestlings and 305 immatures were banded. No individual banded as a nestling was recorded in subsequent years on the study areas. This is in contrast to a return rate in Song Sparrows of 12.6% (Nice 1937) and in Skylarks of 8.8% (Delius 1965). Further, only 4 birds (2 males, 2 females) banded as immatures were recorded in following summers on the study areas.

ESTABLISHMENT OF TERRITORIES AND THE NESTING SEASON

Arrival on the breeding grounds. Clay-colored Sparrows arrived on their breeding grounds in southern Manitoba in early May. Males arrived before females in both 1975 and 1976, the major influx of males occurring from 7 to 10 May and the major influx of females between 12 and 16 May (Figure 2).

Males and females arrived slightly earlier in 1976 than in 1975 (Figure 2). This was possibly a result of the

Figure 2. Dates of arrival of male and female Clay-colored Sparrows, both study areas combined. N = 66 territories in 1975 (open circles), 67 territories in 1976 (solid circles).
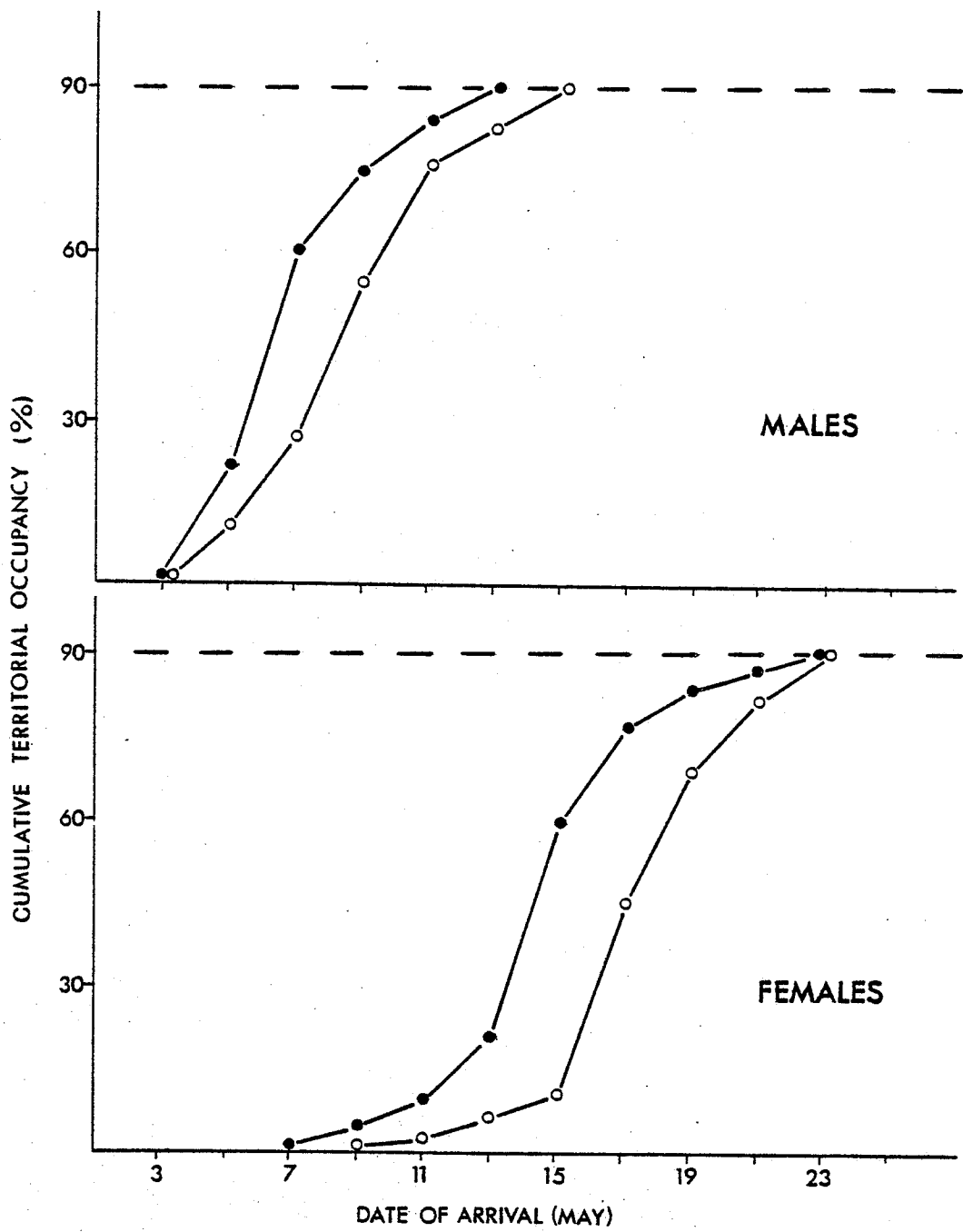
higher mean temperature in April, 1976 (temperatures, in
°C, at Pierson were 0.7 in 1975, 6.7 in 1976). This might
have accelerated the northward migration of the flocks of
Clay-colored Sparrows in 1976 if the warmer temperatures
extended south along the sparrows' migration pathway.

Establishment of territories. Male Clay-colored Sparrows
started to establish territories on the day they were first
observed on the study areas in 1975 and 1976.
Establishment and subsequent defense of the territory
involved singing, especially from perches near the
territorial boundaries, and overt aggression between
individuals. Observations in 1975 indicated that
territorial boundaries between contiguous territories were
established quickly, and once established trespassing by
neighboring males was recorded only rarely. Furthermore,
in 1975, observations suggested that aggressive
interactions between individual Clay-colored Sparrows had
declined considerably by mid-May.

In 1976, I quantified this trend by measuring hostile
encounters throughout the breeding season. I observed 71
aggressive interactions between individual Clay-colored
Sparrows in 1976, 26 on Study Area #1 and 45 on Study Area
#2. Of these, 64 were chases and 7 were fights. In every
case when the birds were identified, the protagonists
proved to be males; in no instance was a banded female
observed in a hostile encounter. Most encounters involved

neighboring territorial males, which were readily identifiable by their colored leg bands. Six encounters involved unbanded birds, and, for the purpose of analysis, an unbanded bird was assumed to be a new male, a reasonable assumption considering that all territorial males in 1975 had been banded and that the conflict area was part of a vacant territory subsequently occupied by a new male. The outcome of most encounters was easily determined; in four instances, however, the chaser became the chased as roles were reversed when territorial boundaries were crossed.

Over 95% of interactions on Study Area #1 occurred in the period 4 to 16 May, and over 85% of interactions on Study Area #2 between 8 and 16 May (Figure 3). No overt aggressive interactions were observed on either study area after May 20. This suggests that most interactions were involved in the establishment of territorial boundaries. Analysis of the protagonists showed that returning males participated in relatively few aggressive encounters among themselves, but encounters between returning males and new males, and among new males themselves, were significantly more frequent (Table 3). There were proportionately more returning males (33) than new males (12) on Study Area #2, yet only 13% of all interactions were between returning males. Similarly, on Study Area #1, returning males (13) outnumbered new males (9), yet produced only 8% of all interactions among themselves.

Figure 3. Total number of aggressive interactions among male Clay-colored Sparrows during the breeding season. Study Area #1, hatched bars; Study Area #2, open bars.
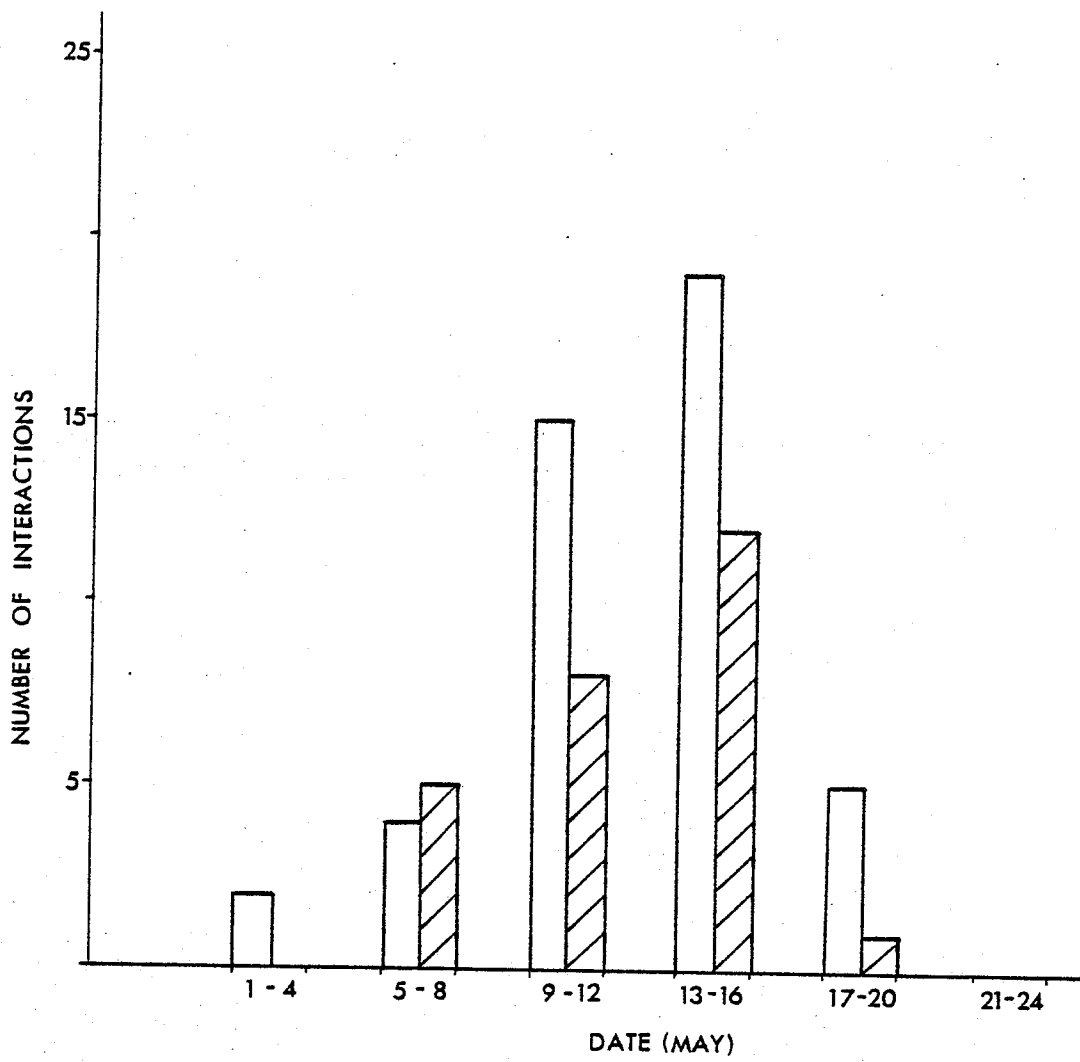
Table 3. Analysis of aggressive interactions of returning (R) and new (N) male Clay-colored Sparrows in 1976.

	Number of returning males	Number of new males	Number of aggressive interactions[1]			
			R vs R	R vs N	N vs N	x^2
Study Area #1	13	9	2	14	10	7.1 $P < 0.05$
Study Area #2	33	12	6	27	12	18.0 $P < 0.001$

1. The method used in calculating expected values is given in Appendix 2.

The nesting season. The nesting season of the Clay-colored
Sparrow in southwestern Manitoba extended from May to early
August. The length of the breeding season may have been
long enough for individual pairs to raise more than one
brood per season. In 1975, however, pairs that
successfully raised young did not attempt a second brood,
even though young were out of one nest by 12 June. In
1976, the situation was almost the opposite; of 20 pairs
that fledged young prior to 23 June, 11 (55%) attempted to
raise second broods. No pair that fledged young after that
date attempted to raise another brood.

An analysis of the start of construction of nests that
ultimately contained eggs (Figure 4) showed that the 1976
breeding season started earlier than in 1975. Of 30 nests
initiated in May 1975, only one was started before 23 May,
whereas in May 1976 14 nests out of 44 were started before
23 May.

Further, in 1975, new pairs took over some territories
mid-way through the breeding season, in late June and early
July, after territories had been vacated by successful
pairs, and attempted to breed. Seven such 'changeovers'
took place. Of the 14 males involved, none of the original
7 males returned the next year, whereas three of the
replacement males returned. No female from either an
original or a replacement pair was resighted; this is
perhaps not unexpected as site tenacity and mate fidelity

Figure 4.   Dates of nest initiation during May of 1975   and
1976.   (A) Study Area #1, (B) Study Area #2.
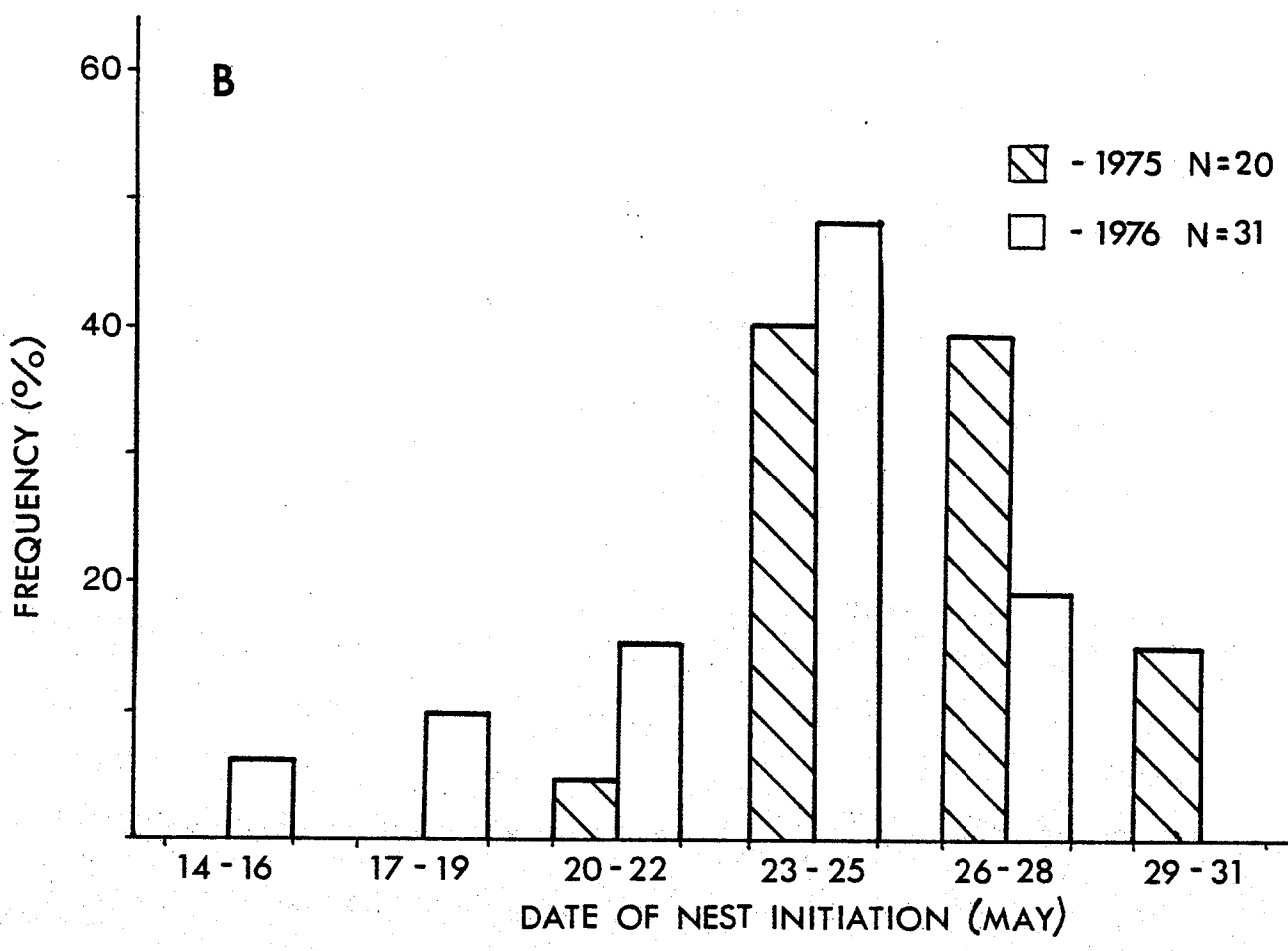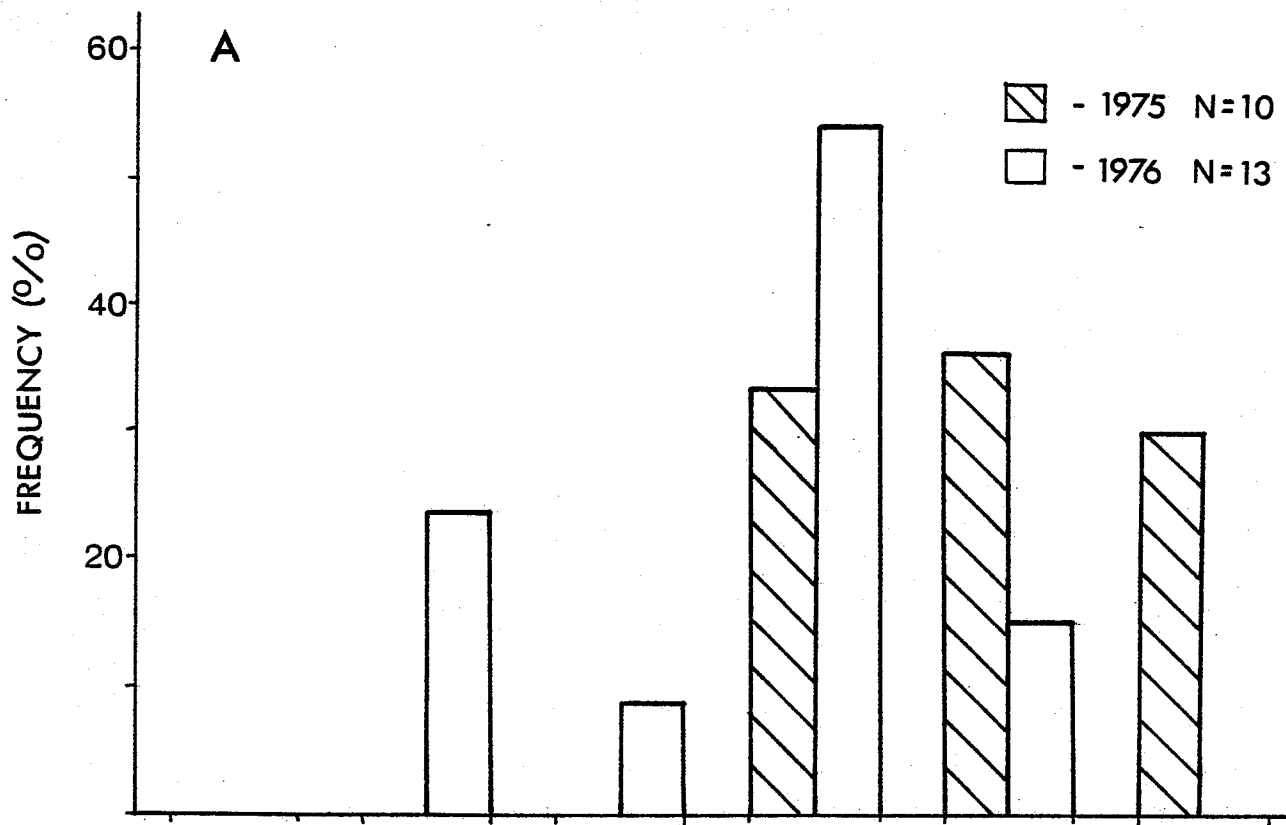
in females was low.

THE MATING SYSTEM.

The pair bond in the Clay-colored Sparrows during the breeding season on my study areas was stable. Once paired, the members of a pair stayed together throughout the breeding season, even if they incurred successive nest losses. Monogamy prevailed on my study areas; no example of any other type of mating system was recorded.

NEST SITE SELECTION

Vegetation analysis of the substrate. Tendencies within a local population of Clay-colored Sparrows to use one type of nesting site above all others have been reported by Walkinshaw (1939), Fox (1961) and Salt (1966). Such a tendency was also evident in both populations I studied in southwestern Manitoba. Out of 125 nests located in 1974 and 1975, 110 were built wholly or mainly in Symphoricarpos; only six nests contained no Symphoricarpos in the support of the nest.

In 1976, I counted the number of branches and/or stems supporting 107 nests. Numbers of supports ranged from 4 (a nest built above the ground in the branches of Symphoricarpos) to a high of 18 (a nest built at ground level and supported primarily by grass stems). I arranged

the nests within six percentage ranges (0, 1-25, 26-50, 51-75, 76-99, and 100) of the three main vegetation types present (Table 4). Once again there is a strong and repeatable use of Symphoricarpos as the nest substrate; 87 nests (81%) were mainly (more than half) or wholly supported by Symphoricarpos, and only 5 (5%) nests did not contain at least one branch of Symphoricarpos in the nest substrate.

In order to show that Clay-colored Sparrows prefer Symphoricarpos as a nest substrate over potentially available sites in other vegetation, it is necessary to compare the frequency with which a particular type of vegetation is used as a nest substrate in proportion to its availability in the habitat. There is a pronounced preference for Symphoricarpos as a nest substrate when compared to other types of vegetation within the study areas (compare open and hatched bars in Figure 5); significantly more nests were built primarily in Symphoricarpos than would have been predicted by chance (X^2 = 15.4, P < 0.001). Symphoricarpos accounted for 58.0% by area of the shrubbery and grassy regions of the study areas, yet 83.7% of the 104 nests used in the analysis were primarily constructed in Symphoricarpos. However, within the area defended by the sparrows, the preference for Symphoricarpos apparently disappears, and selection of nest substrate within the defended vegetation appeared to be

Table 4. Comparison of number of nests of Clay-colored Sparrows and
the proportion of three types of vegetation used as nest substrate.

Amount (%) of vegetation type as substrate	Vegetation Type[1]		
	Symphoricarpos	Elaeagnus/Rosa	Grass/Forbs
0	5	82	22
1 - 25	5	13	40
26 - 50	10	9	31
51 - 75	45	2	9
76 - 99	27	1	2
100	15	0	3

1. Each nest is represented three times, once in each vegetation type,
according to the amount (%) of each vegetation type supporting the nest.
Out of 107 nests, 104 contained more than 50% of one type of vegetation.

Figure 5. Substrate preferences for nests of the Clay-colored Sparrows in 1976. Presented within each of the three types of vegetation (Symphoricarpos, Elaeagnus/Rosa, and grass/forbs) are the percentage of nests (N) which contained 51% or more of one type of vegetation as a nest substrate (open bars), and the percentage of the areas (A, in ha) of the three types of vegetation within the study areas (diagonal bars) and within the area defended by the sparrows (solid bars).
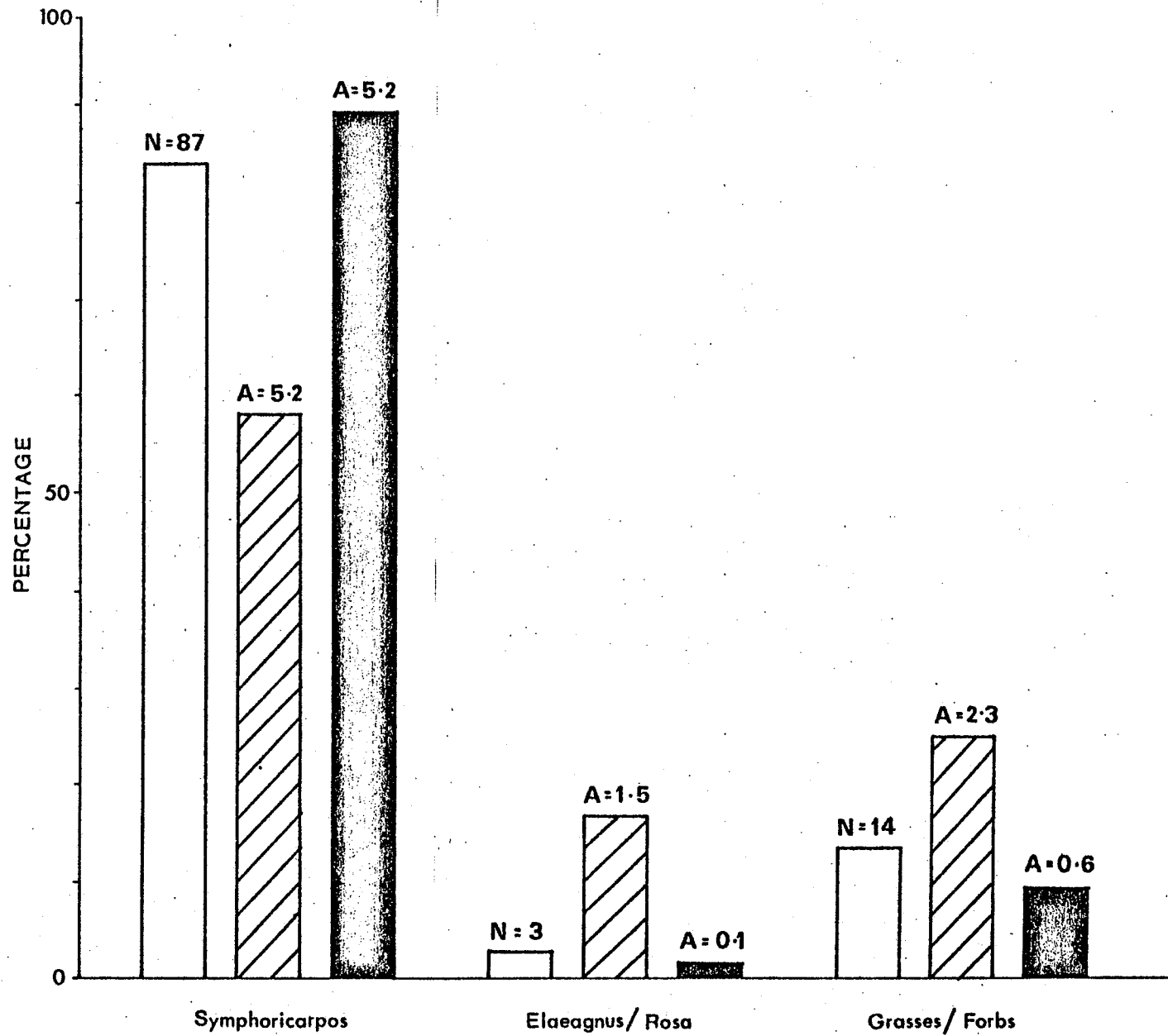
random (compare open and solid bars in Figure 5).
Symphoricarpos accounted for 89.0% of the vegetation
defended by the sparrows, and 83.7% as the primary
substrate of the nests (X^2 = 0.86, not significant). Grass
stems were incorporated into the nest substrate slightly
more than expected, possibly a result of the tendency of
pairs to construct their nests at the edge of a patch of
Symphoricarpos (Part C), where there may have been
proportionately more grass present than in the centre of a
patch.

I next compared light meter measurements between
Symphoricarpos and other types of shrubbery, primarily
Elaeagnus commutata, and found that significantly less
light penetration occurred in Symphoricarpos at all levels
above the ground than in the other vegetation (Table 5).
It is also evident from Table 5 that light penetration
increases with increasing height above the ground (Spearman
rank correlation coefficient r = 0.970, P < 0.005).

Nest location: height above ground and distance from
surface of vegetation. Walkinshaw (1944) and Salt (1966)
reported that early nests are closer to the ground than
later ones. Salt (1966) further suggests that the
Clay-colored Sparrow is more responsive to distance from
the surface of the vegetation than from the ground, so that
nest height increased as the season progressed and the

Table 5. Incident light measurements (foot-candles expressed as log units) in stands of Symphoricarpos and other types of vegetation in 1976.

Height (cm) above ground[1]

	Date	Symphoricarpos						Other						T	P
		10	20	30	40	50	60	10	20	30	40	50	60		
STUDY AREA #1	3 May	18.0	18.5	18.6	19.1	19.4	19.8	19.1	19.6	19.8	19.9	20.0	20.0	0	0.025
STUDY AREA #2	4 May	19.0	19.4	19.8	20.4	20.5	20.6	20.6	20.7	20.8	20.9	20.9	20.9	0	0.025
STUDY AREA #1	24 May	15.6	16.0	16.7	17.7	18.2	19.1	18.9	19.8	20.5	20.1	20.8	20.9	0	0.025
STUDY AREA #2	22 May	17.7	18.1	18.7	18.6	19.5	19.4	19.9	20.6	20.9	21.0	20.7	21.0	0	0.025
	Mean	17.6	18.0	18.5	19.0	19.4	19.7	19.6	20.2	20.5	20.5	20.6	20.7		

1. Each value represents the mean of 10 samples. The highest distance above ground that a nest was built in 1976 was 60cm. Values were compared by Wilcoxon Matched-Pairs Signed Rank test (Sokal and Rohlf 1969).

vegetation grew taller and denser.

No such seasonal trend in nest height was obvious in this study. Height range above ground of the nests at any one time was broad (Figure 6. Study Area #1, r = 0.45, not significant; Study Area #2, r = 0.34, not significant). In general, however, nests were constructed close to the ground throughout the breeding season, only 15% being higher than 30cm above ground in 1976. Similarly, there was no tendency to construct a nest at a set distance below the surface of the vegetation, the 1974 data producing a random scattering of values throughout the nesting season (Figure 7. For both study areas combined, r = -0.07, not significant). Rather, pairs tended to construct their nests at certain heights above ground regardless of the season, individual pairs tending to be consistently ground, low or high nesters within a season (Figure 8. For both study areas combined, r = 0.76, P < 0.01).

There was further no consistency of nest height between years in a particular male's territory. This suggests that females select the nest site since they did not usually nest in the same territory in consecutive years.

CAUSES OF MORTALITY AND THE NATURE OF PREDATION

Adult survival. Once territories had been established and the territorial pairs identified, then adult losses could be monitored over the season. Adult survival during the

Figure 6. Height above ground of nests in relation to date of nest initiation in 1976. (A) Study Area #1, N = 32 nests, (B) Study Area #2, N = 75 nests.

DATES OF NEST INITIATION
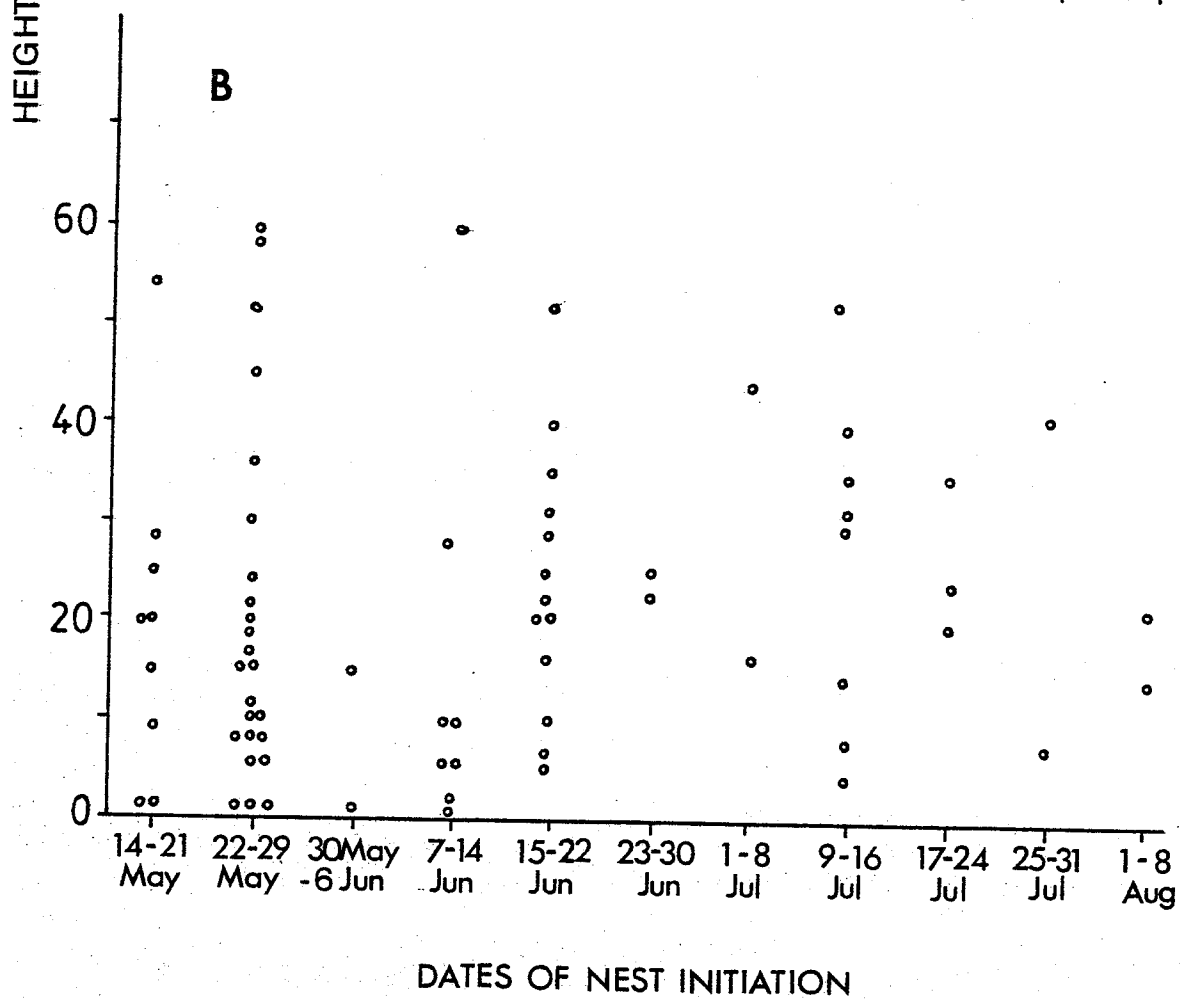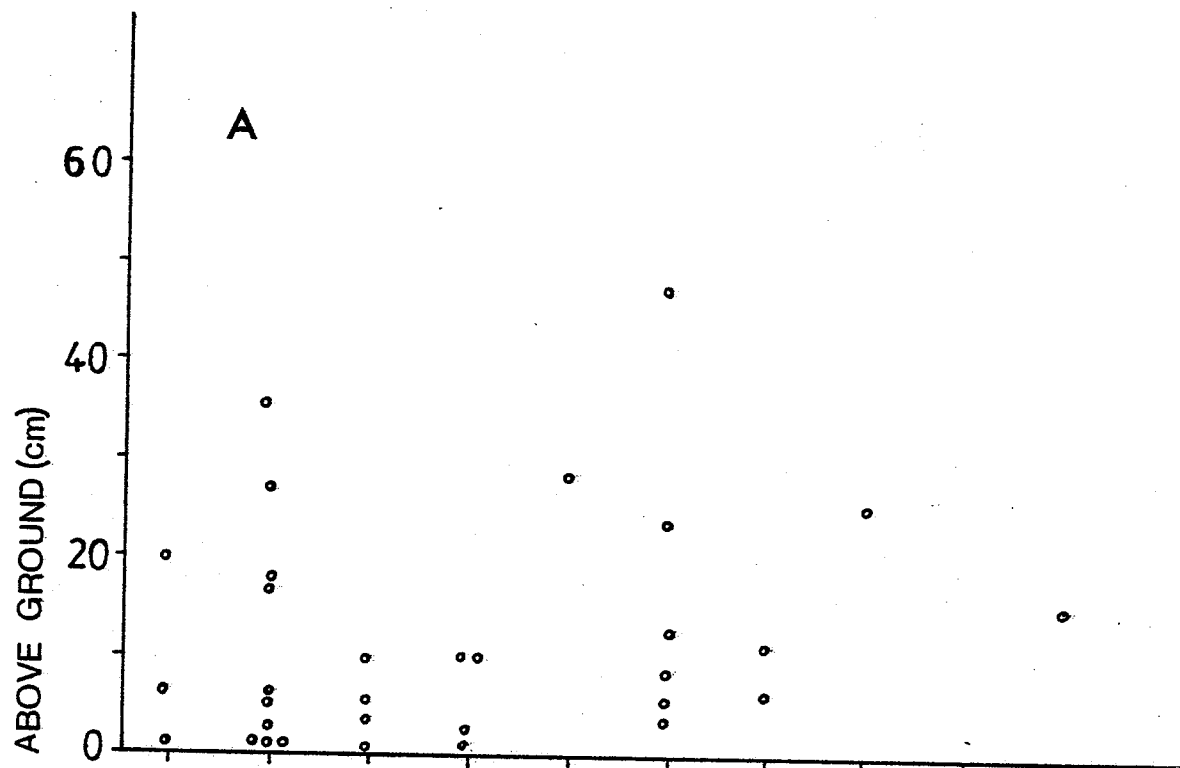
Figure 7. Distance below canopy in relation to nest initiation and advancing season in 1974. Study Areas #1 and 2 combined, N = 41 nests.

DATES OF NEST INITIATION
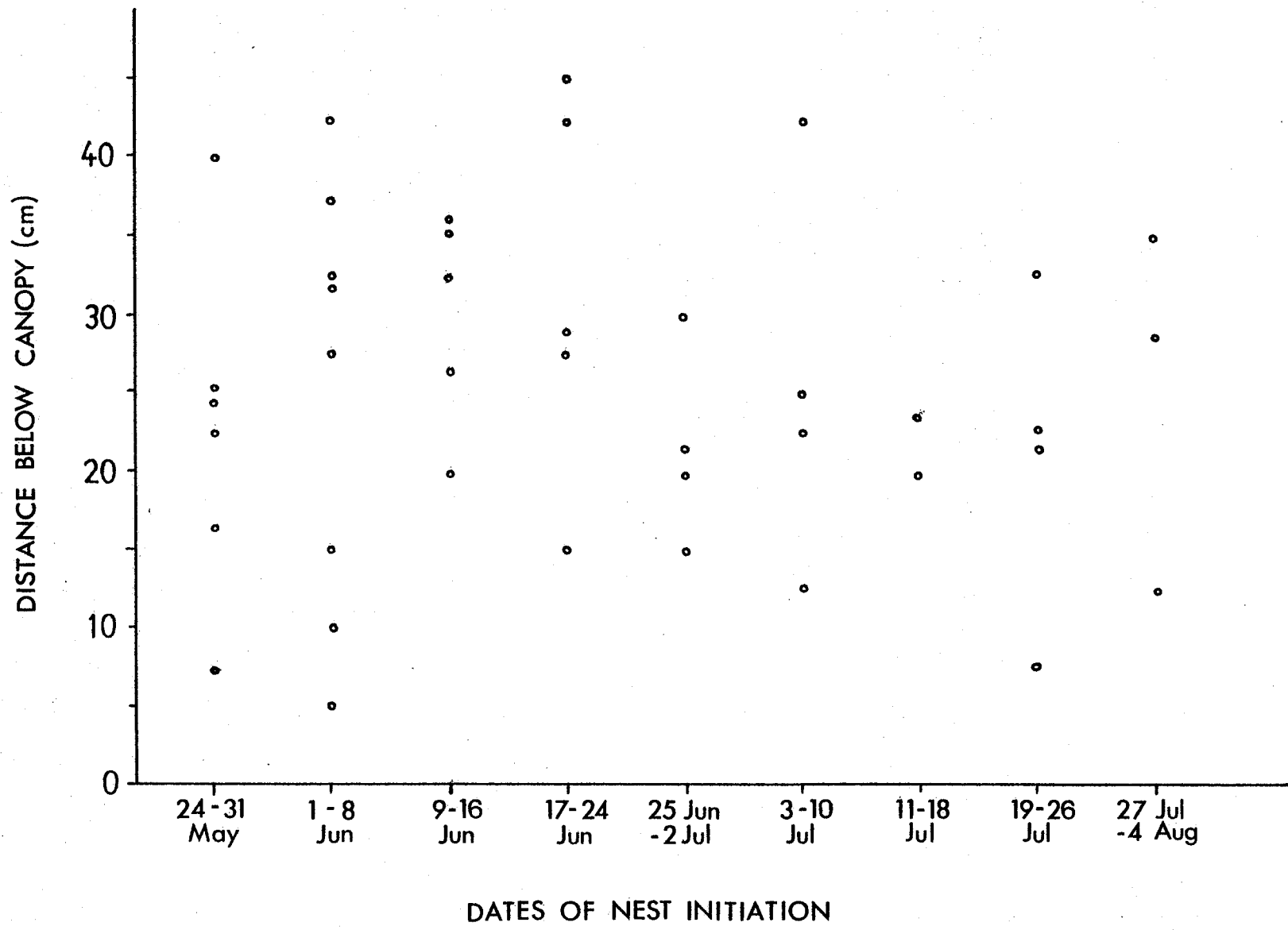
Figure 8. Heights above ground of first and second nests of 35 pairs of Clay-colored Sparrows in 1976, both study areas combined. First nest refers to the first nest located, and second nest to the next nest located, of a pair.
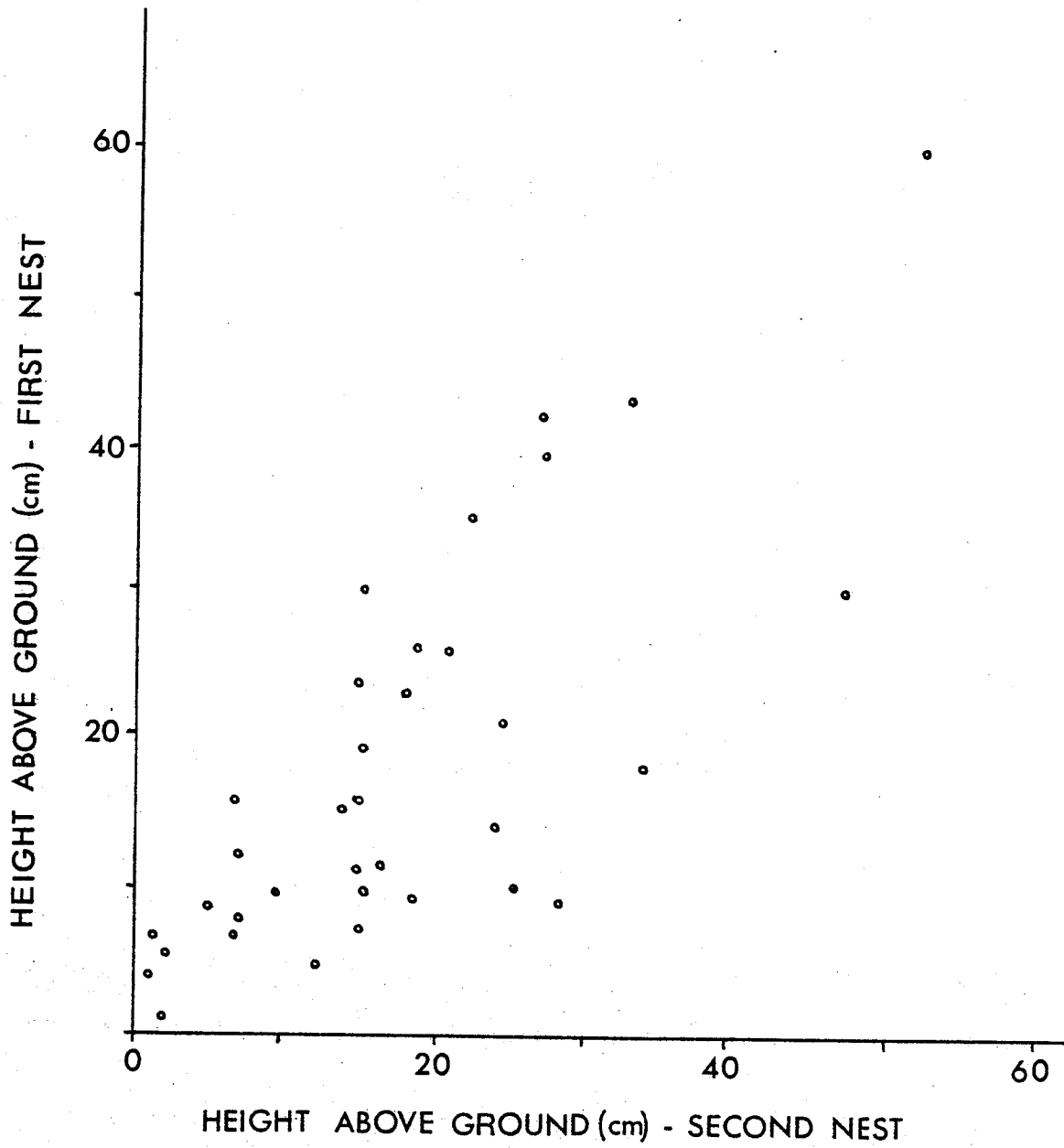
breeding season was high. No adult disappearance during the breeding season could be attributed unequivocally to predation in 1975 or 1976 on either study area. In 1976, no males were lost, whilst the only evidence that a female might have been taken by a predator was at a nest that was destroyed on 18 July and two adult Clay-colored Sparrow retrices found near the nest. The female was not resighted.

Ten males and one female were known to be at least 4 years old at the end of this study, as they were banded as adults in the spring of 1974 and were on territory in 1977. One Clay-colored Sparrow has been known to reach the age of five years (Bent 1968).

Causes of nesting mortality. Table 6 shows the causes of mortality of eggs and young for the 1975 and 1976 breeding seasons. In this analysis cowbird parasitism included only those instances in which a Clay-colored Sparrow nest sustained a known loss (eggs or young) and a cowbird egg was substituted. Predation was the most important factor on both study areas for losses of both eggs and young, although cowbird parasitism contributed substantially to egg loss. For the two areas combined, predation accounted for 59.5% of egg loss and 95.3% of loss of young, and cowbird parasitism was responsible for 21.6% egg loss. Most losses (44.9% for the study areas combined) occurred in the egg stage, the proportions being similar between the

Table 6. Categories of causes of mortality in Clay-colored Sparrows, 1975 and 1976 data for both study areas combined. Format after Ricklefs (1969).

Causes of mortality	Study Area #1	% of Individuals	% of Losses	Study Area #2	% of Individuals	% of Losses
Eggs laid	148			369		
Losses due to:						
Hatching failure	9	6.1	12.7	18	4.9	11.2
Cowbird parasitism	25	16.9	35.2	25	6.8	15.5
Nest-site competition	0			0		
Adult death	0			0		
Weather & desertion	4	2.7	5.6	13	3.4	7.2
Predation	33	22.3	46.5	105	28.5	65.2
Other	0			0		
Total losses (eggs)	71	48.0	100.0	161	43.7	100.0
Young hatched	77					
Losses due to:						
Cowbird parasitism	2	2.6	20.0	1	0.4	1.9
Nest-site competition	0			0		
Weather & desertion	0			0		
Starvation	0			0		
Predation	8	10.4	80.0	53	25.5	98.1
Other	0			0		
Total losses (young)	10	13.0	100.0	54	25.9	100.0
Number of young fledged	67	45.3		154	41.8	

two areas.

The nature of predation. Potential predators on nests of the Clay-colored Sparrow, listed in Bent (1968), are numerous and varied (Appendix 3). Further potential mammalian predators not listed in Bent (1968) on both study areas in southwestern Manitoba include the spermophiles Spermophilus franklini (Sowls 1948, Banfield 1974) and S. tridecemlineatus (Robins 1971a, but see Banfield 1974).

An analysis of the type of predation (simultaneous versus successive removal of nest contents) showed that 41 out of 52 nests appropriate for analysis were robbed completely of their contents at one time. Most simultaneously robbed nests tended to be tipped or damaged, suggesting that ground hunting mammals were the chief predators. The successive removal of eggs from a nest over a number of days is more difficult to explain. Small rodents might have been involved in such predation (Bent 1968:762,1231), as indeed might cowbirds. The only incident of predation witnessed was by a garter snake (Thamnophis sirtalis) discovered swallowing a young Clay-colored Sparrow.

NESTING SUCCESS

In the following analyses, a successful nest is defined as one in which a Clay-colored Sparrow fledged. Two nests on Study Area #2 in 1976 were omitted from the analyses, as

in both cases the nests were empty when I checked them on the ninth day after the young hatched. A prolonged search in the area of the nest failed to reveal the young, but the parents were still present on the territory although not carrying food. Hence the outcome of both nests was classed as unknown.

Nesting success and nest height. Nests with bases constructed within 10cm of the ground were more successful than those constructed higher in the vegetation (Figure 9). When nests above and below 10cm are compared, the differences are significant (Study Area #1: $P = 0.0396$, Fisher's Exact Probability Test; Study Area #2: $X^2 = 7.94$, $P < 0.025$). For both study areas combined, 28 (61%) out of 46 nests constructed within 10cm of the ground were successful, whereas only 18 (31%) out of 59 constructed above 10cm were successful.

Nesting success in returning and in new territorial males. As male Clay-colored Sparrows showed a high degree of site tenacity on both study areas, I was able to compare nesting success of returning males and of new males establishing a territory for the first time on my study areas. As all males in 1975 on both study areas were banded, I used the nesting data for 1976 for comparison. The results (Table 7) indicate that returning males enjoyed a significantly higher degree of nesting success than new males on Study

Figure 9. Nesting success and nest height in 1976. (A) Study Area #1, N = 32 nests, (B) Study Area #2, N = 73 nests.

A

N=20

N= 6

N =4   N=2

B

N=26

N=16

N=14

N=17

NESTING SUCCESS (%)

0-10   II-20   21-30   >3I

HEIGHT ABOVE GROUND (cm)
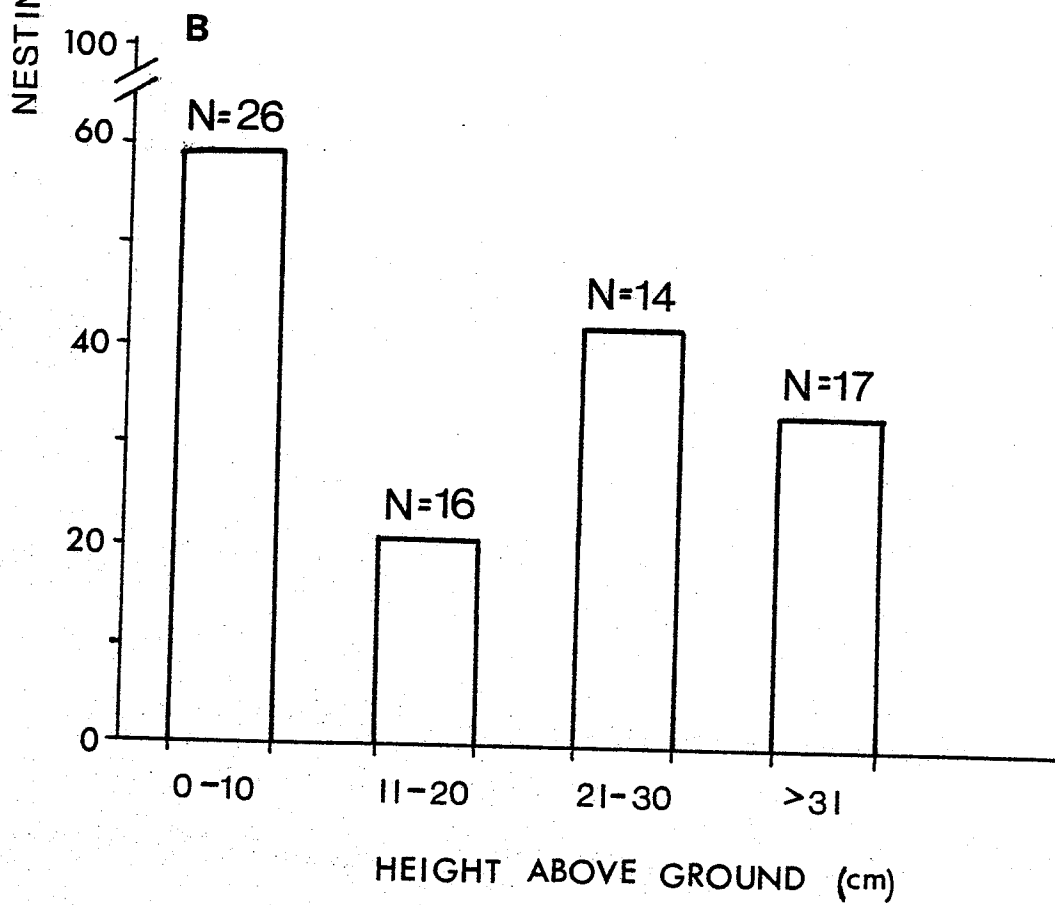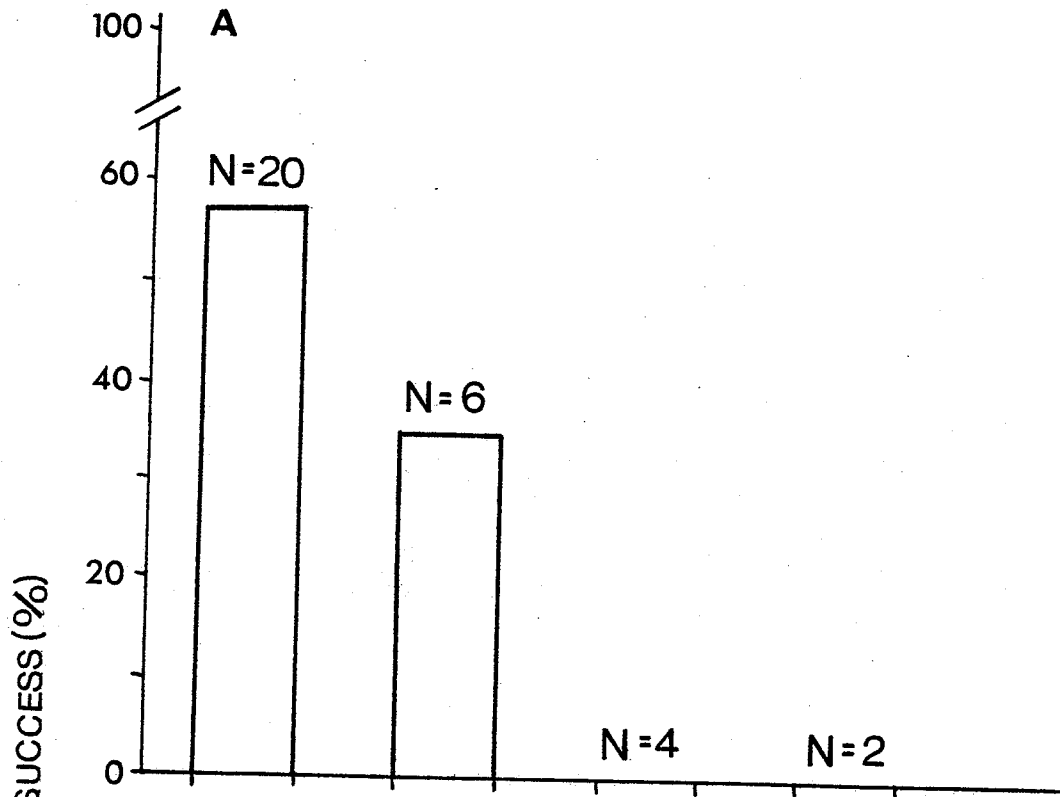
Table 7. Nesting success of returning and new territorial male
Clay-colored Sparrows.

		Successful	Unsuccessful
STUDY AREA #1	Returning	13	7
	New	2	10
STUDY AREA #2	Returning	24	29
	New	7	13

Area #1 (X^2 = 5.23, P < 0.025). On Study Area #2, nesting success was also somewhat higher for returning males (45%) as compared with new males (35%), but the difference was not significant (X^2 = 0.46).

Nesting success and cover afforded by the substrate. As noted earlier, Clay-colored Sparrows on both study areas most often constructed their nests in Symphoricarpos. However, some nests were obviously less well concealed than others, and I hypothesized that open nests would be subject to greater predation pressure than those that were better concealed. I therefore compared light meter measurements between successful and unsuccessful nests in 1976 (Table 8).

Light penetration at successful nests was significantly lower than that at unsuccessful nests on Study Area #1 (t = 2.42, P < 0.05) and on Study Area #2 (t = 2.08, P < 0.05). This suggests that nests built in vegetation that allowed high light transmission were more easily detected by predators.

Cowbird parasitism. Table 9 gives the number of parasitized nests of all species that were located on the study areas. Out of 94 parasitized nests, 84 were Clay-colored Sparrow nests, indicating that the sparrow is the major host for the cowbird in the area.

Cowbird parasitism during the study was significantly

Table 8. Incident light penetration (foot-candles expressed as log units) at successful and at unsuccessful nests of Clay-colored Sparrows in 1976. SD = standard deviation.

	Number of successful nests	Light penetration at successful nests		Number of unsuccessful nests	Light penetration at unsuccessful nests	
		Mean	SD		Mean	SD
STUDY AREA #1	15	15.54	1.12	17	16.62	2.09
STUDY AREA #2	31	15.08	0.99	42	16.93	1.33

Table 9. Parasitized nests of passerines that nested on the study areas. 1974, to 1976 data combined.

Species	Number of parasitized nests	
	Study Area #1	Study Area #2
Western Meadowlark (Sturnella neglecta)	3	0
Red-winged Blackbird (Agelaius phoeniceus)	1	0
Brewer's Blackbird (Euphagus cyanocephalus)	2	0
LeConte's Sparrow (Ammospiza leconteii)	0	1
Song Sparrow (Melospiza melodia)	0	3
Clay-colored Sparrow (Spizella pallida)	54	30
Total	60	34

higher on Study Area #1, averaging 62%, than on Study Area #2, at 22% (Table 10. $X^2 = 30.55$, $P < 0.001$). This difference correlated with the greater number of cowbirds present in Study Area #1 (Table 11), and fewer nests to parasitize. The incidence of parasitism declined considerably from 1974 through 1976 on Study Area #1. This decline may have been due to the fact that there were no cattle grazing after June 1975, and hence vegetation may have provided better concealment for the nest thereafter.

Most Clay-colored Sparrow nests that were parasitized received one or two cowbird eggs (Table 12). In all instances in which the contents of the nest were known before and after parasitism, at least one Clay-colored Sparrow egg, and occasionally two or even three eggs, disappeared, presumably removed by the female cowbird. On three occasions, one of the host's nestlings was removed and an egg substituted, a seemingly maladaptive and wasteful behavior on the part of the cowbird as in all three cases the remaining young sparrows were raised and the cowbird egg abandoned. In only one instance was a young Clay-colored Sparrow raised alongside a cowbird. In all other instances, if a cowbird was hatched and raised, it resulted in the death of the sparrow's own young.

Analysis of the response of pairs to cowbird parasitism revealed the remarkable situation that pairs on Study Area #1 were generally acceptors of cowbird eggs whilst those on

Table 10. Cowbird parasitism on nests of Clay-colored Sparrows for both study areas.

		Number of nests	Number of parasitized nests (%)
1974	Study Area #1	19	16 (84%)
	Study Area #2	22	5 (23%)
1975	Study Area #1	42	23 (55%)
	Study Area #2	42	10 (24%)
1976	Study Area #1	32	15 (47%)
	Study Area #2	75	15 (20%)

Table 11. Numbers of cowbirds counted at biweekly intervals on both study areas.

1974

	15 May	27 May	8 June	19 June	Total
Study Area #1	18	12	15	4	44
Study Area #2	16	9	10	8	43

1975

	14 May	28 May	11 June	25 June	Total
Study Area #1	22	7	8	15	52
Study Area #2	12	11	6	6	35

Table 12. Number of cowbird eggs per parasitized nest for 84 Clay-colored
Sparrow nests. 1974 to 1976 data combined.

| | Number of cowbird eggs per nest | | | |
	1	2	3	4
Study Area #1	29	20	3	2
Study Area #2	22	6	2	0

Study Area #2 were consistently rejectors (in the sense of desertion of nest) (Table 13). The differences between the two areas are significant for both years combined ($X^2 = 14.78$, $P < 0.001$).

FOOD AND FEEDING HABITS

Foraging behavior. Observations throughout the breeding season on several pairs of banded Clay-colored Sparrows indicated that the birds did not obtain food for themselves or for their young in their territories. Up to mid-May, male Clay-colored Sparrows sometimes fed on the grassy areas on the study plots adjacent to their territories, possibly because they were reluctant to fly far from their territories, before territorial boundaries with neighbors were firmly established. The vegetation on the grassy areas was not dense at this time, thereby affording open areas in which the males could forage, presumably for seeds. After mid-May, foraging and food-gathering for the young occurred away from the breeding areas, in a variety of habitats: arable and pasture land, tree bluffs, and around the edges of sloughs and marshes. Interestingly, in the period between territorial establishment and the nestling stage of the reproductive cycle, males of adjacent territories frequently foraged at about the same time of day, in the late morning and late afternoon, off the breeding areas. On 9 occasions, pairs of males from

Table 13. Comparison of parasitized nests and host responses in 63 parasitized nests of Clay-colored Sparrows on the two study areas.

| | Number of parasitized nests | Year | Fate of cowbird egg | | |
			Accepted	Rejected	Unknown
Study Area #1	23	1975	18	3	2
Study Area #2	10	1975	2	7	1
Study Area #1	15	1976	8	3	4
Study Area #2	15	1976	4	8	3

adjacent territories were observed together in the same foraging areas.

Observations of males feeding off territory showed that their behavior was markedly different to their behavior when on their territories. The males did not sing, and they tended to be quite difficult to approach closely, unlike when they were within the confines of the territory where they could be approached often within 10m. If a foraging male was constantly disturbed, he would make a quick return to his territory. No overt aggressive interactions were observed during 15 hours of observation between 6 May and 2 June, 1976, on males foraging off territory. The males fed communally, often within 2m of each other, on the foraging areas. Although individuals seemed to prefer specific foraging locations, there was no indication that males defended feeding territories.

Observations during the courtship and nest building phases indicated that males appeared to have a preference for feeding on arable land adjacent to the nesting habitat, in contrast to the females which most frequently were observed foraging in or around tree bluffs and marshy areas. This suggests that possible partitioning of the foraging areas was in operation in these sparrows.

Adult diet. Adult Clay-colored Sparrows are essentially seed eaters, consuming insects to some extent during the summer months (Bent 1968; personal observations). A wide

variety of vegetable matter (listed in Bent 1968) has been reported in the diet of this sparrow, mainly during the non-breeding season. In this study, I looked mainly at the foods presented to nestlings. However, parents were observed occasionally to eat the food which they had brought back to the nest.

Foods presented to nestlings. Adult Clay-colored Sparrows fed their young a wide variety of invertebrates (Table 14). Predominant foods were lepidopteran larvae, orthopteran nymphs, and various types of Odonata; these three groups comprised 76% of the total number of prey items recorded. A similar breadth of diet is evident in the sample of prey items collected from the nestling cowbirds (Table 15), with lepidopteran larvae and orthopteran nymphs predominating, and thus there was no indication that the adult sparrows brought different sorts of food to the young cowbirds than they did to their own young.

There were substantial differences between pairs in foods presented to nestlings (Table 16). For example, pair #5, whose territory was close to a pond overgrown with Polygonum spp., fed their young almost exclusively on narrow-winged damselflies (Family Coenagrionidae), taking advantage of a readily available and abundant food source which appeared to be localized around the pond. Pair #6 fed their young mostly short-horned grasshoppers (Family Acrididae), whilst lepidopteran larvae predominated in the

Table 14. Food items brought to nestling Clay-colored Sparrows at seven nests in 1976, as determined from direct observations and videocorder information.

Group	Number	Per cent
Orthoptera	108	18.1
Neuroptera	11	1.8
Lepidoptera		
adult	23	3.8
larvae	256	42.8
Odonata	93	15.6
Coleoptera	12	2.0
Hemiptera	1	0.1
Diptera	58	9.7
Araneida	4	0.7
Unidentified	32	5.4
Total	598	100.0

Table 15. Food items brought to four young cowbirds (about 5 - 7 days old) by their Clay-colored Sparrow foster parents.[1]

Group	Number	Per cent
Orthoptera - Tettigoniidae	3	8.1
Acrididae	8	21.6
Lepidoptera larvae	15	40.5
Odonata - Coenagrionidae	3	8.1
Coleoptera - Chrysomelidae	4	10.8
Diptera - Tabanidae	4	10.8
Total	37	100.0

1. 28 samples.

food of the remaining five pairs.

Males and females brought essentially the same type of prey items to their young in roughly the same proportions (Table 16). Horn's (1966) measure of overlap (see Appendix 4) gives an overlap value of 96%, indicating that there is no difference in prey items presented to the nestlings by males and females.

Seasonal distribution of nestling foods contributed by males and females. There was a noticeable change in the relative importance of the major food items during the course of the breeding season (Figure 10). Proportionately more lepidopteran larvae were taken in June, Odonata increased in July, and there tended to be a general increase in the relative numbers of orthopteran nymphs over the breeding season. When the total numbers of the prey items of males and females are combined, the seasonal differences are significant ($X^2 = 52.5$, $P < 0.001$).

Flight lines. Parents were not observed to gather food for their young within the confines of the territory nor over the breeding habitat as a whole. I recorded therefore the lines of flight which the birds followed between the nest and the foraging locations.

There were no major differences between members of a pair in the direction flown from a nest towards the foraging locations (Figure 11). In general, a male and a

Table 16. Foods presented to nestlings by each of seven pairs of Clay-colored Sparrows.

Prey Taxa	Pair #1 M	F	Pair #2 M	F	Pair #3 M	F	Pair #4 M	F	Pair #5 M	F	Pair #6 M	F	Pair #7 M	F	Total M	F
Orthoptera	9	6	5	2	13	10	10	8	1	0	27	17	0	0	65	43
Neuroptera	3	0	0	1	0	1	0	4	0	1	0	1	0	0	3	8
Lepidoptera																
larvae	21	24	26	18	38	30	23	26	0	1	2	6	23	18	133	123
adult	0	0	4	0	4	3	6	2	0	0	1	3	0	0	15	8
Odonata	4	8	5	2	0	1	0	2	30	36	1	2	2	0	42	51
Coleoptera	1	4	0	0	0	0	3	3	0	0	1	0	0	0	5	7
Hemiptera	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0
Diptera	16	6	5	7	0	5	2	7	0	0	1	0	4	3	30	28
Araneida	0	0	0	0	1	3	0	0	0	0	0	0	0	0	1	3
Unidentified	4	2	6	4	2	1	1	1	1	1	3	2	2	1	19	13

58

Figure 10. Seasonal distribution of major foods given to nestling Clay-colored Sparrows by their parents in 1976.
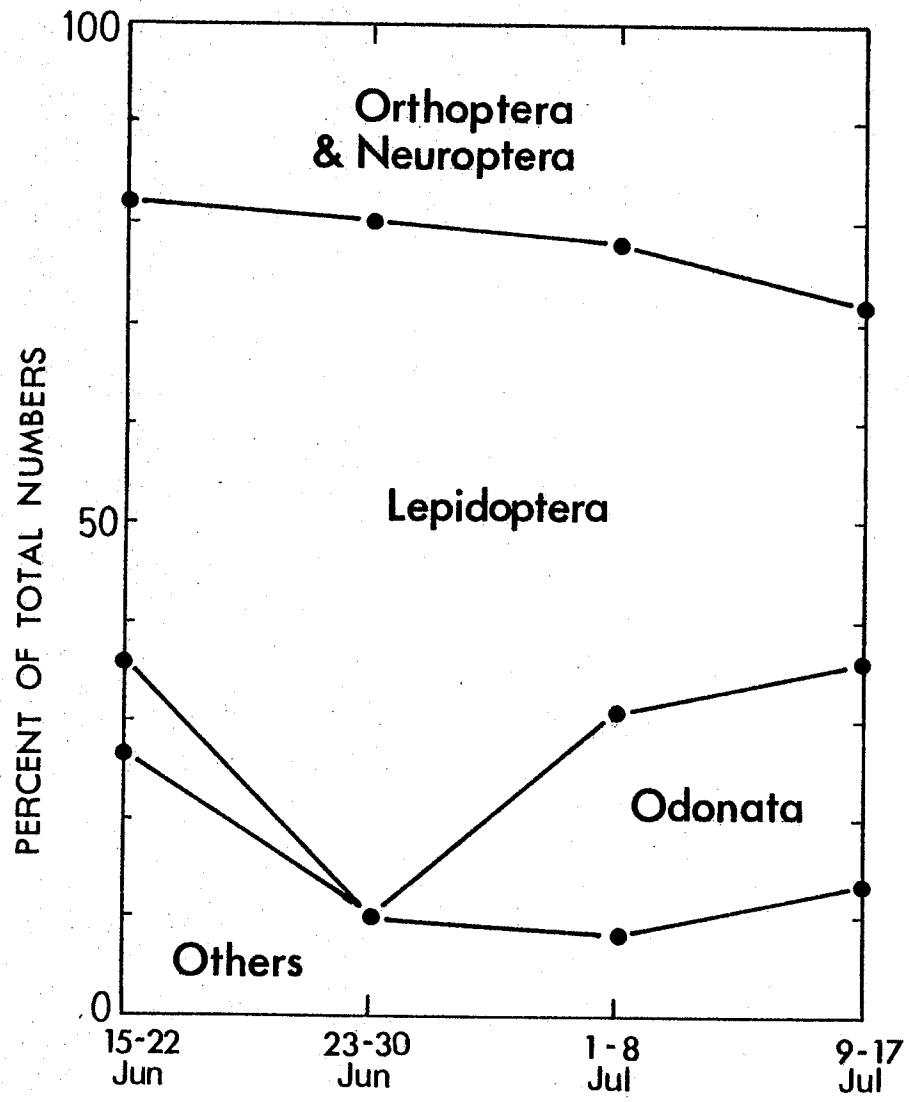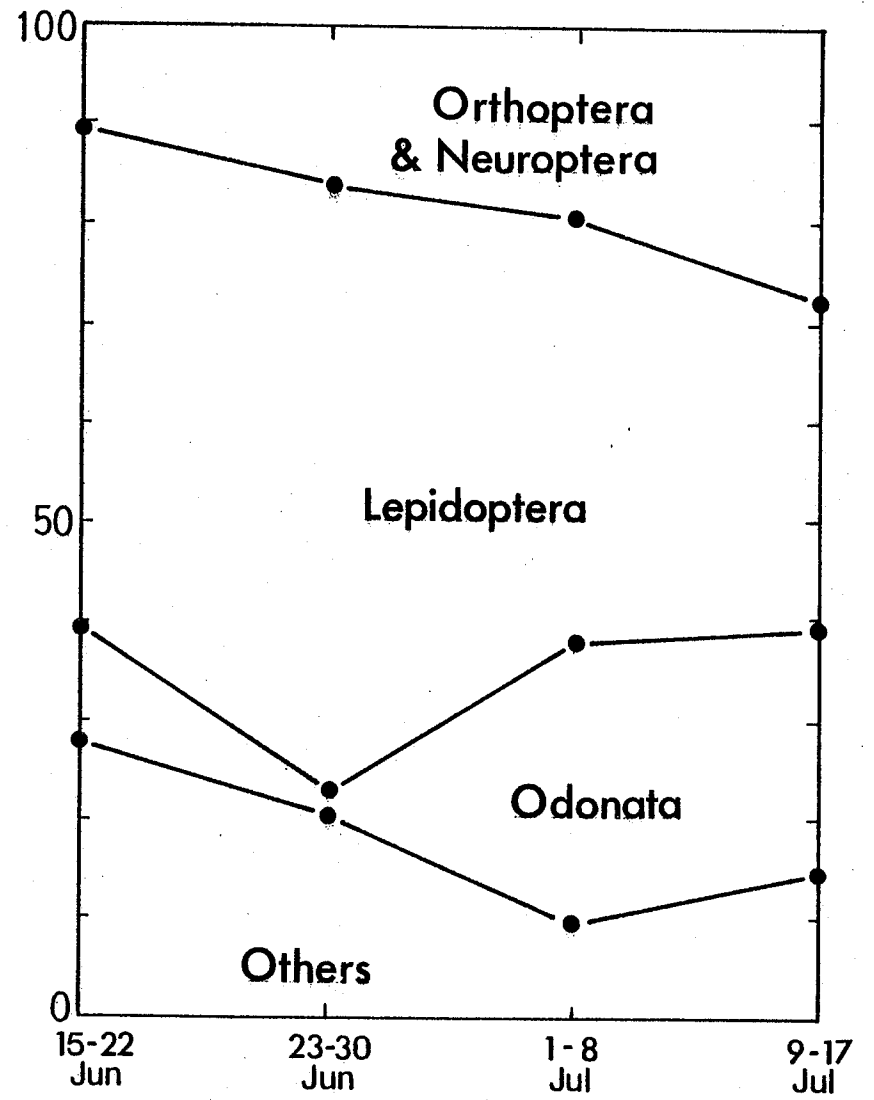
Figure 11. Direction from the nest (in % of total observations for each bird) in which males and females flew to forage during the nestling period. Each circle has a radius of 100%, and there are eight possible directions (north, north-east, east, south-east, south, south-west, west, north-west) in each circle. The solid lines represent males, the dashed lines females. The total number of flights recorded per bird are given below the respective circle.

NEST 1
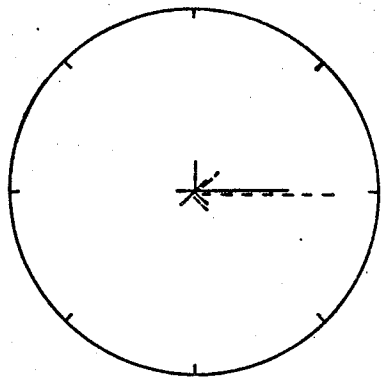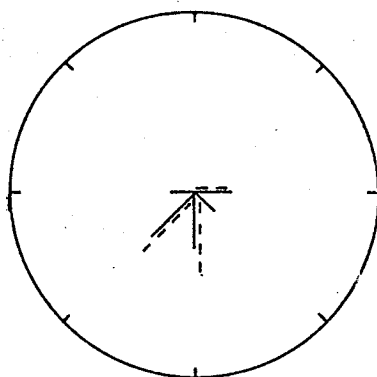
NEST 2

NEST 3

obs. M 35
obs. F 28

obs. M 41
obs. F 38

obs. M 38
obs. F 34

N

W

E

S
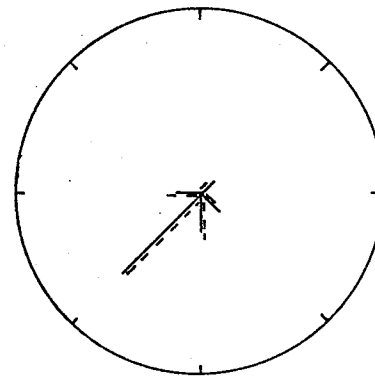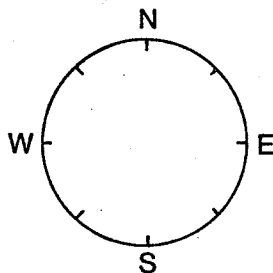
NEST 4
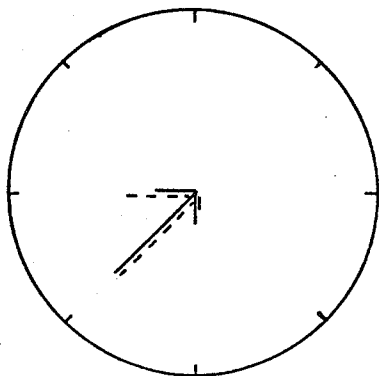
NEST 5

NEST 6

obs. M 29
obs. F 32
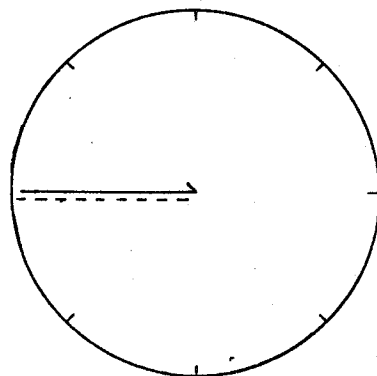
obs. M 30
obs. F 31
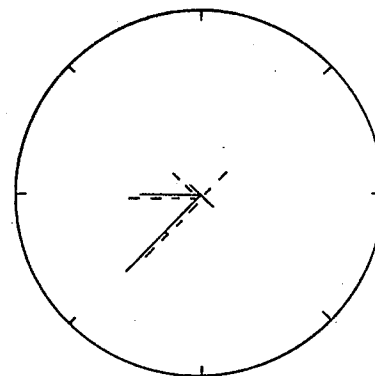
obs. M 18
obs. F 21

female of a pair, whether leaving the nest singly or together, flew predominantly in one and the same direction towards the foraging locations.

There were however substantial differences in the direction of the flight-lines between pairs (Figure 11). This is not surprising as pairs holding peripheral territories (pairs #1 and #5) tended to use feeding areas adjacent to their territories and pairs holding central territories flew to probably the closest available foraging locations. Pairs #3 and #4, which held adjacent territories and were feeding nestlings at the same time, consistently flew to the southwest on leaving their nests, and both pairs foraged in and around a large pond overgrown with vegetation. This suggested that neighboring birds might be following each other to preferred feeding locations. However, the pond was the closest foraging location to both nests, and hence the evidence for following remains inconclusive.

Distances foraged from the nest. In this analysis, pair #7 is omitted, as these birds frequently flew around an intervening bluff on leaving the nest and hence went out of sight. Foraging distances (Table 17) varied between pairs, and this was due partially to the location of the territory. Pairs #1 and #5 held territories on the periphery of the nesting habitat and they flew shorter distances, presumably because foraging locations were

Table 17. Mean distances (m) from the nest that male and female Clay-colored Sparrows flew to forage.

Pair	Male[1]	Female[1]
1	46.2	33.9
2	89.9	78.9
3	56.2	51.6
4	75.3	67.5
5	32.5	31.1
6	94.7	77.3

1. The number of foraging trips made by the males is 182, by the females 172.

closer, than the other four pairs which held territories in the middle of the nesting habitat.

The mean distances from the nest to the foraging areas were compared between mates for each direction flown (Figure 12), and were found to be significantly different (G = 13.28, P < 0.005, goodness-of-fit test, Sokal and Rohlf 1969). In all six pairs, males flew farther on average from the nest to the foraging locations than the females. This was particularly evident when the pair left the nest together; the female alighted first and closer to the nesting area than the male, who flew farther on and then alighted. This suggests that there is spatial partitioning of the foraging areas between members of a pair.

NESTLING ECOLOGY

Young Clay-colored Sparrows left the nest at about nine days of age, while still incapable of flight. They then hopped through the shrubbery, presumably searching for suitable dense cover. After moving a certain distance, they normally stopped at the base of a dense shrub, climbed it, and remained essentially motionless near its crown, waiting to be fed by their parents. The tarsus and feet of the young bird were well-developed, certainly large enough to support an aluminium band of adult size. It seems adaptive for advanced development of tarsi to occur in the

63

Figure 12. Comparison of foraging distances of six pairs of Clay-colored Sparrows in 1976. Each point represents the mean distances flown by members of a pair in one direction. Number of directions flown by each pair ranged from two to six (see Figure 11). Points lying below the line (slope = 1) indicate that males flew farther, points above the line that females flew farther.
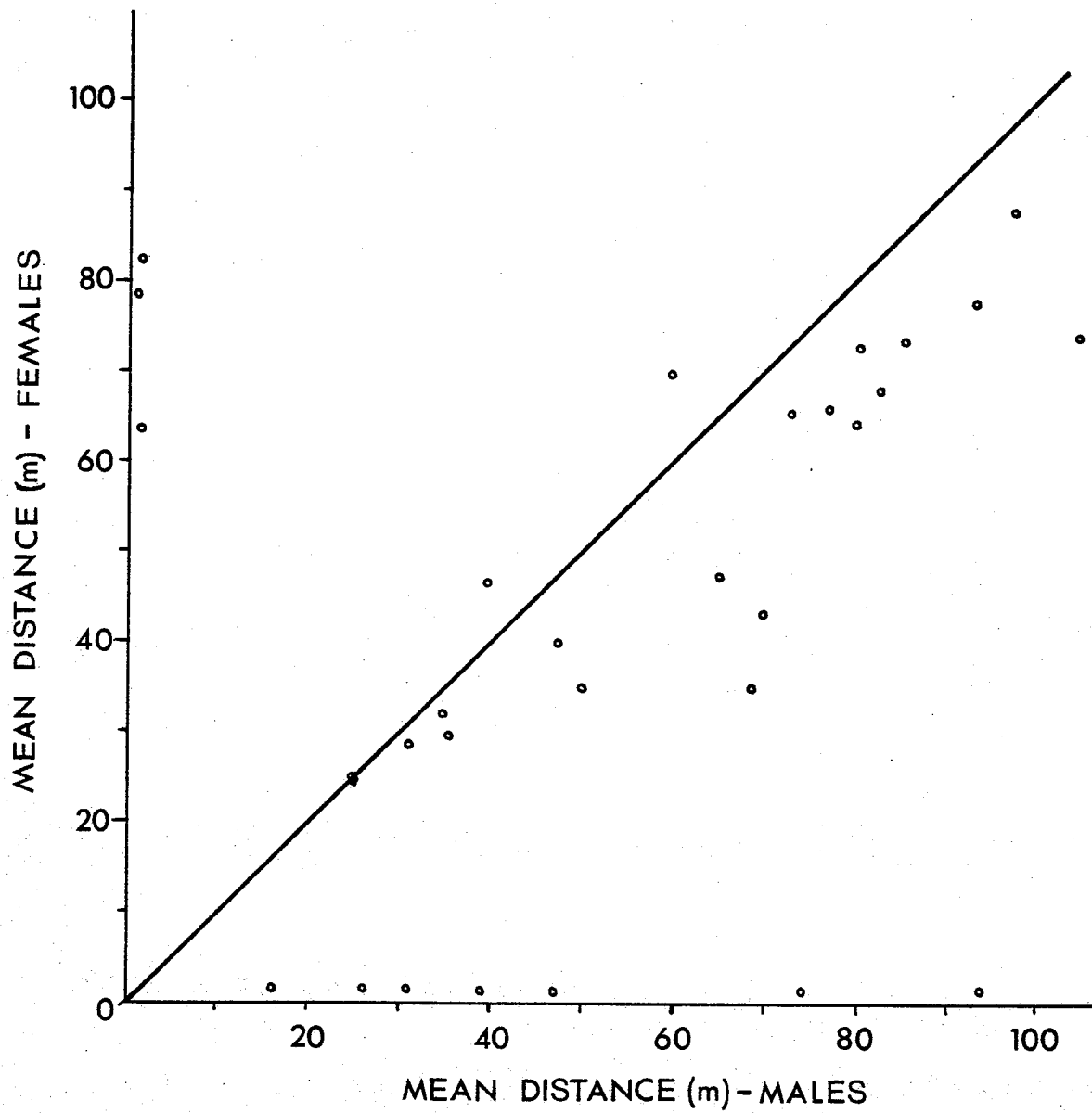
Clay-colored Sparrow young because of their high degree of mobility on leaving the nest (cf. Ricklefs 1969, O'Connor 1977).

The distances from the nest to the selected shrub for 8 young in 1976 averaged 13.6m, ranging from 6 to 21m. These young represented broods from three nests, of 3, 3, and 2 young respectively. In each case, the young dispersed radially out from the nest. The young were not clumped; rather they were widely separated from each other, possibly as an anti-predator mechanism.

Twice I saw parent Clay-colored Sparrows move through the shrubbery with a young bird following closely behind, suggesting that adults occasionally may lead newly-fledged young away from the nest site to a safer place. The young often dispersed out of their parent's territory, across the territorial boundary into an adjacent territory. On no occasion was the male holding the neighboring territory seen to show aggression towards the fledged young nor towards the parents as they flew in with food to feed the offspring. Indeed, on 21 June 1976, a male sang and preened for 20 minutes, but showed no overt agonistic behavior, towards a juvenile some 5m away which had fledged in a neighbor's territory, and was now in this male's territory. An absence of overt aggression by the territorial male persisted even though the juvenile was fed on 5 occasions, three times by its male parent and twice by

its female parent.

DISCUSSION

Site tenacity

Male Clay-colored Sparrows showed a high return rate in successive years to the study areas, and this appears adaptive for numerous reasons. Males returning to the same territory enjoyed higher nesting success than new males. Territorial boundaries between returning males were established quickly with fewer interactions than new males (Table 3).

More surprising is the low rate of return of females. This could perhaps be attributed to a high female mortality rate during the non-breeding season, but one female was known to be at least four years old at the end of the study, and nine others were known to have reached at least the age of three years. For those females that did return to the study areas, mate fidelity was also low. A similar situation exists in the congeneric Field Sparrow (Best 1977), but is in marked contrast to the situation in another grassland passerine, the Skylark, which exhibits 47% mate faithfulness in consecutive years and shows a strong correlation between the breeding success of a pair in one year and the likelihood of its remaining a pair the following year (Delius 1965). This suggests that female

Clay-colored Sparrows return to broad geographic areas, and attempt to form pair bonds with males defending the first suitable territory which the females encounter. A possible reason for this settling pattern was suggested by the data on the 'changeovers' which occurred in 1975. These involved new (= unbanded) females apparently attempting to nest for the first time mid-way through the breeding season. The presence of these females suggests that there would be a premium for the female to occupy quickly any suitable territory when she returned in the spring, rather than rely on the previous year's territory.

Greenwood and Harvey (1976) point out that, in those species in which the male establishes, defends and benefits from retaining the same territory from year to year, selection may operate for the female to disperse to a greater extent than males to avoid inbreeding, as in the case of the European Blackbird (Turdus merula) (Snow 1956). Certainly establishment and maintenance of the territory is the prerogative of the male, and his fitness is apparently enhanced by retention of the same breeding territory from year to year. There is however no evidence in Clay-colored Sparrows that females actively avoid the area in which they bred the previous year. In the Field Sparrow, Walkinshaw (1968) points out that the male would generally accept the first female that arrived on his territory and he believes this to be a causal factor in the smaller return percentage

of females; this is probably also the case in Clay-colored Sparrows.

The lack of return of nestling Clay-colored Sparrows is also surprising. It is possible that fledglings do not form site attachments to their natal area. They wandered extensively in the late summer; one individual banded as a nestling was retrapped thirteen days later 2km southwest of the study area. Also, immatures tended to collect at certain favorite locations around the study areas. Immatures of some other species, for example the Reed Warbler Acrocephalus scirpaceus (Catchpole 1974), have been shown to form site attachments to specific areas in which they congregate in the fall, and return to these areas the following spring. Such a mechanism might be operating in the Clay-colored Sparrow.

It is further possible that the preferred nesting habitat, the stands of Symphoricarpos, is not a stable one. Prairie fires were a major determinant of the distribution and composition of the vegetation in the mixed-grass prairie and aspen parkland (Bird 1961), and shrubs such as Symphoricarpos were burnt to the ground during a fire (Pelton 1953). Thus, if fires occurred frequently enough, selection would favor those first year birds that settled in suitable habitat anywhere on a broad geographic scale over those that returned to their natal area. Adults returning year after year enjoy higher nesting success than

new birds, and this may be a strong enough pressure to cause them to return in successive years to the same area when possible.

Territory establishment and maintenance

Territorial boundaries were established quickly, particularly between returning males, which settled in essentially the same territory as the year before. Common territorial boundaries could be re-established with a minimum of expended energy if neighboring males could recognize each other in successive years. Such recognition could be achieved by song recognition, as males keep the same song in successive years (Part B).

Once territorial boundaries have been established, the territorial system is most likely maintained by song, as few overt aggressive interactions were observed after mid-May. It would certainly seem maladaptive for individuals to constantly expend energy in hostile encounters once boundaries have been fixed (the 'dear enemy' phenomenon, Wilson 1975).

The speed with which male Clay-colored Sparrows established territorial boundaries is consistent with the observation that female Clay-colored Sparrows arrive on average only 5 days after the males. The female does not appear to aid her mate in establishing or defending a territory, and there would seem to be little advantage for

females that attempted to form pair bonds with males if the whole territorial system was in a state of flux. The situation is in contrast to that of some other open country sparrows (Walkinshaw 1939, Potter 1972, Welsh 1975) in which males arrived 20 days or more before the females, but also in which the territorial establishment phase was prolonged, taking much longer than in Clay-colored Sparrows.

Female arrival and a decline in aggressive interactions between males appear to coincide temporally. Catchpole (1972) noted a similar correlation between pairing and a marked decrease in male aggression in Reed Warblers. There were many instances of rival male Reed Warblers gaining portions of territories from newly paired males, whereas prior to pairing they were vigorously repulsed. This led to some shrinkage of territories after pairing. The situation in the Clay-colored Sparrow differs as territories once established did not change, and pairing and courtship both occurred without shrinkage of the territory.

No overt aggressive interactions were observed on either study area after 20 May. This contrasts sharply with the findings of Morse (1976) who found increases of intraspecific interactions in two species of wood warblers of the genus Dendroica during the fledging stage. His interpretation is that, although the warblers synchronize

their breeding season to periods of maximum food abundance,
they do not have access to such a strong pulse of food as
do, for example, Great Tits (Parus major) (Perrins 1965,
1970), with the result that searching for food requires a
great proportion of their time (Morse 1968) and probably
places a consequent premium upon maintaining a large
exclusive space to the end of the breeding season. The
situation in the Clay-colored Sparrow more closely
resembles the situation in the Great Tit (Hinde 1952) and
the Blue-gray Gnatcatcher (Polioptila caerula) (Root 1967),
where territorial defense appears to be non-existent at the
time the young fledge. This would be particularly adaptive
for the Clay-colored Sparrow as the territory is not used
to gather food. This is further supported by observations
of dispersal of young Clay-colored Sparrows after they have
left the nest, as neighboring males showed no overt
aggression to either juveniles wandering into their
territories or parents attempting to feed the juveniles,
which might have been predicted if food were an important
resource within the territory.

It is not clear why pairs should have attempted second
broods in 1976, but not in 1975. It is possible that the
shortened breeding season in 1975 was below a threshold
value needed if double-broodedness was to occur. Moreover,
'changeovers' took place, indicating that it might have
been adaptive for the original pairs not to expend energy

in attempting a second brood, whereas the energy cost on the replacement pairs would be proportionately less, if this was their first nesting attempt of the season.

Nest site selection and nesting success

Nesting losses due to predation were greatest during the egg stage, hence the predators did not appear to be cueing in on either the increased activity of the parents as they fed nestlings or on the presence of nestlings rather than eggs in the nest. This suggests that predators are not locating Clay-colored Sparrow nests primarily by olfactory or auditory cues.

There is evidence to support the hypothesis that predators were locating nests by sight. Pairs of Clay-colored Sparrows which have the highest nesting success are those that selected nest sites which offered a high degree of nest concealment. Most pairs appeared to minimize the chance of having their nests detected by predators hunting by sight by constructing their nests primarily in Symphoricarpos, which allowed less light penetration than other shrubs. However, females may not have been selecting Symphoricarpos per se as a nest site, but rather could have chosen sites which offered a high degree of nest concealment, with Symphoricarpos offering better nest concealment than the other vegetation.

Pairs that nested close (within 10cm) to the ground

enjoyed higher rates of nesting success than those nesting higher in the vegetation. The visual outline of the nest might not have been easy to detect if the nest was close to the ground as light penetration was lower there than higher in the vegetation. Thus, it is possible that the major nest predators were ground dwelling mammals locating the nest from beneath and seeing it as a dark silhouette against the sky.

Spermophiles were thought to be involved in nest predation on another species of grassland sparrow, Passerherbulus henslowii, (Robins 1971a), and Robins (1971a:44) adds that ground squirrels may be important predators on ground nesting birds because of their diurnal foraging behavior. Franklin's Ground Squirrel is an omnivorous feeder (Banfield 1974), and its depredations can be quite severe on ground nesting birds (Sowls 1948). The animal was fairly common on both study areas in all three years of my study and may have been responsible for the loss of many nests, particularly those in which all the contents of the nest disappeared simultaneously and the nest was tipped or damaged.

A comparison between returning and new males showed that returning males enjoyed greater nesting success than new males; it seems reasonable, although not indisputable, that returning birds can be equated with older, and hence more experienced, birds whilst new birds are younger, possibly

nesting for the first time. Thus, older birds probably
have a higher nesting success that younger ones, as found
by other workers investigating differential reproductive
success with age of birds (e.g. Coulson 1966, Mills 1973).

Cowbird parasitism

When Clay-colored Sparrows hatched and raised cowbird
young, it almost invariably resulted in the death of the
sparrow's own young. It would therefore be adaptive for
the sparrows to evolve some mechanism to counteract
parasitism. Certainly the eggs of the two species are
vastly different in color and size. The sparrows' eggs are
blue, sparingly marked with spots of dark brown at the
large end of the egg whereas the cowbirds' eggs are whitish
densely speckled with various shades of brown. Bent (1968)
gives the average measurements for 50 sparrow eggs as
17.1mm by 12.7mm, and for 127 cowbird eggs as 21.45mm by
16.42mm (Bent 1965). Thus, there is no doubt as to the
identity of the egg.

Rejection of the parasite's egg by the sparrows, by
removal or desertion, would prevent an unnecessary
channelling of the parents' energy and time into raising
the cowbird at the expense of their own young. The
Clay-colored Sparrow is probably not physically equipped to
remove a cowbird's egg, therefore the only avenue
apparently open to it would be to desert and then renest.

Rothstein (1974) classified most hosts of the cowbird into either acceptors or rejectors. Only a few species fell in the area between these two designations. Although not listed by Rothstein (1974), the Clay-colored Sparrow appears to be one such species. On a broad geographic scale, this species has been reported as incubating and/or raising cowbirds in Saskatchewan (Fox 1961), Manitoba and North Dakota (Bent 1968), whereas in Alberta they are reported as being 'wholly intolerant of parasitism' (Salt 1966). The birds in southwestern Manitoba appear to be a combination of both.

Although one population (Study Area #1) were generally acceptors whilst the other (Study Area #2) were consistently rejectors, there is little evidence that the two populations are genetically programmed to deal with the parasite's egg in different ways. No individual banded on one area was observed on the other, although the two areas are only 12km apart, but there was also no evidence that young returned to their natal area to breed, a necessary requisite if gene flow between populations is to be restricted.

Individual pairs within one season were consistently either acceptors or rejectors of the parasite's egg, thus Shortt's comment (IN Bent 1968) that Clay-colored Sparrows seemed more tolerant of cowbird parasitism towards the close of the season is not borne out. Interestingly, of

six females that were parasitized in both 1975 and 1976, the same four were acceptors and the same two rejectors in both years.

It is possible that effective defenses against cowbird parasitism may not have fully developed in passerine species inhabiting brush areas and forest edges. Species of the grassland edge may have been only partially exposed to the cowbird over the ages (Mayfield 1965, Friedmann 1963); such possibly is the case in the Clay-colored Sparrow.

Food and foraging behavior

Clay-colored Sparrows presented a wide variety of prey items to their young, and they collected the prey in a variety of foraging locations off territory.

It is possible that the differences in prey items brought to the young by different pairs is a reflection of the age of the young: a change in the proportion of prey items in the nestling diet might occur as the young grow older (Betts 1955, Royama 1970, Robins 1971b, Best 1977a). However, similar aged nestlings did not receive the same foods. For example, the oldest nestlings in nests #1, #4 and #6 were about the same age (about 6 days) during the observation periods, yet orthopterans were more prominent in pair #6's prey items than in the other two in which lepidopteran larvae predominated. Moreover, the oldest

nestlings in nests #2, #5 and #7 were about 5 days of age, yet Odonata were the chief food in nest #5 and lepidopteran larvae in the other two. Finally, the young in nest #3, at about 3 days old, also received predominantly lepidopteran larvae. This raises doubts that the birds were selectively choosing prey according to the age of the nestlings. Interestingly, nestlings of pair #3, the youngest nestlings under observation, were the only young to receive spiders, which is consistent with Royama's (1970) suggestion that spiders have special nutritional value important for nestling growth at an early age.

Males and females did not differ either in the type or the proportion of prey items presented to their young (Table 16). Hence the sexes did not appear to select different food items in order to reduce intersexual competition. This is perhaps not surprising as the sparrows are essentially monomorphic in culmen depth and length, and in length of tarsometatarsus (Appendix 1).

Although males and females used essentially the same foods, possible reduced intersexual competition for food was evident early in the breeding season when males and females foraged in different habitats. More evidence for reduced intersexual competition for food appears during the nestling stage, when males and females again used different localities in which to collect food. Equally important is that females foraged closer to the nesting site than the

males (Figure 12), a tendency reported in some other passerines (e.g. Morse 1968, Wiens 1969, Robins 1971b, Busby 1978). The energy demands on the two sexes are not the same. The female does practically all the brooding of the young, and she expends energy in creating heat for the young. On the other hand, territorial defense, the prerogative of the male, is minimal during the nestling stage. It would therefore appear to be most advantageous to the Clay-colored Sparrow if measures to conserve energy during foraging were selectively in operation in females. As the adults followed the same flight lines from the nest to the closest available feeding areas, avoidance of intersexual competition was possible merely as a result of the male's tendency to forage at a slightly greater distance from the nest than the female.

PART B

DIALECTS, INDIVIDUAL DIFFERENCES IN SONG,

AND SONG REPERTOIRE

IN THE CLAY-COLORED SPARROW, Spizella pallida

INTRODUCTION

Topics of avian acoustical behavior that have received considerable attention in recent years include the existence and function of dialects (e.g. Thielcke 1969, Nottebohm 1972, Lemon 1975, Avery and Oring 1977), differences in vocalizations between individuals (e.g. Armstrong 1973, Thorpe 1968, Beer 1970, Evans 1970, Harris and Lemon 1972), and the width and significance of song repertoires (e.g. Bertram 1970, Armstrong 1973, Hartshorne 1973, Dobson and Lemon 1975, Krebs 1977). In this study, I investigated these topics in the Clay-colored Sparrow, *Spizella pallida* (Fam. Fringillidae).

Dialects are widespread in the Fringillidae (e.g. Marler 1952, Marler and Tamura 1962, Dittus and Lemon 1969, Milligan and Verner 1971), but their existence has not been examined in Clay-colored Sparrows. I therefore examined the question of whether dialects exist in this species. Individual variation, both within a population and between years within the same individual, was also examined to determine the relationship, if any, between individuals and group (dialect) differences.

Casual observations during the 1974 breeding season

revealed that some males had more than one song type in their repertoire, and that they often appeared to be countersinging by matching neighbor's songs. Other studies (Walkinshaw 1939, Willing 1970, but c.f. Bent 1968) have reported only one song type in the repertoire of this species; however, none of these studies systematically investigated size of song repertoire in individually marked birds. I therefore investigated in more detail the song repertoires of a sample of males to see if a male had more than one song type in his repertoire, and I attempted to determine the context in which each song type, if more than one, was used. I also investigated matched counter-singing by playback experiments and monitoring responses, and by comparing the songs of neighboring birds to identify similarities, if any, between them.

The Clay-colored Sparrow has several characteristics that make it ideal for investigations of avian acoustical behavior. Its song has a simple and repetitive structure (see below), and is relatively easy to analyze (c.f. Marler and Mundinger 1970). This is unlike the more elaborate songs of other members of the Fringillidae which have been intensively studied (e.g. Thompson 1970, Emlen 1971a, Harris and Lemon 1972, Lemon 1975, Mundinger 1975). During my study, no female was ever observed to sing; all tape-recordings used in the analyses were of territorial males. A male usually sang from conspicuous elevated

perches and repeated the same song in regular succession, in the order of 6 to 9 songs per minute. In addition the males defended small territories with well defined boundaries, and they showed a high return rate from one year to the next (Part A), all features which aid in the functional analysis of the species' acoustical behavior.

METHODS

Clay-colored Sparrows were studied on two research areas, about 12km apart, in extreme southwestern Manitoba near Lyleton (see Figure 1, Part A). Tape-recordings of songs of color-banded males were made in May and June in 1975 and 1976. For each male whose songs were used in the investigation of song repertoires, I determined the size and boundary of its territory (Part C), and thus I could plot the position of each song perch within the territory.

On 29 May 1977, I tape-recorded three territorial males near the University of Manitoba Campus in Winnipeg, Manitoba. On 6 June 1977, I tape-recorded four territorial males at the University of Manitoba Field Station, about 5km west of Delta, Manitoba (see Figure 1, Part A).

All songs were recorded at a tape speed of 19cps on a Uher 4400 tape recorder, using a Uher M539 microphone placed at the focal point of a 60cm parabolic reflector. For analysis of the songs, I used a Kay Electric Company 675 sonagraph at the wide band-pass filter setting. Each song was analysed at two speeds, at 2.4 seconds to allow measurements of the whole song, and 0.8 seconds to allow finer measurements of the structure and frequency range of the song.

Songs of Clay-colored Sparrows are usually described in

terms of a series of buzzes (e.g. Borror 1961, Bent 1968).
However, Davis (1964a) refers to buzzes as motifs. Borror
(1961) describes each buzz as consisting of a series of
similar phrases, each phrase comprised of two or three
notes whereas Davis (1964a) uses the term figure for phrase
and segment for note.

Some attempts have been made to standardize the
terminology used to describe bird song (e.g. Davis 1964b,
Shiovitz 1975, Verner 1976). In this paper, I follow
Verner's definitions of terms, and use the terms buzz,
syllable and note in referring to parts of a Clay-colored
Sparrow's song. Figure 1 presents sonagrams useful in
reference to terms used in the text. The term buzz is
particularly convenient, not only because of the
descriptive nature of the word and the fact that it is
ingrained in the literature in describing a Clay-colored
Sparrow's song, but also because it fits Verner's
(1976:265) definition of 'a sound utterance with
notes....repeated from about 56 to 267 per second'. A
syllable was comprised usually of two notes, the first an
ascending frequency modulation and the second a descending
frequency modulation (Figure 1). Occasionally a syllable
was comprised of up to six notes, each note the same, the
notes making a distinct identifiable unit. All
Clay-colored Sparrow songs analyzed in this study were
monosyllabic, consisting of the same syllable repeated.

Figure 1. Sample sonagram with identification of terms used in this study to designate parts of songs of Clay-colored Sparrows. Sonagram of song of a territorial male on 19 May 1975. For explanation of a syllable, see text.
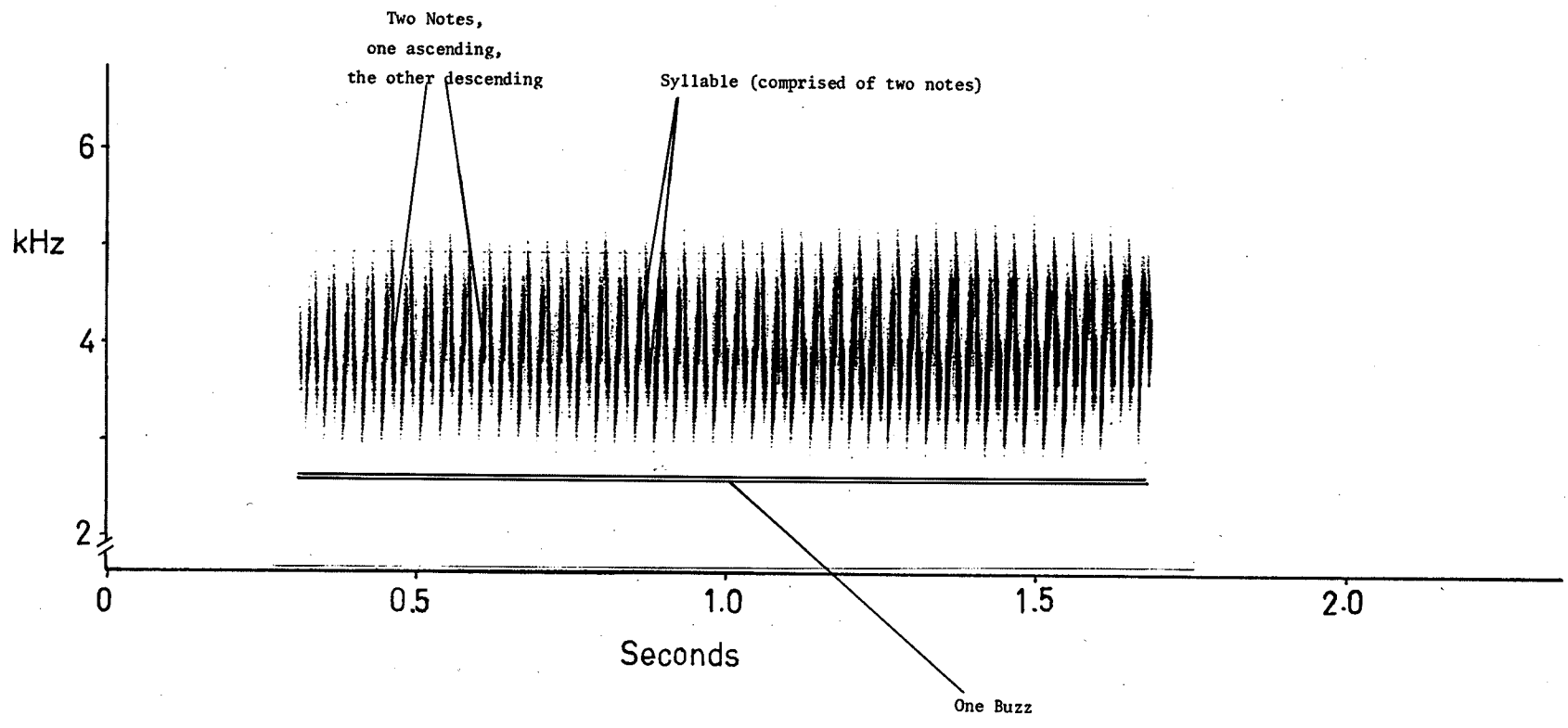
Each song was analyzed for the following eleven characteristics. (1) Total length of the song. This was measured in seconds from the beginning of the first buzz to the end of the last buzz, including intervals between buzzes. (2) Length of the first buzz, in seconds. (3) Interbuzz intervals, in seconds. For songs of only two buzzes, the interval was one measure. For songs consisting of more than two buzzes, the mean of the grouped interbuzz intervals was used. (4) Number of syllables per song. (5) Number of notes per syllable. (6) Number of buzzes per song. (7) The rate of note utterance, expressed as the number of notes per second. (8) The upper frequency limit, and (9) the lower frequency limit. Both (8) and (9) were measured to the nearest 500hz, and assigned to the closest value on a scale from 0 to 10khz in half kilohertz increments. (10) The ascending frequency modulation of a note within the syllable (FM ascending), and (11) the descending frequency modulation of a note within the syllable (FM descending). Both (10) and (11) are expressed as rates of change of frequency modulation in hertz per millisecond. This was achieved by measuring the absolute value of the slope of the note. Most birds had a FM descending component, but several birds lacked a FM ascending component, in their songs.

Two analyses were run to attempt to identify differences, if any, between the songs of different

populations of Clay-colored Sparrows. The first was between the two study areas in southwestern Manitoba. In this analysis, I used ten males per study area and five songs per male. All the songs were tape-recorded in the morning between 22 and 29 May 1976. However, as these two study areas were in the same geographic area, I decided to run an additional analysis. This was between the two populations in southwestern Manitoba, a sample of territorial birds from Delta, and a fourth sample of territorial birds from Winnipeg. The distance from Winnipeg to Delta is about 135km, from Delta to Lyleton 240km, and from Lyleton to Winnipeg 295km. To equalize sample sizes, three males with three songs per male were chosen from each population. The songs of an individual male used in the analyses were sung consecutively from one song perch, representing therefore only one song type per male.

In 1975, I carried out playback experiments on 9 territorial males on the study areas, to assess their response to two different song types. The rationale behind the experiment was that if different song types conveyed different information, then the recipients of the stimulus should respond differently. The experiments were undertaken between 0700 and 0900 hours between 18 and 24 May, when nest building and clutch initiation were under way (Part A), thus removing the time of the breeding cycle

as a potential variable affecting a bird's response to the playback (c.f. Verner and Milligan 1971, Petrinovitch et al. 1976). The songs used in the experiment were probably unfamiliar to the test birds, as they were tape-recorded from a male holding a territory about 8km from the nearest study area.

Two experimental tapes were used, one of two-buzz length and the other of eight-buzz length, each of three minute duration. The eight-buzz tape was made by duplicating the second buzz of the two-buzz song six times. The experimental tapes were played back through a loud speaker from the Uher 4400 tape-recorder at a constant volume. The speaker was placed about 30cm above the ground, and a mount of a Clay-colored Sparrow in a perching position was secured on top of the speaker. The speaker and the mount were placed centrally in the territory of each test bird.

Males were tested on consecutive days with the two tapes presented in random order. Data were taken on each test bird for three periods (before, during and after playbacks), each period being of three minutes duration. I recorded three visible responses: the latency of response, the closest approach to the speaker and mount, and the number of flights over the speaker and mount. Each response was ranked on a scale of one point to three points (Table 1), indicating an increasing intensity of response. The scores for each response were then summed for each

Table 1. Ranking of interactions within each of three visible responses to experimental playbacks.

Visible Responses		Rank[1]
Latency of response (seconds)	0 - 5	3
	6 - 10	2
	more than 10	1
Closest approach to speaker and mount (cm)	0	3
	1 - 50	2
	more than 50	1
Number of flights over speaker and mount	more than 10	3
	6 - 10	2
	0 - 5	1

1. Higher ranks within each behavior category were assumed to reflect higher intensity of response.

bird, thus providing an index of response intensity for each bird. I also recorded two audible responses, the rate of singing and the number of buzzes per song during each period. This method of evaluating the intensity of the agonistic response by an individual to a playback has been used by Emlen (1971b) and Heidemann and Oring (1976).

Finally, the movements of six males on their territories were observed, and their songs tape-recorded after they had changed perches, in early June 1976. The songs of each bird were all recorded on the same day, between 0600 and 1000 hours. Although I tried to record songs at all perches, some songs at certain perches were missed, thus some songs in an individual's repertoire may have been missed. Perches were classed as being centrally or peripherally located in relation to the territorial boundaries of the test bird, and the position of the perch relative to the nest was determined.

For the purpose of analyses, songs from the repertoire of an individual male were frequently chosen by the quality of the tape-recording. If one song during a recording session produced a clear sonagraphic trace, with minimal interference from external noise, then successive songs in the same recording session generally produced clear analyzable traces. Thus, there was no set pattern in selecting songs, unless otherwise specified, other than the clarity of the sonagram.

RESULTS

The existence of dialects

There were no significant differences in either analyses between the two study areas at Lyleton, or between the Lyleton, Delta, and Winnipeg populations, for any of the eleven characteristics measured (Tables 2 and 3). In the comparisons between the two main study areas (Table 2), no characteristic approached significance. One characteristic approached significance in the comparisons between the widely spaced populations (Table 3): the number of syllables per song ($0.05 < P < 0.1$). These results indicate that dialects are not evident in at least a large part of the Clay-colored Sparrow's breeding range in southern Manitoba. This lack of evidence for the existence of dialects is probably not because all songs are similar between the various areas, but because there are large variations between the individuals within the different populations (see below).

Songs of males within and between years

Recordings of 12 males at Lyleton in 1975 were analyzed for comparisons between individuals. The twelve males were all recorded in the early morning in late May on one study area. Sonagrams of five songs were made for each individual male. The five songs per male were sung

Table 2. Comparison of songs between two populations of Clay-colored Sparrows from the two main study areas at Lyleton.

Song Characteristic	Study Area #1		Study Area #2			
	Mean[1]	SD	Mean[1]	SD	F[2]	P
Total song length (sec)	1.72	0.26	1.74	0.19	1.86	ns
Length of first buzz (sec)	0.75	0.19	0.81	0.21	2.99	ns
Interbuzz interval (sec x 10^{-2})	9.9	0.9	10.1	1.9	1.88	ns
Number of syllables/song	133.4	48.4	129.1	47.7	3.21	ns
Number of buzzes/song	2.6	0.5	2.6	0.6	2.48	ns
Number of notes/syllable	2.7	1.5	2.9	1.5	*	*
Number of notes/second	199.1	33.1	202.9	36.7	3.67	ns
Upper frequency limit (khz)	6.3	0.3	6.4	0.3	0.96	ns
Lower frequency limit (khz)	2.2	0.2	2.2	0.2	1.28	ns
FM(ascending) (hz/sec x 10^{-2})	2.22	1.38	1.96	1.03	1.73	ns
FM(descending) (hz/sec x 10^{-2})	1.85	0.78	1.73	0.62	3.16	ns

1. Each mean value is the mean of measurements for 10 birds (five songs per bird). The means for individual birds are listed in Appendix 5.
2. The data were analyzed by a two-factor mixed design, with repeat measures on one factor (Bruning and Kintz 1968). ns = not significant. F = F(between areas).
* The number of notes per syllable did not vary between songs of each bird; $t = 0.29$, not significant.

Table 3. Comparison of songs between four populations of Clay-colored Sparrows.

Song characteristic	Study Area #1		Study Area #2		Delta		Winnipeg		F[2]	p
	Mean[1]	SD	Mean[1]	SD	Mean[1]	SD	Mean[1]	SD		
Total song length (sec)	1.64	0.29	1.66	0.17	1.74	0.29	1.71	0.29	3.18	ns
Length of first buzz (sec)	0.80	0.22	0.88	0.18	0.95	0.16	0.91	0.22	2.37	ns
Interbuzz interval (sec x 10^{-2})	10.1	1.4	9.2	1.2	10.5	0.8	9.5	1.1	0.67	ns
Number of syllables/song	117.4	60.6	114.3	59.1	182.4	104.7	149.7	31.0	3.42	ns
Number of buzzes/song	2.3	0.6	2.1	0.2	2.3	0.6	2.7	0.6	0.45	ns
Number of notes/syllable	3.3	2.3	3.0	1.7	2.3	1.5	2.0	0.0	——*	—*
Number of notes/second	214.4	48.5	182.7	29.5	205.6	18.5	195.6	25.7	2.88	ns
Upper frequency limit (khz)	6.1	0.1	6.2	0.3	6.6	0.1	6.3	0.3	1.24	ns
Lower frequency limit (khz)	2.2	0.3	2.1	0.1	2.4	0.1	2.4	0.2	1.66	ns
FM(ascending) (hz/sec x 10^{-2})	2.81	2.64	2.22	0.82	1.88	0.12	2.07	1.39	2.10	ns
FM(descending) (hz/sec x 10^{-2})	1.90	1.22	1.69	0.32	0.97	0.42	1.67	0.98	2.42	ns

1. Each mean value is the mean of measurements taken on three birds (three songs per bird). Three males lacked a FM(ascending) component in their songs. Means for individual birds are listed in Appendix 5.
2. The data were analyzed by a two-factor mixed design with repeat measures on one factor (Bruning and Kintz 1968). F = F(between areas). ns = not significant.
* The number of notes per syllable did not vary between songs of each bird. One-way analysis of variance, F = 0.16, not significant.

consecutively from one perch, and thus were of one song type per male.

Of the 11 characteristics used in the analysis, there were greater differences between than within individuals in all but the upper and lower frequency limits (Table 4). The most significant differences between the songs of individuals occurred in the number of syllables per song, the rate of note utterance, and the frequency modulation of both the ascending and descending notes in a syllable.

No two individuals had songs which were similar in all song parameters, and an individual male could be discriminated, by a combination of characteristics, from any other male. To my ears, at least one song type of a male seemed to be individually distinct from that of any other male, including neighboring territory holders, and I could individually recognize many territorial males by their songs. It seems more than likely that the birds themselves could do likewise.

Male Clay-colored Sparrows showed a high rate of return from 1975 to 1976 on the two main study areas (Part A), and therefore presented an opportunity to investigate the hypothesis that songs are retained unchanged from one year to the next. Songs used in this analysis were all recorded in late May or early June. As some song types within an individual male are quite variable (see below), song types between years within the same males were matched, primarily

Table 4. Analysis of individual differences among 12 Clay-colored Sparrows.[1]

Song characteristic	BIRD #			F	P<
	1	2	3		
Total song length (sec)	1.67 ± 0.08	1.92 ± 0.13	1.39 ± 0.08	5.66	0.01
Length of first buzz (sec)	0.79 ± 0.02	1.14 ± 0.04	0.87 ± 0.03	100.74	0.001
Interbuzz interval (sec x 10^{-2})	8.8 ± 0.3	13.3 ± 0.3	8.6 ± 0.2	52.47	0.001
Number of syllables/song	127.2 ± 4.2	111.4 ± 6.0	52.8 ± 2.4	444.33	0.001
Number of buzzes/song	2.0 ± 0	2.4 ± 0.6	2.0 ± 0	20.97	0.01
Number of notes/syllable	2.0 ± 0	2.0 ± 0	6.0 ± 0	—*	—*
Number of notes/second	160.1 ± 16.7	124.4 ± 3.2	245.2 ± 2.9	389.46	0.001
Upper frequency limit (khz)	6.2 ± 0.6	5.9 ± 0.2	6.4 ± 0	2.62	ns
Lower frequency limit (khz)	2.3 ± 0.3	2.3 ± 0.3	2.5 ± 0.4	1.75	ns
FM(ascending) (hz/sec x 10^{-2})	0.96 ± 0.07	——	——	350.60	0.001
FM(descending) (hz/sec x 10^{-2})	1.54 ± 0.07	1.08 ± 0.07	1.25 ± 0.1	190.50	0.001

1. Each value represents the mean of measurements taken of five songs per bird, with standard deviations given per mean. The songs of three males are represented in this table: the songs of the remaining nine are given in Appendix 6. One-way analysis of variance (Sokal and Rohlf 1969) was applied to each of the 11 characteristics of the song for all 12 birds.
* The number of notes/syllable did not vary within each bird.

on the basis of the number of buzzes per song.

Out of the 20 males which had been tape-recorded in 1975, 13 returned in 1976. A comparison of their songs showed that there was a high correlation between the two years for all ten characteristics (Table 5). Although songs within the repertoires of individual males were not chosen at random, and were deliberately matched between years, nevertheless the result that no other differences between years appeared indicated that at least one song type for each male was retained from one year to the next. Tape-recordings in 1975 were not sufficient to allow comparisons of all song types within a male's repertoire between the two years.

Song repertoire and song matching

Observations in 1974 suggested that individual male Clay-colored Sparrows had more than one song type in their repertoire. In 1975, observations on 13 males in mid-May indicated that at least one characteristic, the number of buzzes per song, was variable for 11 (85%) of the males (Table 6). Therefore in early June 1976 the repertoires of six males were recorded, from different perches within their territories. The repertoires of two males are given as examples in Table 7, and the repertoires of the remaining four in Appendix 7. An interesting pattern emerges from these results. Some individual males appear

Table 5. Similarities in songs between years in Clay-colored Sparrows.

Song characteristic	Number of males	1975 Mean[1]	1976 Mean[1]	Paired t-test	r
Total song length (sec)	13	1.71	1.70	0.38	0.84
Length of first buzz (sec)	13	0.72	0.72	0.37	0.99
Interbuzz interval (sec x 10^{-2})	13	11.3	11.4	0.05	0.84
Number of syllables/song	13	137.8	141.8	0.65	0.99
Number of notes/syllable	13	2.8	2.8	0	1.00
Number of notes/second	13	201.0	200.2	0.58	0.99
Upper frequency limit (khz)	13	6.1	6.0	0.94	0.90
Lower frequency limit (khz)	13	2.3	2.5	0.97	0.86
FM(ascending) (hz/sec x 10^{-2})	6	2.66	2.62	1.16	0.98
FM(descending) (hz/sec x 10^{-2})	11	1.69	1.68	0.35	0.99

1. Each value represents a mean of the song measurements of 13 males, except for the FM(ascending) and FM(descending) characteristics which were absent in some songs. None of the t-tests is statistically significant (P > 0.05), whereas all of the correlations are (P < 0.01).

Table 6. Frequency of occurrence of various numbers of buzzes per song for 13 males observed for varying time periods in mid-May 1975.

Date	Male	Number of buzzes/song										Total number of songs	Duration of observation period (min)
		1	2	3	4	5	6	7	8	9	10		
14 May	A	—	39	7	20	2	—	—	—	—	—	68	12
	B	—	83	13	—	—	—	—	—	—	—	96	15
	C	35	—	—	—	—	—	—	—	—	—	35	7
	D	—	49	1	—	—	1	4	4	31	—	90	15
	E	—	65	10	—	—	—	—	—	—	—	75	11
	F	—	—	34	—	6	1	14	1	—	—	56	10
	G	—	86	7	—	—	—	—	1	—	1	95	12
15 May	H	—	92	43	—	—	—	—	—	—	—	135	21
	I	—	24	6	—	—	8	—	—	—	—	38	10
	J	—	19	9	—	—	—	—	5	—	—	33	6
	K	—	20	—	—	—	4	7	—	—	—	31	6
	L	—	72	6	—	—	—	—	—	—	—	78	13
	M	44	—	—	—	—	—	—	—	—	—	44	7
	Total	79	389	136	20	8	14	25	11	31	1	874	145

Table 7. Comparison of songs delivered from different perches (a - d) for two males.[1]

Song characteristic	Male #1						Male #2					
	a	b	c	d	F	P<	a	b	c	d	F	P<
Total song length (sec)	1.82	3.28	2.63	1.86	51.6	0.001	1.96	2.92	1.30	1.81	111.7	0.001
Length of first buzz (sec)	0.95	0.53	0.66	0.94	54.6	0.001	0.61	0.34	0.56	1.09	29.3	0.01
Interbuzz interval (sec x 10^{-2})	12.3	14.7	14.0	12.0	29.8	0.01	12.5	21.7	12.6	11.5	191.1	0.001
Number of syllables/song	75.0	286.3	250.0	78.3	373.7	0.001	143.0	261.3	98.7	135.7	405.7	0.001
Number of buzzes/song	2.0	6.0	3.7	2.0	129.0	0.001	3.0	5.0	2.0	2.0	65.0	0.001
Number of notes/syllable	2	1	1	2	—	—*	1	2	1	2	—	—*
Number of notes/second	90.8	111.6	112.3	89.9	46.3	0.001	81.9	279.6	84.6	253.2	317.8	0.001
Upper frequency limit (khz)	6.5	6.2	6.5	6.3	1.8	ns	6.0	6.0	6.0	6.0	—	—*
Lower frequency limit (khz)	2.2	2.0	2.0	2.3	1.8	ns	2.3	2.0	2.7	2.0	7.3	0.05
FM(ascending) (hz/sec x 10^{-2})	0	2.62	2.50	0	31.4	0.01	0.75	0.62	0.88	0.84	398.8	0.001
FM(descending) (hz/sec x 10^{-2})	1.46	1.03	1.06	1.51	85.8	0.001	0.68	1.28	0.66	0.78	520.8	0.001

1. Each value represents a mean of measurements taken of four songs from a given perch for each bird. The data were analyzed by one-way analysos of variance (Sokal and Rohlf 1969).
* The values for these characteristics did not vary within song types.

to have more than one song type, and they sing these song types from different song perches. However, they may also sing the same song type from more than one perch. Male #1 had essentially two song types, the first sung on perches a and d, and the other on perches b and c. The only differences between the songs on perch b and c appear to be a result of the number of buzzes per song, and hence song length and the number of syllables per song, all other characteristics being similar (Table 7). Birds #2 and #5 also had two song types, sung on different perches, whereas birds #3 and #4 sang essentially one song type, almost all variation in the analyses being caused by a change in the number of buzzes per song, the structure of the syllable remaining unchanged (Appendix 7).

Bird #6 had the most variation of all birds. There appeared to be three song types, one on perch a and c, which varied only with respect to the number of buzzes per song, a second on perch b, and a third on perch d (Table 7).

In only one case (bird #5) did a male sing a type of song on a centrally located perch that was not also sung on at least one peripherally located perch (Table 8). One male did not sing from a central perch during the observation and tape-recording sessions. The other four males sang one type of song on a central perch and the same song type on at least one peripheral song perch. Thus

Table 8. Summary of song types and song perches in relation to the position of the perches in the territory.

Male #	Location of song perch		Number of song types	Number of song types sung from:	
	Central	Peripheral		central perches	peripheral perches
1	1	3	2	1	2
2	1	3	2	1	2
3	1	4	1	1	1
4	0	3	1	0	1
5	1	2	2	1	1
6	1	3	3	1	3

there was no consistent pattern of different song types with central versus peripheral areas of the territory.

As nests tended to be built at the periphery of the territory (Part C), it was possible that a change in song type with change in song perch was related to the distance of that perch from the nest, and hence the female. The number of song types given from perches on the half of the territory lying nearest to the nest and those given from perches on the half of the territory lying furthest from the nest for five males are given in Table 9. I did not locate the nest of one male (#5) until six days after I had tape-recorded his songs, hence I have omitted this bird from the analysis.

Males #3 and #4 had only one song type in their repertoires, which they sang on both near and far song perches. Of the remaining three males, two (#2 and #6) sang different song types on near and far perches and one male (#1), with two song types in his repertoire, sang both types near to the nest but only one far from the nest. In each of these three males, one song type was given exclusively near to the nest. There was a similarity in the song type given exclusively by these three males (#1, #2, #6) on near perches. This song type was the longest (in seconds) and had the most number of buzzes in each of the bird's repertoire.

It is also possible that the occurrence of different

Table 9. Comparison of number of song types with distance of singing perch from the nest in the Clay-colored Sparrow.

Male #	Total number of song types	Near Perches		Far Perches	
		Number of near perches	Number of song types	Number of far perches	Number of song types
1	2	2	2	2	1
2	2	1	1	3	1
3	1	2	1	1	1
4	1	2	1	3	1
6	3	1	1	3	2

song types was in some way related to a tendency for neighboring birds to share or match at least some characteristics of their songs. To test this possibility, songs of neighboring territorial males were compared. As all territory holders in 1975 were color-banded, it was possible to identify returning as well as new territory holders in 1976. The songs of both groups were recorded, and the tape-recordings compared between pairs of new and returning neighbors, between pairs of new neighbors, and between pairs of returning neighbors.

There was no evidence from the analyses (Table 10) that neighboring males sang 'like' songs if the males were both new territory holders or if they were both returning territory holders; they did not match songs, at least with the neighbor against which the test bird was tested. There was only weak evidence of similarity between neighbor's songs when new and returning males were compared. Only one characteristic, the frequency modulation of the ascending note of the syllable between returning and new males, is significant ($P < 0.05$).

Observations in 1974 suggested that neighboring males were countersinging by matching the number of buzzes per song. To test this hypothesis, I carried out playback experiments with songs of different numbers of buzzes. I also simultaneously collected information on the hypothesis that a different number of buzzes within a song conveys

Table 10. Comparison of songs of neighboring Clay-colored Sparrow territory holders.

Song characteristic	New[1]	New	r	Old[2]	New	r	Old	Old	r
Total song length (sec)	1.80	1.85	0.11	1.67	1.79	0.19	1.69	1.75	0.50
Length of first buzz (sec)	0.82	0.92	0.45	0.78	0.68	0.16	0.70	0.69	0.11
Interbuzz interval (sec x 10^{-2})	11.2	10.9	0.02	12.1	11.3	0.54	10.3	11.9	0.46
Number of syllables/song	170.4	126.2	0.10	177.0	150.5	0.31	121.3	163.0	0.53
Number of buzzes/song	3.2	2.8	0.15	2.6	2.3	0.13	2.7	2.9	0.14
Number of notes/syllable	2.8	2.8	0.33	1.8	2.8	0.33	2.7	2.3	0.39
Number of notes/second	206.4	212.3	0.32	197.7	225.3	0.12	204.7	193.1	0.46
Upper frequency limit (khz)	6.2	6.0	0.23	6.2	6.1	0.21	6.1	6.2	0.11
Lower frequency limit (khz)	2.3	2.3	0.26	2.3	2.2	0.45	2.3	2.4	0.25
FM(ascending) (hz/sec x 10^{-2})	1.89	2.04	0.47	2.42	2.25	0.72*	2.88	2.43	0.35
FM(descending) (hz/sec x 10^{-2})	3.02	2.87	0.56	2.00	1.98	0.19	2.22	1.68	0.25
Number of pairs analyzed		9			12			11	

1. 'New' refere to a territory holder establishing a territory for the first time, and 'old' refers to a male returning to the territory he held the year before on the study areas.
* $P < 0.05$. None of the other r values is significant.

different information to the recipient, and hence might elicit a different response.

The general response of a male to the playback was to stop singing and fly close to the loud speaker and mounted bird. Some test birds remained close to the loud speaker for the duration of the three-minute playback period, constantly flying back and forth over the mount, without uttering an audible vocalization. Others would fly to a perch close to the speaker, after making a few flights over the mount and speaker, and there begin to sing.

The visible responses are summarized in Table 11. There was no significant difference between the responses of individual males to a 'short' song (two-buzz) as opposed to a 'long' song (eight-buzz), (T = 11.5, Wilcoxon matched-pairs signed rank test). Individual males tended to be consistent in their level of response to both of the playback tapes. Thus, differences in number of buzzes per song did not invoke different visible responses from territorial males.

The audible responses to the playback tapes are summarized in Table 12. One individual (male #2) did not leave his song perch during either of the playback experiments, nor did he change his song. He did however increase his rate of singing during the playback period with the 'long' song, and maintained it at pre-test levels for the 'short' song on the following day. This was in

Table 11. Indices of visible responses of individual males to playbacks of two experimental tapes.[1]

Male #	'Short' song[2]	'Long' song[2]
1	7	7
2	3	3
3	8	9
4	6	8
5	9	9
6	8	9
7	7	7
8	6	5
9	8	9

1. Each value represents the sum of three ranks, obtained as outlined in Table 1.
2. 'Short' song = 2-buzz experimental playback, 'Long' song = 8-buzz experimental playback.

Table 12. Audible responses of individual male Clay-colored Sparrows to playbacks of two experimental tapes.

	Male #	Number of songs delivered per three minute period			Mean number of buzzes per song		
		Before	During	After[1]	Before	During	After[1]
'Long'[2] song	1	18	4	30	3	6	3.2
	2	19	28	24	2	2	2
	3	15	0	10	—	—	—
	4	15	0	12	—	—	—
	5	12	0	10	—	—	—
	6	10	3	12	2	5.5	2.2
	7	12	2	15	3	3.4	3.2
	8	19	12	15	3	3	3
	9	12	4	15	2	7	2
	Total	131	53	143	15	26.9	15.6
	Mean	14.7	5.9	15.9	2.5	4.5	2.6
'Short'[2] song	1	17	6	18	3	3	3
	2	16	18	18	2	2	2
	3	17	0	5	—	—	—
	4	16	4	15	2	3	2.4
	5	17	0	15	—	—	—
	6	12	6	10	2	2.5	2.2
	7	15	10	10	3	3	3
	8	18	6	12	3	2.6	2.8
	9	15	3	13	2	2.4	2.2
	Total	143	53	116	17	21.5	17.6
	Mean	15.9	5.9	12.8	1.9	2.4	2.0

1. Before, During and After refer to three minute time intervals before, during and after playback of each experimental tape.
2. See Table 11 for definitions of 'long' and 'short' songs.

contrast to the general response of the eight remaining test birds, all of which reduced their rate of singing during the playbacks. For all birds combined, the reduction in the amount of singing during the playback period was significant ('long' song, $F = 5.73$, $P < 0.05$; 'short' song, $F = 9.40$, $P < 0.01$).

There is some evidence that males changed their songs by increasing the number of buzzes per song when responding to the 'long' song ($F = 5.01$, $P < 0.05$), whereas there were no changes in numbers of buzzes when the 'short' song was played back ($F = 0.41$, not significant). This result is consistent with the hypothesis that the number of buzzes in one male's song is influenced by the number of buzzes in another male's song, and hence provides some evidence for song matching.

DISCUSSION

Dialects and individual differences

Several members of the Fringillidae exhibit song dialects (review in Lemon 1975; Mundinger 1975, Eberhardt and Baptista 1977). In the Clay-colored Sparrow, however, there is a lack of conformity in the songs of birds within a locality, and dialects apparently do not exist, as the differences in songs of Clay-colored Sparrows more than 200km apart are no greater than the differences within localities. Further, there is at best only weak experimental evidence that males match songs (there is some copying of the number of buzzes per song). There is very little evidence that they do so under natural conditions (Table 10).

The lack of evidence for the existence of dialects in this sparrow correlates with large variations between individual males within an area. Individual variation in song between adjacent individuals within a population has been shown to occur in almost all studies conducted on passerines (c.f. Marler and Hamilton 1966). Most studies on dialects, in spite of this individual variation, have however been able to identify some characteristic which has less variation within a population than between populations. No such characteristic was identified from among the eleven song parameters measured in this study.

If populations are isolated geographically or ecologically, dialects can develop (Nottebohm 1972, Mundinger 1975). Isolating mechanisms such as geographical separation or ecological differences are probably not in operation on a local population level in the Clay-colored Sparrows in the central plains of North America, as populations are not widely separated and occur in the same sorts of habitat on a broad geographic scale.

There is a high return rate of adult males to the territory which they held the previous year (Part A), and males retain the same song from one year to the next (Table 5). However, no evidence was obtained of young returning to their natal areas; no banded nestling, from a total of 146 banded over 3 years, was subsequently located on either study area in any year (Part A), thus no information on the transmission of song types from father to son is available. The essential questions then are where and when does a male Clay-colored Sparrow crystallize his song. If song learning in the Clay-colored Sparrow occurs in the bird's first fall, and the young birds do not show site tenacity, then dialects could not easily occur. On the other hand, if song learning occurred in the bird's first spring, then dialects could develop (see Kroodsma 1974, Thompson 1976). However, new territory holders in the Clay-colored Sparrow did not copy an established neighbor's song (Table 10). Thus, whenever the sensitive period for song learning

occurs in the Clay-colored Sparrow, it does not appear conducive to the establishment of dialects.

Nottebohm (1969, 1972) and Nottebohm and Selander (1972) hypothesized that dialects function to promote local adaptation. The difference in songs between populations inhabiting adjacent but different habitats might limit gene flow, and thus enhance the adaptation of each population to its own local conditions. Dialectal differences correlate with genetic differences among populations of the White-crowned Sparrow _Zonotrichia leucophrys_ (Baker 1974, 1975), and changes in song pattern occur at points of abrupt habitat shifts in the Chingolo _Z. capensis_ (Nottebohm 1969). In the Clay-colored Sparrow, then, one would not expect that dialects would develop across the great plains of North America, which is a broadly homogeneous area, but they could presumably occur in populations occupying habitats on the fringe of the central plains, such as the mountain valleys of British Columbia or in the young forest plantations of eastern North America (Bent 1968). Comparisons of songs between these fringe areas remain to be made.

Finally, the apparent lack of dialects in the Clay-colored Sparrow suggests that 'dialect-specific assortative mating' (see Nottebohm 1969, Avery and Oring 1977), in which a female's choice of a mate is influenced by his song dialect, is not in operation in the

Clay-colored Sparrow. This may be partially due to the low rate of return between years of female Clay-colored Sparrows (Part A).

The significance of song repertoires

Much information is coded in the song of a bird (e.g. Emlen 1971b, Falls 1969, Shiovitz 1975), and it is generally acknowledged that different songs or variants of a given song may carry different information, especially modifying information such as probability (Smith 1977) or motivation level (Falls 1969). Moreover the same 'message' in the song from one individual may have different meanings to the recipient, depending on the context given, and the meaning may differ for different recipients (Smith 1969, 1977). In the Clay-colored Sparrow, the change in song with change in song perch is intriguing. What type of information change, if any, is associated with different songs given from different perches, and what is the functional significance of the different songs?

Morse (1970) contended that, in the Black-throated Green Warbler (Dendroica virens), separate song types are used in different functional contexts, one type for territorial defense and the other for courtship and pair-bond maintenance, whereas Lein (1972) argued that song types in this warbler represent segments of a motivational continuum. As the first of these interpretations is

functional, and the second causal, they need not be mutually exclusive. One can predict that, for both of these arguments, songs uttered from centrally located song perches would be different from those uttered from peripherally located ones within a male's territory. Morse's argument would predict that a central song perch would be closer to the nest, and hence the female, thus a song type functioning in pair-bond maintenance should be given more frequently on central rather than on peripheral song perches. Lein's argument, which is partly based on sensory stimuli (presence or absence of males nearby), would predict that where a bird feels most secure, or less aroused (the centre of his territory), he should give one type of song, and this type should gradually change as he moves into areas in which he feels less secure, or more aroused (the periphery of his territory).

In the Clay-colored Sparrow, there is some evidence that song types are being used in different functional contexts. Three out of five males used one song type exclusively whilst on a song perch close to the incubating female, which is at least consistent with the idea that a song type is used in pair-bond maintenance, but is also consistent with other interpretations. There is also some evidence that male Clay-colored Sparrows may have been using special songs to convey information to the female later in the breeding cycle. On 13 occasions, whilst I was collecting

information from blinds on nestling foods (Part A), I observed the following behavior: a male presented food either to the nestlings whilst the female was also present or to the female who then fed the food to the young. After doing so, the male flew to a conspicuous perch close to the nest, uttered a 'long' song in the form of many short buzzes (between 8 and 15) and with short interbuzz intervals (for three songs, a mean of 0.057 seconds), and then flew off towards a food gathering area. The song was never uttered when the male was alone at the nest, and it thus appeared as if the male was passing information to the female by means of this song type. However, playbacks of songs differing in the number of buzzes per song failed to elicit different levels of response in territorial males, hence the difference may not lie in the number of buzzes per song per se, but in a combination of the characteristics of the song.

Motivational information could probably be conveyed by modification of one song type, and Clay-colored Sparrows do change the parameters of songs sung consecutively of one song type in numerous subtle ways, as well as changing song types themselves. However, different song types were not related to position within the territory (central versus peripheral). It remains possible that song types are related to distance of the perch from the nest and the female, and hence may relate to different motivational

states of the male.

Whether or not we accept that the different song types can be explained by either or both of the above hypotheses, other non-mutually exclusive interpretations remain possible. Krebs (1977) discussed some major current hypotheses in addition to those outlined above, that have been put forward to explain the significance of a varied song repertoire. These additional hypotheses are individual recognition, sexual selection, habituation, matched countersinging, and Krebs' own 'Beau Geste' hypothesis.

Individual recognition of individual males by females and/or other males could be facilitated by having a small repertoire consisting of more than one song type if a single song type is common to all males in a given population (Verner 1976). A large song repertoire, however, would presumably make individual recognition more difficult, and, as Krebs (1977) points out, it is probably the least likely explanation for a large song repertoire. The fact that a male sometimes changes his song type when changing perches argues against individual recognition as a major selective factor favoring a large song repertoire.

The idea that sexual selection is involved in song repertoire rests on the assumption that females might choose males on the basis of the size of the male's singing repertoire (Kroodsma 1977). For example, males with larger

or 'better' territories might have larger song repertoires
and thus could be better at attracting females (e.g.
Howard 1974, Catchpole 1976, Krebs 1977). Whether the
female's choice is influenced by the size of the male's
repertoire or the size or quality of the territory in the
Clay-colored Sparrow is not clear. In my study, all
territorial males attracted a female, irrespective of the
size of their song repertoire or the size of the territory
(Part A). Further, no male attracted two females. Also,
neither the size of the territory nor the number of young
fledged per male showed any consistent relationship with
repertoire size for six test males (Table 13).

Hartshorne (1956,1973) suggested that a varied
repertoire could function to reduce habituation in the
listeners. According to this hypothesis, if a bird sings
the same song repeatedly, the song will tend to lose its
effectiveness as a signal because of habituation by the
responders. In Clay-colored Sparrows, no two consecutive
songs, even within one song type, are identical, and most
birds examined had more than one song type. Thus, reduced
habituation appears to be a possible hypothesis to explain
variations both within and between song types in this
species. Why such a reduction in habituation should be
favored by natural selection remains less clear, however,
since habituation provides a potentially adaptive means of
reducing unnecessary responses to individually recognizable

Table 13. Comparison of repertoire size with size of territory and number of young fledged per territory (as calculated in Part C) in a sample of Clay-colored Sparrows.

Male #	Number of song types	Size of territory (m^2)	Number of young fledged/territory
1	2	645	4
2	2	585	2
3	1	648	0
4	1	545	2
5	2	786	0
6	3	760	3

neighbors (Falls 1969). Further, retention of song from year to year, as occurs in the Clay-colored Sparrow, may function in reducing aggressive encounters between returning males, and habituation is possibly the basic mechanism involved in maintenance of lowered aggression levels between adjacent territory holders.

Song type matching by countersinging neighbors, which has been found in numerous species (review in Verner 1976), provides another possible interpretation for the occurrence of a varied song repertoire. Verner argues that matched countersinging has been important in the evolution of different song types in the Long-billed Marsh Wren Telmatodytes palustris, by functioning to maximize attentiveness between neighbors (1976:289).

There is some evidence that matched countersinging occurs in Clay-colored Sparrows, as some males altered their songs, at least in the number of buzzes per song, to approximately match an experimental playback. However, comparisons of song types between adjacent territory holders revealed no obvious pattern. If matching during countersinging is important in territory maintenance, then one might expect it to occur most obviously in those males which are establishing territories for the first time. Extensive similarities in song figures have been found between old and new territory holders in several passerines (e.g. Thompson 1970, Lemon 1965, 1967, Kroodsma 1974).

This is not the case in the Clay-colored Sparrow. Only one characteristic of the songs of new territory holders was significantly correlated with those of adjacent returning territory holders. Countersinging, by increasing the number of buzzes, thus occurred only when a male appeared "threatened" inside his own territory during playback experiments.

The 'Beau Geste' hypothesis, proposed by Krebs (1977), states that repertoires have evolved in the context of density assessment. According to this hypothesis, territorial birds may increase the apparent density of singing territorial males in a given area by use of a varied repertoire, so that non-territorial birds, using song as a means of assessing density (see Fretwell 1972) and hence suitability of an area for nesting, may be dissuaded from attempting to establish a territory there.

The evidence from this study is consistent with the 'Beau Geste' hypothesis. Firstly, there must presumably be a surplus of males which are prevented from taking a territory by the territory holders. Removal experiments (Part C) showed that such a surplus existed. Secondly, Krebs (1977) predicted that changes in perches should synchronize with changes in song types, which is evident in this study. Lastly, Krebs argues that the hypothesis should apply to discontinuous singers with small repertoires. The Clay-colored Sparrow is a discontinuous

singer, as its continuity value (calculated by dividing song length by its cadence[1], Hartshorne 1973) is less than 0.20. Its repertoire is also small, up to three song types per male, although it is difficult to see how this is a prediction (Krebs 1977) of the hypothesis, as fewer song types per male means less 'Beau Geste' effect. Krebs (1977) also states that the hypothesis is most likely to apply to birds living in dense habitats, where singing males are not easily visible. This is not the case in the Clay-colored Sparrows, which inhabit a relatively open type of habitat.

The differences between the 'Beau Geste' and matched countersinging hypotheses relate primarily to the targets at which the songs are aimed, the first at non-territorial males and the latter at a neighboring territory holder. But the end result could be the same in both cases, in the maintenance of the territorial system by matching songs with neighbors whilst simultaneously creating a false impression of density to non-territorial birds. The same system could simultaneously be favored by sexual selection. Moreover, these evolutionary explanations are consistent with the possibility that song types also differ in functionally meaningful ways, according to the proximity of the female, which could in turn provide a motivational

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1. Cadence is defined as song length plus length of the following silent interval (Dobson and Lemon 1975)

basis underlying the causation of the different song types. Thus it is probably not practical to search for any single 'function' of song repertoire, but rather to consider its adaptive consequences by asking the question: how does the size of an individual's repertoire maximize that individual's fitness?

In summary, then, I have found that dialects do not occur in the Clay-colored Sparrow in localities widely separated from each other, in spite of the fact that some conditions exist for the establishment of dialects, such as the retention of at least one song type from one year to the next and a high return rate of males in consecutive years. The lack of dialects is not because all males have a similar song type, but rather is associated with a large amount of variation in songs between individuals both within and between populations. The hypothesis that song dialects function to promote adaptation to local environmental conditions is at least consistent with the situation in the Clay-colored Sparrows, for one would predict that in a homogeneous environment occupied by contiguous populations, as is the case for the populations I studied, dialects would not easily develop.

I next found that most Clay-colored Sparrows examined had more than one song type in their repertoires. Several possible selective forces could be active in determining the width of song repertoire. Individual recognition and

sexual selection appear unlikely in view of the change of song type with the change of song perch. Some evidence was obtained that was consistent with matched countersinging (under experimental conditions only) and the conveyance of different information to specific targets, but the data are perhaps most consistent with Krebs' 'Beau Geste' hypothesis as an explanation of the significance of song repertoire in the Clay-colored Sparrow.

PART C

OPTIMUM SIZE OF TERRITORY IN THE CLAY-COLORED SPARROW,

Spizella pallida

INTRODUCTION

Spacing systems in populations of animals are products of the relationship between ecological and behavioral forces. Several reviews of avian social systems have concluded that the spacing system in a bird population is a joint adaptation to food distribution and safety from predators afforded by available nesting sites (Crook 1965; Lack 1968; Horn 1968; Orians 1971; Brown 1975; Wilson 1975). Size of territory in a territorial spacing system should then be a compromise between these forces of food and predation. Within a given nesting habitat, there should presumably be a certain size of territory which is more frequently defended than others, and this size could be optimum in terms of reproductive success. I examined this postulate for two populations of Clay-colored Sparrows in southwestern Manitoba.

I first determined the size of the territory defended by the sparrows. I determined the position of the nest within the territory, and I then investigated the hypothesis that nest spacing was influenced by predation on the nest contents (e.g. Horn 1968, Post 1974). I also tested the hypothesis that variability in size of territory is a

result of different levels of aggression of individual territorial males. I then investigated several other proximate factors which could influence size of territory, such as pressure from neighboring males, variations in habitat structure, and age of the territorial male.

As food is not gathered within the territorial boundaries (Part A), territories located around the periphery of the nesting habitat might be favoured over ones located in the centre of the nesting habitat, as the birds might have shorter flight lines to feeding areas, and hence expend less energy. There should therefore be more potential competition for peripheral territories, and I hypothesized that this would result in peripheral territories being smaller, enjoying higher reproductive success, and/or being occupied first.

It is possible that all birds present on the area established territories, territorial behavior working merely to distribute the population evenly. The size of the population and hence the territories could have been determined by other factors, such as mortality on the wintering grounds. An experimental demonstration of a surplus population, potentially capable of breeding but prevented from doing so by the territorial behavior of the territorial birds, constitutes one effective method of experimentally refuting this hypothesis (e.g. Watson and Moss 1970). I therefore carried out removal experiments to

test for the existence of such a surplus.

Finally, I investigated the possibility that the most frequently defended size of territory was optimal in terms of reproductive success, individuals maximizing their reproductive fitness by defending a particular size of territory.

Size of territory in this sparrow has been reported as being quite small, between 0.1 and 0.4 ha (Fox 1961; Salt 1966; Bent 1968), although in none of these studies were individually marked birds used nor were the boundaries of defended territories determined. Hence estimates of the sizes of territories have been, at best, rough approximations. Analysis of sizes of territories in the populations of Clay-colored Sparrows in southern Manitoba indicated that on average they were smaller than those reported elsewhere in the literature (see below).

The Clay-colored Sparrow is a particularly appropriate species for this kind of functional study as territories are small and are exclusive areas once boundaries between territorial males have been established during mid-May. The birds are relatively easy to capture, and nests are not difficult to locate (Part A). Further, the birds are conspicuous, they allow close approach, and they are easy to observe in the structurally simple habitats in which they occur.

METHODS

Two populations of Clay-colored Sparrows were studied in southwestern Manitoba near the town of Lyleton during the breeding seasons of 1974, 1975 and 1976. The two areas were about 12km apart, between 5.6 and 5.9ha in size, and each contained extensive stands of low shrubs, principally Symphoricarpos occidentalis. The male Clay-colored Sparrows established their territories over these stands. Over 800 birds were banded during the study, and all territorial pairs during the last two summers of research were color-banded, thus permitting recognition of individuals. Males showed a high rate of return from one year to the next, and in general returned to the territory they held the year before. Females on the other hand showed a low rate of return, and rarely returned to either the same territory or the same mate in succeeding years. During the course of the study, 232 nests were located, and for each nest its outcome and its position within the territory were determined. More details are given in Part A.

Determination of territorial boundaries and sizes

Territorial boundaries were determined after the majority of males had arrived. Males established territories quickly (Part A): no trespassing of

neighboring males was recorded after 20 May, and the territory did not vary in size or shape until late into the breeding season, at the time when adults were occupied in feeding fledged young. Determination of territorial boundaries was greatly facilitated by the topography, which was essentially flat and thus allowed a wide uninterrupted view of large portions of a study area and greatly aided observations on the movements of individual birds and of pairs of adjacent territorial males. Also, the computation of size of territory was helped by the fact that there was a very small vertical component in the low shrub communities defended by the sparrows.

Territorial boundaries were determined using the following information. The most important criteria were the number and location of song perches. Males perched conspicuously whilst singing and they frequently changed song perches between bouts of singing. Song perches were the exclusive property of particular territorial males; no two males were ever observed to use the same song perch once territories had been established. Boundaries were fixed at the mid-point between the nearest song perches of adjacent territorial males, and these perches were rarely more than 5m apart. Several observations on the behavior of territorial males tended to support this procedure. When a non-territorial bird appeared on the nesting habitat, it would be chased out of one territory into the

next, the neighboring male taking over the chase once the intruder had been chased across the territorial boundary into his territory. Also, males could be flushed from shrub to shrub within the territory (the 'territory flush' technique of Wiens 1969, 1973). Each male was flushed no fewer than ten times, and the male kept within a clearly delineated area. If a male was driven to his territorial boundary, he either doubled back behind the observers or made a prolonged flight directly to a neighboring bluff, soon returning once the disturbance had passed. In all these instances, males would not venture beyond their peripheral song perches for more than a metre or so, indicating that the song perches around the periphery of the territory were a reasonable guide to the extent of the territory.

As few as six peripheral song perches and ten flushes were sufficient to determine with a high degree of assurance the boundaries of some males' territories, especially those with particularly small territories or those which had peripheral territories with an undefended boundary (see below). The boundaries of other males' territories were less easily discovered. Thus, in order to obtain a more precise measure of the boundary between some neighboring males, I placed a tape recorder at what I judged to be the boundary between two territories. I placed a mount of a Clay-colored Sparrow close by, then

played back a tape of a territorial Clay-colored Sparrow song. In most instances, both males approached the tape recorder, perched close by, and often sang; this was interpreted as indicating that the tape recorder was close to, or on, the mutual territorial boundary between neighboring males. In one instance, a male approached and attacked the stuffed bird, evidently indicating that the tape recorder had been placed far into that male's territory. This playback method has been used successfully to determine boundaries in other territorial passerines (see Dhondt 1966; Krebs 1971; Cederholm and Ekman 1976).

Once territories appeared settled, that is when a pair of sparrows could be consistently and reliably found within an exclusive area of the nesting habitat, and males repeatedly used a number of song perches within that area, I plotted the territorial boundaries on aerial photographs, and determined size of territory by compensating planimeter. The photographs were taken directly overhead and verified by actual ground measurements on the study areas.

Figure 1 shows an example of territories on one study area. Territorial boundaries are contiguous, and territories cover the nesting habitat, which closely corresponds with the distribution of _Symphoricarpos_ on the study areas. Areas surrounding the nesting habitat, such as marshes, tree bluffs, weedy fields, and pure stands of

132

Figure 1. Aerial photograph of Study Area #2, showing
extent of nesting area (thick black line) and the
territorial boundaries (thin black lines) of the
territorial males. The most prominent clumps of vegetation
are aspen bluffs. Peripheral territories are marked 'p'.

Study Area 2   1976   45 Territories

other shrubs such as <u>Elaeagnus</u> <u>commutata</u> were not defended.
The locations of peripheral territories are also indicated
in the figure.

Internest distances and nest predation

One method used to investigate the possibility that
predaticn is correlated with nest spacing is to look for
different rates of predation on nests at different
distances from nearest neighbors (Horn 1968; Krebs 1971;
Post 1974). I therefore took direct field measurements of
the distances between nearest active nests, after the young
had fledged, and compared these distances between
successful and unsuccessful nests. I analyzed one time
period, early June, in 1975, and three time periods over
the course of the breeding season in 1976. In all
analyses, I only considered blocks of contiguous
territories such that the distances between the closest
active nests were known. No nest was used in more than one
analysis, and I used the largest number of contiguous
territories containing active nests at one time within each
time period.

I also analyzed nest locations to see if the birds
themselves were actively spacing out their nests within the
boundaries of their previously established territories. To
do this, I first determined whether nests were selectively
placed within 5m of the periphery (cortex) or nearer the
centre (core). In addition, I generated hypothetical

random distributions of nests within the territories, and compared the distances between pairs of nests from the hypothetical and the actual distributions. I used two blocks of contiguous territories for these analyses. Both blocks were on Study Area #2, and the territories contained active nests during the early part of the breeding season. All nests were thought to be first nesting attempts.

I generated a hypothetical random distribution of nests by dividing the boundary of each territory into 12 sections, assigning a number to each section, and determining in which section a nest was to be located from tables cf random numbers. Each hypothetical nest was arbitrarily located on the territorial boundary, as the Clay-colored Sparrow had a pronounced and repeatable tendency to nest at the edge of the territory (see below). The distance between two nests was determined from randomly picked pairs of numbers between adjacent territories. The data were analyzed by comparing the distances between the corresponding pairs of nests from the hypothetical and the actual distributions.

Determination of aggressive responses to a test stimulus

To test the hypothesis that males with larger territories are in some way more aggressive than those holding smaller ones, I conducted playback experiments in 1976 on 12 males (8 returning and 4 new territorial males) on Study Area #1 and on 32 males (25 returning and 7 new

territorial males) on Study Area #2. The experiments were carried out between 17 May and 23 May, between 0600 and 0900 hours. The experiment consisted of two test periods, a three minute control period followed by a three minute experimental playback. The test song was a three-buzz song of a male which was tape recorded about 30km southeast of Study Area #2. The tapes were played back through a loud speaker at constant volume. The speaker was placed centrally in each territory, and a mount of a Clay-colored Sparrow in a perched position placed on top of the speaker. This experimental design is similar to the one used in 1975 in Part B. Four responses were measured: the closest approach to the speaker/mount, the latency of response, the number of flights over the speaker/mount, and the change in song rate between the control and the experimental time periods. Information was recorded into a portable Sony tape recorder and later transcribed.

Vegetation structure analysis

Variations in habitat structure have been shown to influence size of territory in some passerines (e.g. Wiens 1973, Martin 1974). In 1974, casual observations on size of territory and vegetational features of the study areas suggested that the Clay-colored Sparrows defending large territories appeared to incorporate areas in which Symphoricarpos was sparsely distributed. Conversely, small territories were often to be found in dense homogeneous

stands of Symphoricarpos. Therefore, I ran line transects the following year on both study areas in order to test the hypothesis that size of territory is influenced by the relative amounts of Symphoricarpos. The transect method I used was the line intercept technique, as it is both rapid to perform and well suited for analysis of low shrub stands (Smith 1974).

Line transects were run in early May 1975, in an east-west direction. Twenty transects, about 12m apart, were run on each study area, and each transect was 210m in length. A tape was laid over the vegetation, and the percent ground cover which laid directly below the transect was visually estimated by perpendicular projection from the tape onto the vegetation. The transects were transferred onto a map of the study area in question, and a map of the territorial boundaries was superimposed onto each study area map. Thus, each territory overlay part of at least one transect.

The vegetation within a territory was measured at intervals of approximately one metre in length along the transects. For the purpose of analysis, I expressed each intercept length as a function of the amount of Symphoricarpos present within that length. For example, a one metre intercept of grass alone would be recorded as 0% Symphoricarpos, one in which 70% of the ground cover was Symphoricarpos and 30% some other vegetation would be

recorded as 70% _Symphoricarpos_, and so on. More details of the analysis are given in Appendix 8. I then totalled the amounts of the different percentages of _Symphoricarpos_ within each territory, and compared these totals between territories of different sizes.

The_removal_experiments

In order to test the hypothesis that territorial pairs are actively spacing themselves out, I carried out removal experiments on both study areas in 1975. On one study area, five territorial males were shot on 19 May and on the other study area four males were captured, transported 250km east of Lyleton, and then released, on 20 May. The identity of each removed male was known before the removal, as was the boundary of his territory. Two of the males from each removal experiment held peripheral territories, and territories experimentally made vacant did not share common territorial boundaries. No attempt was made to estimate the size of the surplus, merely its existence. The numbers of replacements, the dates of settling, and the area claimed by the replacement birds were monitored.

RESULTS

Size of territory

Mean sizes of territories were 971 m² and 1053 m² on Study Area #1, and 739 m² and 676 m² on Study Area #2, for 1975 and 1976 respectively. When numbers of territories were plotted against size of territory (Figure 2), it was evident that there were ranges of sizes of territories which were more frequently defended than others. On Study Area #1, the most frequently defended range was 800 - 1000 m² in both years. On Study Area #2, the commonest size range was 400 - 800 m² in 1975, and from 400 - 600 m² in 1976.

Size of territory and location of territory within the nesting area

Peripheral territories were, on average, larger than central ones on both study areas in both years (Table 1). The differences were significant in 1976 (Study Area #1, t = 2.28, P < 0.05; Study Area #2, t = 2.68, P < 0.01), and were marginally insignificant in 1975 (Study Area #1, t = 1.46; Study Area #2, t = 1.37; for both study areas, 0.1 > P > 0.05). There were no significant differences (X² tests, P > 0.05) in all four analyses of success rates of nests between peripheral and central territories in two years (Table 2). Thus, if there was greater competition for peripheral territories because of their proximity to

139

Figure 2. Frequency distribution of sizes of territory of Clay-colored Sparrows on both study areas during 1975 (hatched bars) and 1976 (open bars).
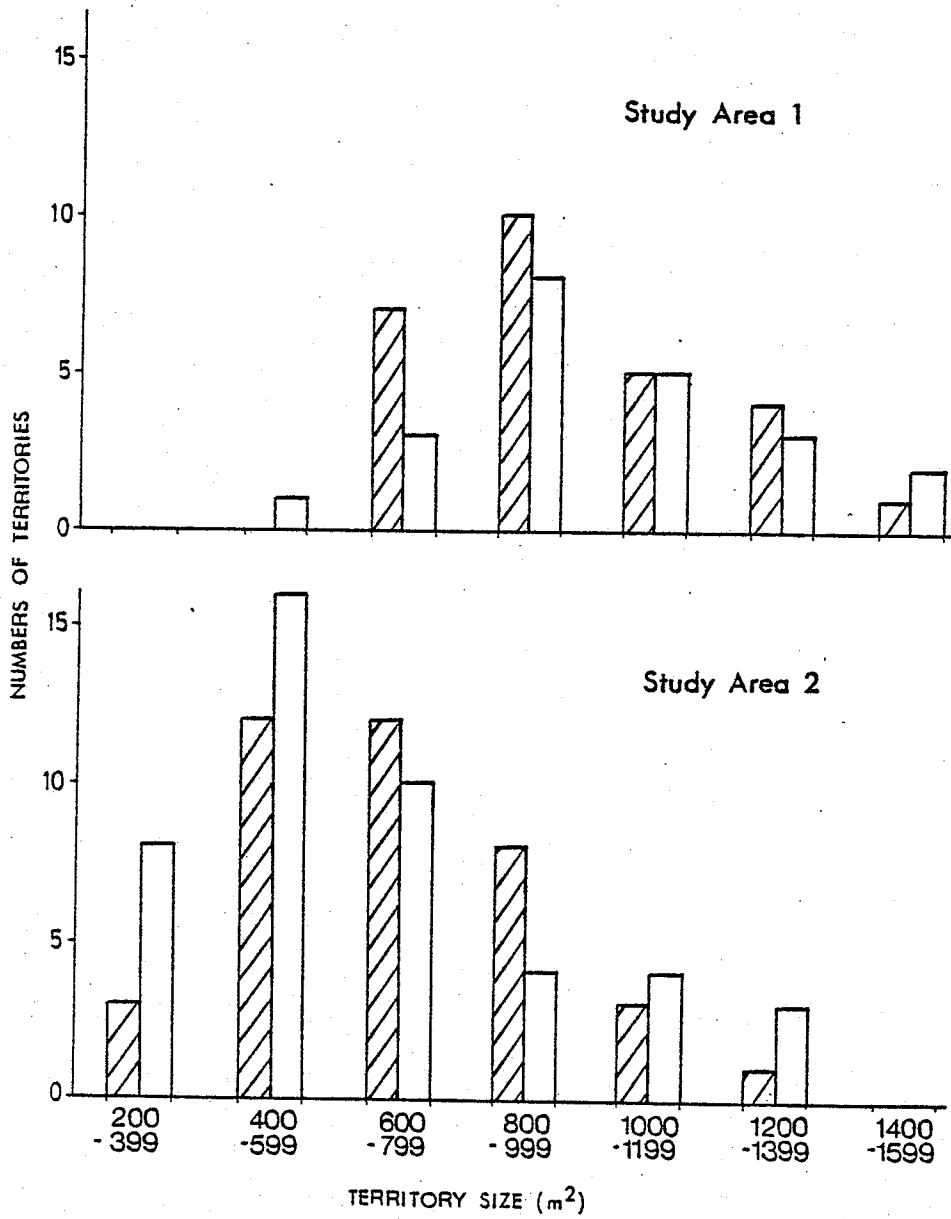
Table 1. Comparison of size of territory between peripheral and central territories.

		Peripheral Territories			Central Territories		
		Number of territories	Territory Size (m^2) Mean	SD	Number of territories	Territory Size (m^2) Mean	SD
Study Area #1	1975	15	991.7	476.3	12	945.8	233.3
	1976	14	1052.6	316.0	8	863.1	240.4
Study Area #2	1975	19	781.6	232.6	20	698.8	286.3
	1976	22	788.7	285.6	23	537.5	308.4

Table 2. Analysis of frequency of successful nests[1] between peripheral and central territories.

		1975		1976	
		Peripheral	Central	Peripheral	Central
Study Area #1	Successful nests	7	6	8	7
			*		*
	Unsuccessful nests	17	11	10	7
	Total	24	17	18	14
Study Area #2	Successful nests	6	10	18	14
			*		*
	Unsuccessful nests	15	10	24	19
	Total	21	20	42	33

1. A successful nest is defined as one in which one or more nestling Clay-colored Sparrows fledged.
* Not significant (X^2 test).

the feeding areas, it did not result in peripheral territories being smaller or enjoying higher nesting success.

There was no difference in dates of arrival in 1976 between males occupying central or peripheral territories (Table 3. X^2 =0.25, not significant). Returning males reclaimed their territory of the previous years, wherever its location, and new birds claimed whatever area remained undefended. Moreover, in 1976, returning males reoccupied 23 out of 31 central territories (74%) and 26 out of 36 peripheral territories (72%), indicating that the location of territory did not affect rates of return. Thus, there was no evidence to support the hypothesis that peripheral territories were favored over central ones.

One of the more plausible explanations why peripheral territories should average larger than central ones is that pressure from neighboring males is greater in central positions and so causes a reduction in size of central territories (e.g. Krebs 1971, Wiens 1973). On my study areas, there was a significant difference between those territories with few (0 - 2) and those with many (3 - 6) neighbors on Study Area #1 in both years (respectively, $P = 0.00002$ and $P = 0.003$, Fisher's exact probability test) (Table 4). There was a similar trend on Study Area #2 in both years (Table 4), although the differences were not significant (X^2 tests, $0.1 > P > 0.05$ for each year).

Table 3. Arrival dates (early or late) and location (peripheral or central) of territory occupied by Clay-colored Sparrows in 1976, both study areas combined.

| | | Location of territory | | |
		Central	Peripheral	Total
Date of [1] Arrival	Early	17	23	40
	Late	14	13	27
	Total	31	36	67

1. 'Early' is from 1 - 7 May, 'late' from 8 - 16 May.

Table 4. Comparison of size of territory with numbers (0 - 2, 3 - 6) of adjacent territorial males.

	Median size of territory (m^2)	1975		1976	
		0 - 2	3 - 6	0 - 2	3 - 6
Study Area #1	$<$ 900	5	9	0	6
	$>$ 900	12	1	12	4
Study Area #2	$<$ 750	9	12	8	18
	$>$ 750	12	6	10	9

Central territories on average have more adjacent territories than peripheral ones, as the latter generally have a length of undefended boundary. Thus, there may have been more compression of central territories, resulting in their average smaller sizes.

Location of nest within territory in relation to predation

Casual observations on nest locations in 1974 indicated that nests were most frequently positioned at the edge of territories. Quantitative analysis of nest locations in 1975 and 1976 revealed that nests were built significantly more often in a five metre band around the edge of the territory (the cortex) than in the centre of the territory (the core) on both study areas in both years (Table 5). As many territories encompassed a complete patch of Symphoricarpos, most nests were also constructed at the edge rather than in the centre of a patch of Symphoricarpos. It is possible that this tendency to nest at the periphery of the territory was a result of nest spacing in response to potential predation pressure, an aspect that I consider next.

Predation on adult Clay-colored Sparrows during the breeding season was minimal; however, the chief cause of nesting mortality was predation (Part A). I therefore examined the relationship between nest predation and territory size.

Comparisons between successful and unsuccessful nests

Table 5. Comparison of nest locations within the territory (cores versus cortices).

		Number of nests		x^2 *	
		Core	Cortex		
Study Area #1	1975	12	30	8.43	$P < 0.01$
	1976	10	22	6.15	$P < 0.01$
Study Area #2	1975	9	32	8.80	$P < 0.01$
	1976	14	61	19.50	$P < 0.001$

* The expected values for the number of nests in each area were calculated from the relative areas of cores and cortices (see Appendix 9)

(Table 6) indicated a significant relationship between predation and distances from nearest neighbors in three out of the four analyses, and a similar trend in the other one. There was also no seasonal effect, as the relationship occurred throughout the breeding season. Thus, nests closer together were less successful than those farther apart.

Table 7 presents results of the further comparison between actual inter-nest distances and hypothetical distances generated by assuming nests are placed randomly around the periphery of the territory. Actual internest distances averaged larger than the hypothetical distances in both analyses (1975 analysis, $T = 13.5$, $0.1 > P > 0.05$; 1976 analysis, $T = 15.5$, $P < 0.05$; Wilcoxon matched-pairs signed rank test, one-tail). It is thus possible that the birds were not positioning their nests randomly around the margins of the territory, but were influenced by the location of their neighbor's nest(s), such that inter-nest distances were greater than random.

Territory size and aggression

I investigated, by means of playback experiments, the premise that territory size is related to the aggressiveness of individual males. Responses to the playback/mount revealed large differences between individual birds in each of the four behaviors monitored (Table 8). In general, an individual male that responded

Table 6. Summary of nest spacing and nesting success during 1975 and 1976. Presented are the number (N) of nests used in the analysis, the mean of the distances in metres between nests in adjacent territories, and the standard deviation.

Time period	Unsuccessful			Successful				
	N	Mean	SD	N	Mean	SD	t	
30 May - 10 June 1975	4	26.5	4.6	6	35.5	6.2	2.68	P < 0.05
25 May - 10 June 1976	6	14.7	5.8	9	19.7	6.8	1.64	0.1 > P > 0.05
11 June - 30 June 1976	9	13.8	4.9	12	18.4	5.9	2.14	P < 0.05
1 July - 20 July 1976	4	15.4	4.6	7	20.9	5.9	2.53	P < 0.05
1976 data combined	19	14.6	5.1	28	20.2	6.3	2.86	P < 0.005

Table 7. Comparison of internest distances between the actual and the hypothetical nest distributions.

		Actual distances	Hypothetical distances[1]
Internest distances (m) 1975 (N = 10)	Range	12.4 - 53.4	11.7 - 36.2
	Mean	31.7	23.9
	SD	13.4	6.7
Internest distances (m) 1976 (N = 12)	Range	8.2 - 37.6	9.6 - 24.5
	Mean	20.6	16.2
	SD	8.8	5.1

1. See Methods.

Table 8. Frequencies of occurrence of responses of male Clay-colored Sparrows to experimental playbacks on the two study areas.[1]

Response		Study Area #1	Study Area #2	
Percent decrease in song rate	0 - 25	4	5	
	26 - 50	1	7	K = 0.50
	51 - 75	3	6	
	76 - 100	4	14	
Closest approach (cm)	0 - 25	7	16	
	26 - 50	2	6	
	51 - 75	0	1	K = 0.24
	76 - 100	1	4	
	100	2	5	
Number of flights	0 - 3	4	11	
	4 - 6	2	11	
	7 - 9	2	6	K = 0.62
	9	4	4	
Latency of response (sec)	0 - 10	6	13	
	11 - 20	2	2	
	21 - 30	0	5	K = 0.59
	31 - 40	1	6	
	40	3	6	

1. The samples for the two study areas were compared by the Kolmogorov-Smirnov two sample test (Sokal and Rohlf 1969). None of the K values is significant. 12 birds were tested for each of the response categories on Study Area #1, 32 for each category on Study Area #2.

within 10 seconds of the start of the playback would also approach the loudspeaker/mount within 25cm, often within 10cm, and would make numerous flights over the loudspeaker/mount and would have the highest percent change in song rate. Conversely, other individuals would respond weakly in all the response parameters measured. Birds on the two study areas did not differ significantly (Table 8), thus the fact that territory size averaged larger on Study Area #1 than on Study Area #2 cannot be attributed to the greater 'aggressiveness' of the territory holders on the former area, which might have resulted in the defense of larger territories.

Differences between individuals were not correlated with territory size (Table 9). No value approached significance for either study area. If there is a correlation between territory size and the ability of a male to defend a particular size of territory, then it was not evident in the measures taken during the playback experiments.

Further, the differences between individuals could not be equated with new versus returning territory holders (Table 10). There were some pronounced differences between the two groups; returning males approached the test stimulus much closer than did new males, for example. None of these differences in the responses measured was significant, however, and this is probably a result of the wide differences between individuals within each group.

Table 9. Correlation values (r) for size of territory versus response to playbacks. None of the r values is significant. Data used in the analyses are given in Appendix 10.

Response	Study Area #1	Study Area #2
Percent decrease in song rate	0.16	0.08
Closest approach	0.13	0.04
Number of flights	0.26	0.16
Latency of response	0.09	0.07

Table 10. Comparison of responses to playbacks between new and returning territorial males.[1]

		New males		Returning males		
	Responses	Mean	SD	Mean	SD	t
Study Area #1	Percent decrease in song rate	68.8	26.3	44.2	28.6	1.43
	Closest approach (cm)	87.5	42.7	60.3	44.4	1.66
	Number of flights	3.3	3.4	7.4	3.4	0.98
	Latency of response (sec)	18.6	18.1	20.1	24.0	0.66
Study Area #2	Percent decrease in song rate	78.7	17.3	63.6	30.1	1.18
	Closest approach (cm)	101.4	176.8	45.9	51.8	1.56
	Number of flights	6.2	4.6	5.6	3.4	0.35
	Latency of response (sec)	16.5	15.0	27.7	30.5	0.87

1. For Study Area #1, N(returning males) = 8, N(new males) = 4. For Study Area #2, N(returning males) = 25, N(new males) = 7. None of the t values is significant.

Territory size and habitat structure

In this section, I test the hypothesis that larger territories contain proportionately less dense Symphoricarpos than do smaller territories.

The line transects on each study area totalled 4200m. However, the transects frequently crossed parts of the study areas which were not defended by the Clay-colored Sparrows. These parts were grassy areas, tree bluffs, stretches of standing water and marsh habitat, and pure stands of Elaeagnus commutata; 2016m on Study Area #1 and 1428m on Study Area #2 were not defended. Only defended portions were used in the analyses.

Two categories of Symphoricarpos were identified; sparse (lower than 50% cover) and dense (50% and higher cover) (see Appendix 8). On both study areas, there was an inverse relationship between proportion of dense Symphoricarpos ground cover and territory size (Figure 3); larger territories had proportionately less dense ground cover than smaller territories. A comparison of the ratio of sparse to dense Symphoricarpos between the two study areas showed close agreement within each range of territory sizes. The hypothesis that larger territories contain proportionately less dense ground cover of Symphoricarpos appears to be supported.

Territory size and other proximate factors

Older males are reported to defend territories which are

155

Figure 3. Frequency distribution of the proportion (%) of dense _Symphoricarpos_ in relation to size of territory. The number of territories in each size range of territories is given above each bar.
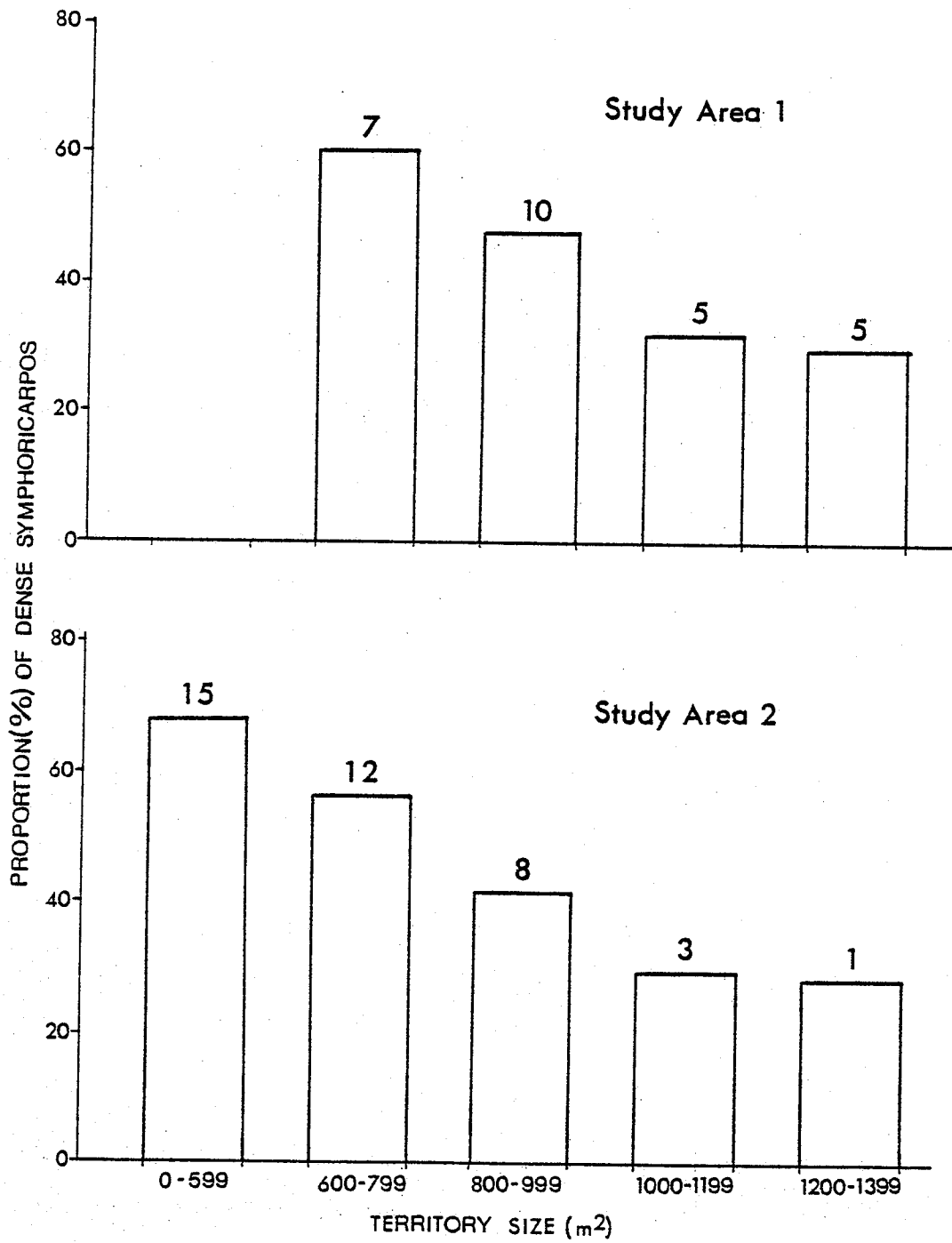
on average larger than those of first year males in the Great Tit _Parus_ _major_ (Dhondt and Huble 1968) and in the Field Sparrow _Spizella_ _pusilla_ (Best 1977b). In the populations of Clay-colored Sparrows at Lyleton, individuals nesting for the first time were not distinguished from older birds, partially because no fledgling banded on either of the study areas was ever resighted in subsequent years. However, as males showed a high rate of return to the same territory in subsequent years (Part A), a not unreasonable assumption is that new territory holders can be equated with first year birds holding territories for the first time. A comparison of territory sizes of new and returning territory holders, however, revealed no obvious trends (Table 11). In one area, new birds defended larger territories, and in the other returning birds defended larger ones, but neither difference was significant. There is thus no evidence that age, as assumed above, consistently influenced territory size.

This finding is consistent with the observation that returning males took essentially the same territory with the same boundaries from one year to the next. When a male did not return, new males would claim the now vacant territory. Usually the territory would be occupied by one new male, but occasionally the territory would be divided between two new males, as happened in 1976 on Study Area

Table 11. Comparison of sizes of territory of new and returning territorial males in 1976.

	Class of males	Number of territories	Territory size(m^2) Mean	SD	t^1
Study Area #1	Returning	16	888.1	260.6	
					0.94
	New	6	1023.1	360.4	
Study Area #2	Returning	33	746.8	331.5	
					0.71
	New	12	606.6	278.7	

1. Neither t value is significant.

#2. This resulted in more territories being taken (45 in 1976, 39 in 1975) and possibly the smaller territory size for the new territory holders (Table 11).

One reason why fledglings were banded was to test the hypothesis that territory size was a heritable characteristic. The total lack of fledgling return prevented any further investigation of this idea.

Interspecific territoriality has been suggested as being important in determining territory size in a given population of some species of birds (e.g. Orians and Willson 1964, Yeaton and Cody 1974). The expanses of low shrubbery which the Clay-colored Sparrows inhabited were virtually devoid of potential avian competitors, and no overt agonistic interactions were observed between the sparrows and any other passerine species on the nesting or the foraging areas. This suggests that interspecific competition between Clay-colored Sparrows and other cohabiting species is minimal.

Patterns of settling can influence territory size in some passerines (e.g. Knapton and Krebs 1974). The fact that most male Clay-colored Sparrows arrived over a short space of time and established their territories very quickly is at least consistent with this hypothesis. The fact that males take the same size territory in consecutive years suggests that the relative importance of this proximate factor is probably minimal.

Replacement of removed territory holders

Within three days of each experimental removal, unbanded replacement males had occupied all the territories experimentally made vacant on the study areas (Table 12). Replacement occurred on a 1:1 ratio with removals on both study areas. There was no detectable shift in territorial boundaries of neighboring males into the vacant areas, indicating that territories were fixed and well established before the removals were carried out. Each replacement male subsequently attracted a female. All replacement birds were unbanded, thus their origin was not known.

One of the four males removed on 20 May died during transportation. The remaining three males were not seen again during 1975. However, one of these males returned in 1976, and reoccupied his territory from which he had been removed.

The identities of two females of the removed males were known before the removals. Both females deserted the territories after their mates had been removed, to be replaced by new unbanded females.

The fact that the experimentally emptied territories were filled within four days after the original territories had been established suggests that there was a surplus of non-territorial birds. This is evidence that the territory holders were actively spacing themselves by defending a particular size of territory, and that territory size was

Table 12. Number and dates of removals of males from breeding territories[1] in 1975.

	Number of males removed	Removal dates	Number of replacement males	Replacement dates
Study Area #1	4	20 May	4	21 – 23 May
Study Area #2	5	19 May	5	20 – 22 May

1. For location of experimentally vacated territories within the study areas, see Methods.

not merely a result of passive settling by all available males onto a given area.

Territory size and reproductive success

In this analysis, I define reproductive success as the number of fledged young per territory. Thus, in this particular analysis, if two pairs each fledged one or more young from a territory, the combined output of both is used. On Study Area #1, the number of fledged young per territory was greatest in the range of territory sizes between 800 and 1000 m² (Figure 4), which also corresponded with the largest number of territories (37%) taken, as indicated in Figure 2. Similarly, on Study Area #2, the greatest number of fledged young per territory corresponded with the most frequently defended territory size (33%) (compare Figures 2 and 4).

This seems to indicate that the birds were tending to maximize reproductive fitness by preferentially defending territories of an optimum size. The ranges of these 'optimum' territories differ between the two study areas, indicating that optimal territory size is not necessarily fixed at one size for different populations of Clay-colored Sparrows.

The greater number of fledged young per territory was not a result of multiple broods within certain ranges of territory size and not in others, as the number of young fledged per nest (Figure 5) was also greatest in the range

Figure 4. Distribution of numbers of fledged young per territory during the breeding season. Data for 1975 and 1976 are combined. The total number of territories for both years for each size range of territories is above each bar.
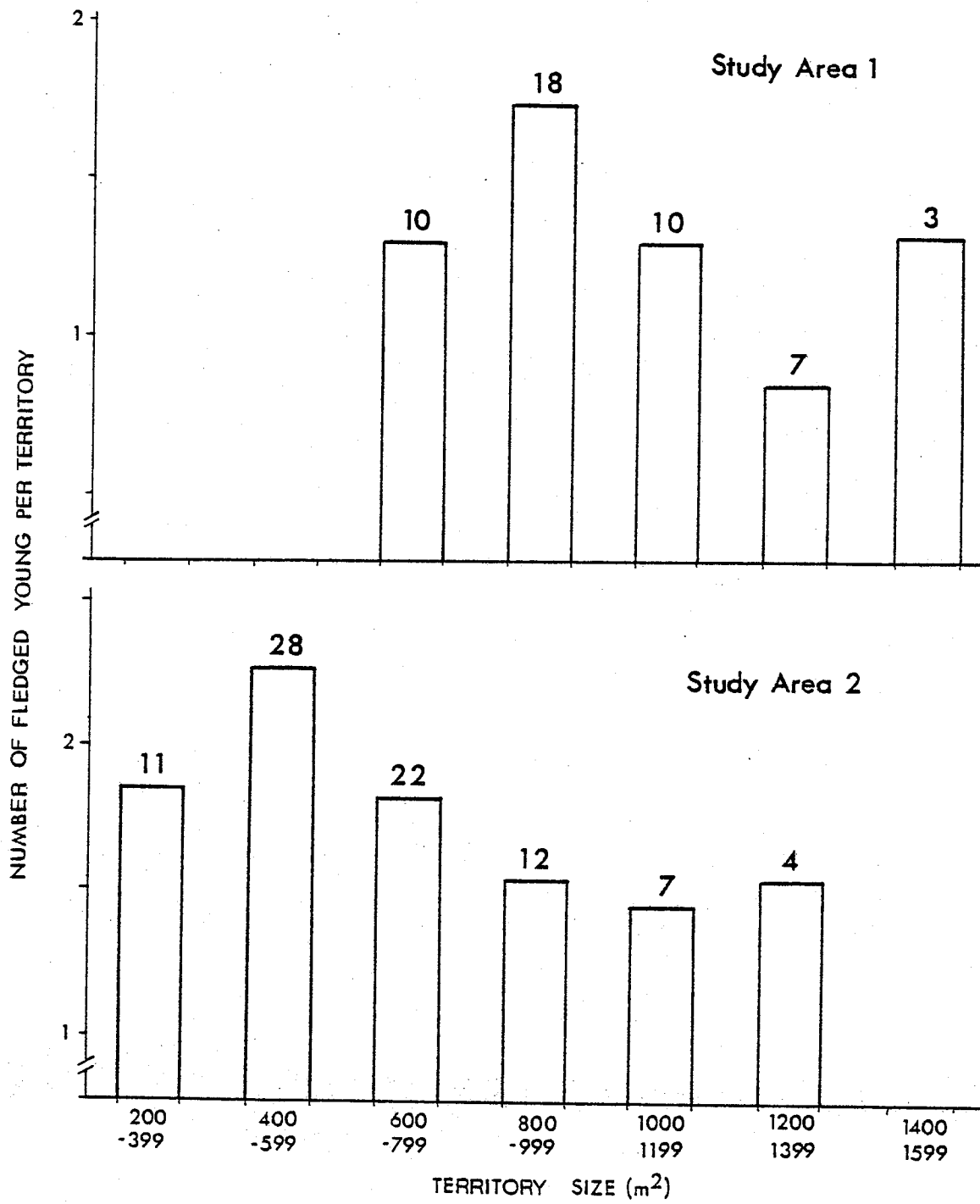
Figure 5. Distribution of numbers of fledged young per nest. Data for 1975 and 1976 are combined. The total number of nests for each size range of territories is given above each bar.
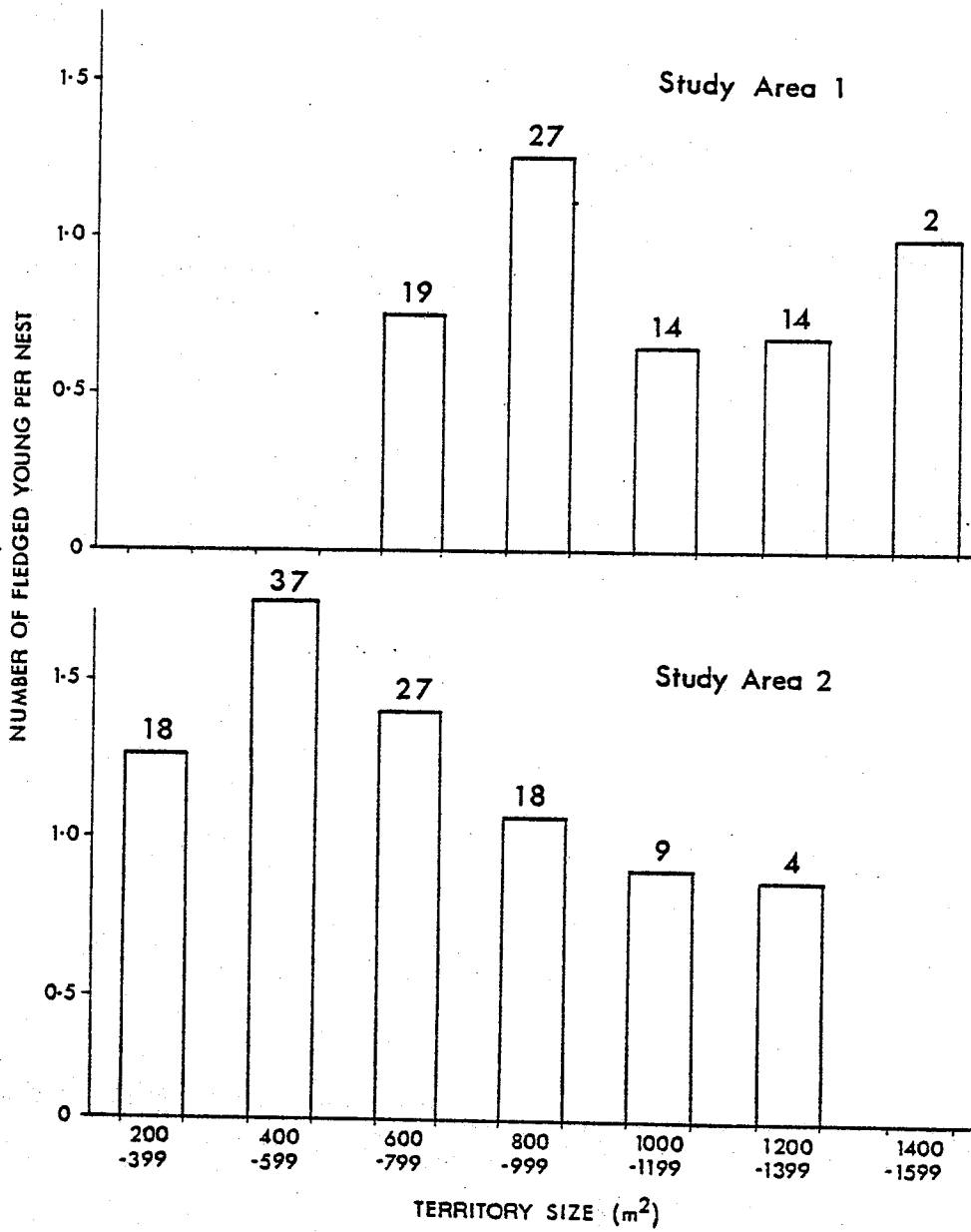
of territory size which was most frequently taken.

DISCUSSION

If we make the reasonable assumption that spacing systems are the products of natural selection (e.g. Smith 1968, Holmes 1973, Barash 1974), then we can further deduce that they should be adaptive. Why is it adaptive for a Clay-colored Sparrow to defend so small a territory? Why is it adaptive to be territorial in the first place? Why is there an apparent optimum range of territory size?

Food and territory size

Clay-colored Sparrows were not observed to use their territories as food gathering areas. Adults foraged and collected food for their young on feeding areas away from the nesting areas (Part A).

As the territory is not used as a feeding area, then there is presumably no selection pressure on the birds to defend a large area to supply food for the nestlings (Howard 1920, Hinde 1956, Brown 1975). I therefore compared this system of the Clay-colored Sparrow in southwestern Manitoba with those systems of 11 other populations of seven species of open country sparrows for which territory size, its range and mean, had been determined, and I arranged these populations according to whether the birds foraged within the territorial boundaries, part within and part outside the territory, or

outside the territory (Figure 6). There appears to be a connection between territory size and the relative amounts of food collected within the boundaries of the territory. The population of Clay-colored Sparrows in southwestern Manitoba represents the sole example of essentially all food being collected off territory, and it also has the smallest mean territory size. It seems reasonable that the removal of the need to protect a food gathering area has resulted in the Clay-colored Sparrow defending a size of territory that is very small relative to that of other open country sparrows. Thus, food is not a factor acting directly on the size of the territory, and it would therefore not be adaptive for an individual male to expend large amounts of energy in defending an unnecessarily large territory. Hence the size of the territory could collapse.

It is possible that the amount or availability of food off territory could in some way influence the number of breeding pairs on the islands of nesting habitat. If food were repeatedly in short supply during part of the breeding season, then selection could have favored a few pairs with large territories. No nestlings were lost to starvation (Part A), a result that suggests (Ricklefs 1969, Emlen and Demong 1974) that there was no shortage of food, at least during most of the breeding season.

It is also possible that the pattern of territorial dispersion in Clay-colored Sparrows is related to the

Figure 6. Foraging locations during the breeding season and size of territory (range and means) for 12 populations of eight species of open-country sparrows.

FORAGING LOCATION

ON TERRITORY
- Tree (Weeden 1965)
- Savannah (Wiens 1969)
- Seaside (Post 1974)
- Henslow's (Wiens 1969)

ON & OFF TERRITORY
- Vesper (Wiens 1969)
- Grasshopper (Wiens 1969)
- Field (Best 1977b)
- Field (Walkinshaw 1944)
- Henslow's (Robins 1971b)
- Savannah (Welsh 1974)
- Seaside (Post 1974)

OFF TERRITORY
- Clay-colored (This study)

0   5000   10,000 15,000   20,000 25,000

SIZE OF TERRITORY (m^2)
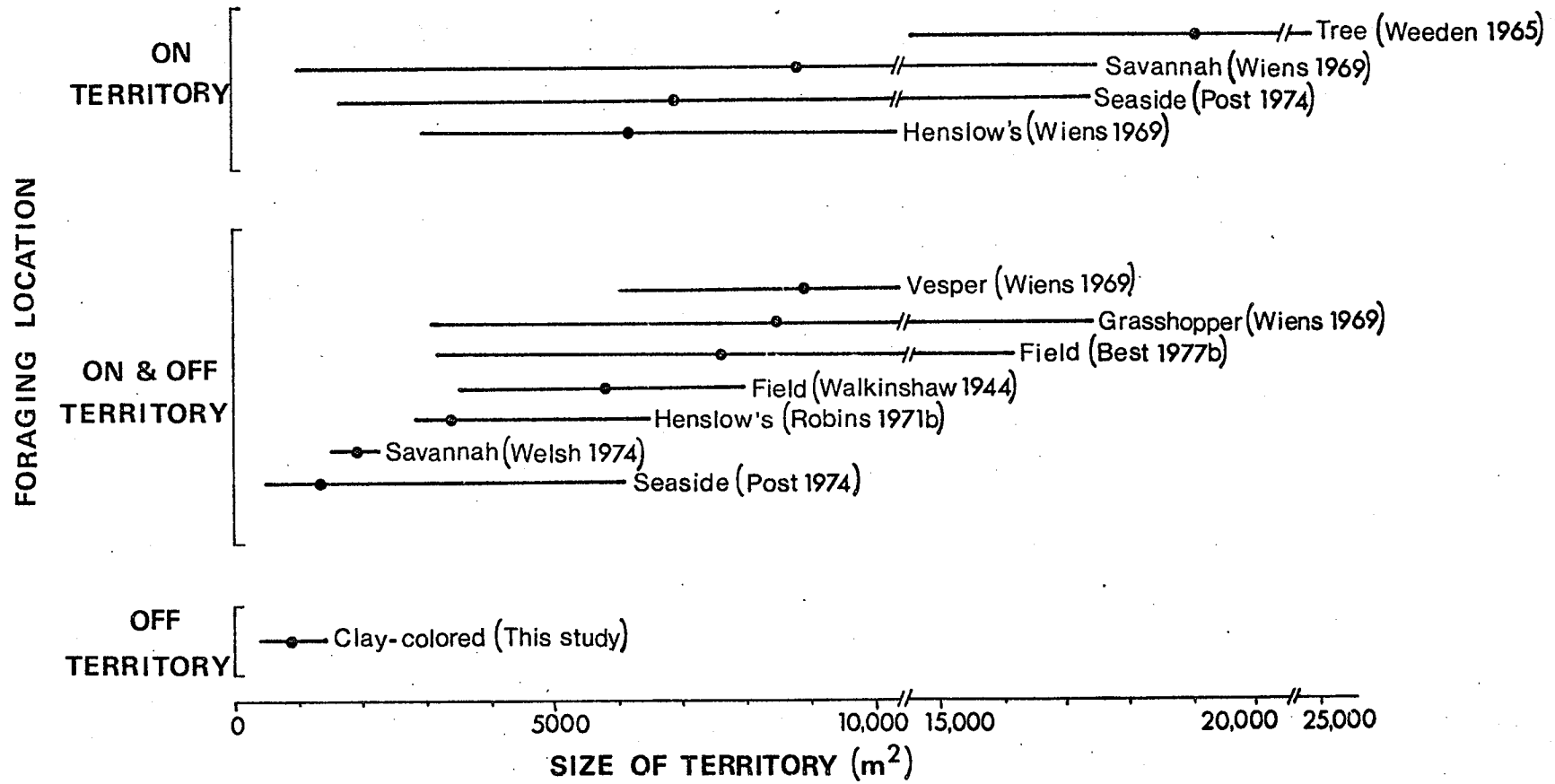
distribution and stability of the food supply, as described in Horn's (1968) energy budget model. However, Horn's model is less relevant to situations involving small islands of breeding habitat surrounded by a feeding area, as in the Clay-colored Sparrow. The clumped dispersion pattern of territories in this species is better explained as a direct result of the distributional pattern of Symphoricarpos, which provides protected nesting sites, rather than as a direct result of local food distribution.

The adaptive functions of territory

There are several proposed functions of territoriality (e.g. Hinde 1956, Krebs 1971, Maynard Smith 1971, Brown 1975). One plausible explanation for the selective value of territoriality in the Clay-colored Sparrow is the 'predator-buffer' hypothesis (see Hinde 1956, Wilson 1975). The hypothesis is supported by the evidence of lowered rates of predation with increasing distances between nests, and of a possible active spacing of nests. Thus territory could have a selective advantage in spacing out nests as a defense against predators. This might act as a buffer to prevent territory size from decreasing to a point at which predation pressure outweighs the benefits accrued from not having to defend a feeding territory.

Predation is an important selective pressure shaping the breeding biology of many avian species (Crook 1965, Lack 1968, Ricklefs 1969, Windsor and Emlen 1975). Birds such

as Clay-colored Sparrows, which are gregarious outside the breeding season, typically become territorial for breeding when preferred nest sites are relatively accessible to predators, thus achieving a measure of protection by means of nest dispersion and nest concealmant. In the Clay-colored Sparrow, group mobbing of a predator was not observed although the opportunity arose when potential predators such as spermophiles (see Part A) were seen frequently in the nesting areas during the breeding season. Direct defense of the easily accessible nests seems generally ineffective, and only occasionally were distraction displays (involving injury-feigning) noted, principally during the late nestling stage. The birds appeared to be relying on both concealment and dispersion of their nests to avoid nest predation, as less well concealed nests suffered predation rates higher than did better concealed ones (Part A), and there was a significant tendency for more widely dispersed nests to be less subject to predation (Table 6).

One argument that is at least consistent with the observation (Table 1) that peripheral territories averaged larger that central ones is that predation is often most severe at the edge of a breeding population (Kruuk 1964, Horn 1968, Hamilton 1971, Buckley and Buckley 1972, Erwin 1977). Hence, to compensate for possible increased predation pressure, it would be adaptive for peripheral

territory holders to defend slightly larger territories. There were however no differences between peripheral and central territories in success rates of nests (Table 2).

The 'sufficient-resource' hypothesis (e.g. Wilson 1975) predicts that a selective value of territoriality is the defense of an adequate supply of some resource, usually food. Some studies (e.g. Smith 1968, Gass et al. 1975) have shown that territory size was closely correlated with the food requirements of an individual territory holder, thus supporting this hypothesis. Food however did not appear to be a defended resource in the Clay-colored Sparrow, and it is difficult to imagine any other resource, such as nest sites, being in short supply.

The 'polygyny hypothesis' of McLaren (1972) argues that a sufficient force favoring defense of very large and/or resource rich territories would be to increase the likelihood of a male attracting many mates. This is not supported in the Clay-colored Sparrow. No territorial male was unpaired and no male attracted more than one female during the breeding season at any one time, no matter how small or large the territory. Further, large territories, for whatever reason, are associated with a reduced reproductive success rate as compared to the modal (smaller-sized) territory. It does not seem likely that polygyny is the adaptive strategy of territoriality in this species.

On both my study areas, replacements occupied territories experimentally made vacant. One of the consequences of territoriality was thus that would-be breeders were excluded from territories. This is consistent with the 'super-territory hypothesis' (Verner 1977).

Verner (1977) has argued that natural selection can favor those individuals that defend territories that are larger than the size that would be predicted to include resources just sufficient for survival and/or reproduction. He refers to these large territories as 'super territories', and argues that they are favored not because a super territory holder produces more young, but because its relative contribution to future gene pools is larger because some other, excluded individuals do not reproduce at all.

Some aspects of my study are at least consistent with Verner's idea. The removal experiments indicated that some birds were being excluded from the breeding population. Further, the hypothesis assumes some cost to defending a larger than necessary territory, which is supported by the observation that birds defending large territories on my study areas produced slightly fewer young than those defending smaller ones.

Even under this hypothesis, there must still be an optimum size, and some territories must be too large. The

real question then is whether this idea can explain the modal (= optimum) territory size in the Clay-colored Sparrow. Is the optimum territory size in the Clay-colored Sparrow a 'super-territory'?

One of the tenets of Verner's hypothesis is that the super-territory holders are more aggressive than those birds holding smaller territories. No correlation was found in this study between levels of aggression and territory size, at least in the form of response to playback experiments. A further conclusion is that levels of aggression manifested in the defense of different-sized territories is heritable. This remains to be shown in the Clay-colored Sparrow.

Perhaps the real flaw in Verner's idea is the problem of 'cheaters'. Those that revert back to smaller, less costly territories achieve the same benefit from super-territory exclusion as do those simultaneously holding the super-territories in the same areas, and yet they pay no added cost. If super-territory holders and cheaters are equally aggressive, then selection could work against the super-territory holders. The problem of cheaters suggests that this hypothesis may not be viable in the real world.

Optimality and territory size

It still remains to be explained why a certain range of territories appears to be optimum in terms of reproductive success, and why this range should be different between the

two study areas. My working hypothesis is that most individual Clay-colored Sparrows preferentially defend a particular range of size of territories in which they apparently maximize their reproductive fitness. No banded fledgling was seen in subsequent years, thus no information could be collected on mortality rates of fledglings relative to the different sizes of territories. Thus, as a first approximation, I assume that mortality of Clay-colored Sparrow fledglings after they have left the nest is independent of the size of territory in which they were raised.

Individuals defending territories smaller than the optimum were subject to a lowered reproductive rate that was most likely a result of predation pressure (Table 6). It would not therefore be adaptive to defend too small a territory. The question then remains why the largest territories do not enjoy the highest rate of reproductive success. Defense of an area by a bird requires expenditure of a certain amount of time and energy that might profitably be used to other ends (Orians 1971). It is conceivable that those individuals with large territories spend more time in defending the territory, or patrolling its boundaries, than those individuals with smaller ones, and this in some way effects overall reproductive activities. No direct evidence is available to support or refute this idea for the Clay-colored Sparrow, but it

remains a plausible consideration.

The idea that overly aggressive individuals may have a reduced rate of reproductive success (the 'aggressive neglect' phenomenon) has been discussed by Brown (1975). No differences in response to an experimental playback were determined between males defending different sized territories, thus individual variability in the size of the defended area could not be related to differing levels of aggression.

It is possible that the larger territories are suboptimal due to lack of concealment afforded by potential nest sites. Larger territories incorporate a lesser proportion of dense Symphoricarpos than do smaller territories in both the study areas. Also the total ratio of dense to sparse Symphoricarpos is proportionately smaller on Study Area #1 (1.01:1.00) than on Study Area #2 (1.23:1.00), which could partially explain the larger average size of territories on Study Area #1 than on Study Area #2. There is reason to believe that nests are more easily detected in sparse Symphoricarpos (Part A), and thus it may be necessary to defend a larger area in order to gain benefits from dispersion of nest sites to compensate for reduced nest concealment.

When the two presumed anti-predator mechanisms of nest spacing and nest cover (as explained above) are combined, a general model can be generated to predict optimal territory

size (Figure 7). Pressure from predators for nests to be spaced out is assumed to be greater at low sizes of territory, then becomes progressively weaker as territory size increases until it reaches an asymptote. Increase above this asymptotic size of territory would presumably provide little additional protection from nest predation. The relationship between nest cover and reproductive fitness shown in Figure 7 is derived from the assumption that protection from nest predators provided by nest concealment was relatively greater in dense than in sparse Symphoricarpos (Part A) combined with the finding (Figure 3) that density of Symphoricarpos varied inversely with territory size, thus the apparent decrease in fitness with increasing territory size. The shape of the curve is drawn to approximate the trend evident in Figure 3, in which the ratio of dense to sparse Symphoricarpos appears initially to decline linearly with increasing territory size, then approaches an asymptote at large territory sizes.

One would predict that the territory size at which the two lines in Figure 7 intersect would be optimal. This prediction from the modal is consistent with the situation encountered in this study, in which optimal territory size was intermediate in size.

A further intriguing aspect is why returning males should take the same size of territory in successive years, if ranges of territories differ in reproductive success.

Figure 7. Model of two parameters (nest cover and nest spacing) which could potentially affect fitness, and thereby predict an optimal size of territory when fitness is maximized at the point where the two measures intersect. For an explanation of the shape of the curves, see the text.
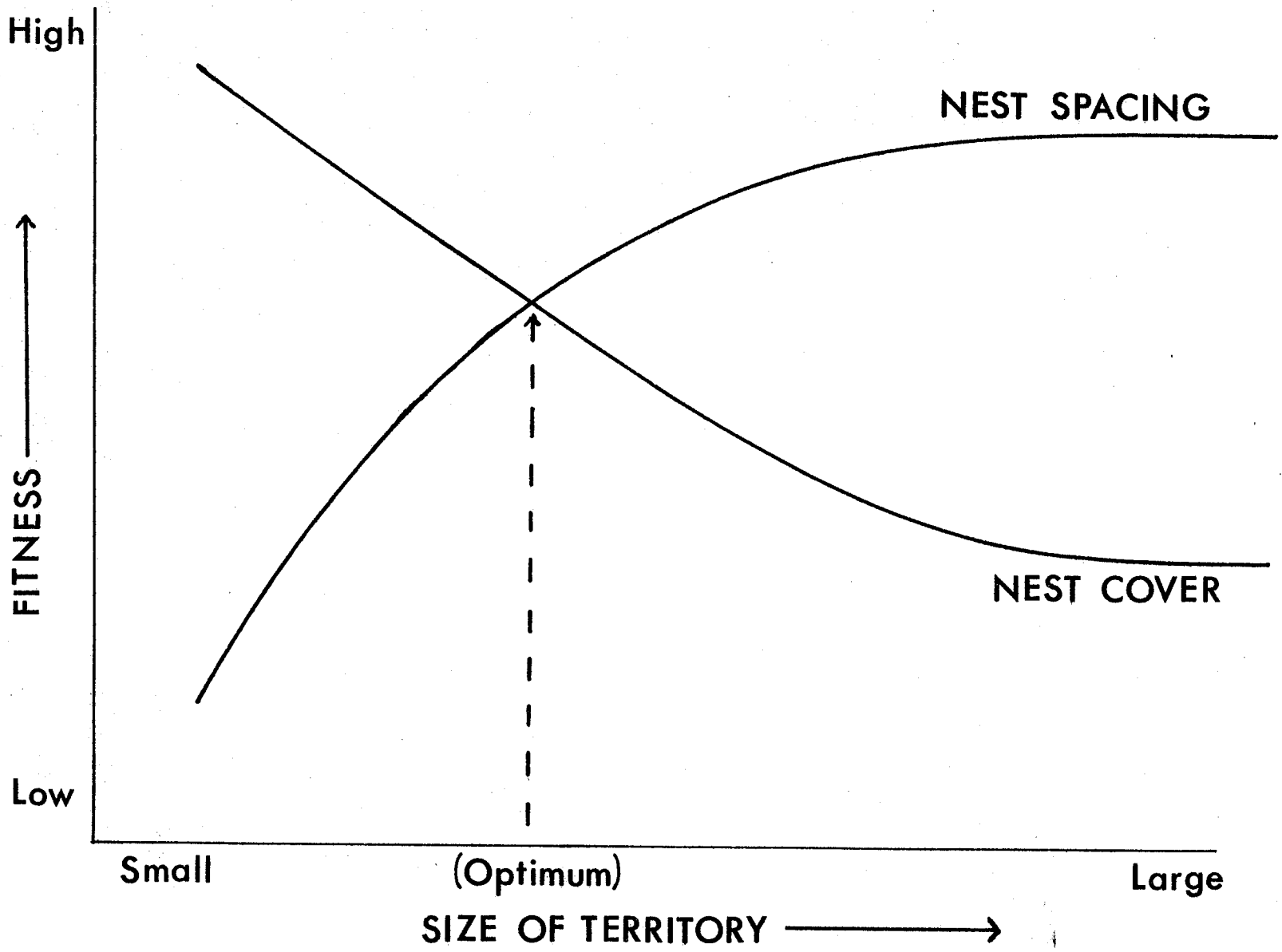
In this situation, a male defending a sub-optimal territory
is faced with a choice of alternatives: retain the same
territory from one year to the next and retain a slightly
below optimum reproductive output, or take a chance on
claiming another territory which may or may not result in
an increased reproductive success. It seems as if, at
least in the Clay-colored Sparrow, the benefits are
weighted in favor of claiming one's territory in successive
years.

In summary, territoriality in the Clay-colored Sparrow
has most likely evolved or is at least maintained as a
predator-buffer mechanism, with predation being the most
important factor in preventing the territory from becoming
a very small size. The upper limit to the size of the
territory is probably determined ultimately by the amount
of time and energy expended in defending a large territory,
and proximately by a number of factors, such as nesting
cover and pressure from adjacent territory holders or
intruders. The results of this study indicate that most
individual Clay-colored Sparrows preferentially defend a
particular range of size of territories in which they
apparently maximize their reproductive fitness. This
optimum range can be largely predicted by a simple a
posteriori model using two parameters relating to the
anti-predator behavior of this species.

GENERAL DISCUSSION

By investigating the ecology and behaviour of a single species, one can attempt to deduce adaptive relationships of the social system of an animal to its environment. The spacing system of the sparrows in the genus Spizella, which includes the Clay-colored Sparrow, is one of territorial dispersion over the nesting habitat, but the use of the territory and the corresponding territory size are quite different between Clay-colored Sparrows and other members of the genus Spizella which have been studied in depth. The Field Sparrow (Spizella pusilla) (Best 1977b), the Tree Sparrow (S. arborea) (Weeden 1965), and the Chipping Sparrow (S. passerina) (C. Keller, personal communication) all defend territories which average three to twenty times larger than those defended by the Clay-colored Sparrow in southwestern Manitoba (Part C). In each of the former three species, the territory is used both for reproductive activities and for food gathering, and it seems probable that, within a nesting territory, food is an economically defendable resource.

The situation in the Clay-colored Sparrow is different. The distribution of food does not coincide with the distribution of the nesting habitat. Thus, there are three options open to the Clay-colored Sparrow:

(1) to defend a large area incorporating not only an area

of nesting habitat but also an area of sufficient size to provide enough food for both parents and young.

(2) to defend both a nesting territory and a separate, disjunct feeding territory.

(3) to defend just a nesting territory, and feed and collect food in communal feeding areas.

For a male to defend a very large territory incorporating the necessary resources for feeding and nesting would require a large expenditure of time and energy (Orians 1971), and may result in insufficient time being devoted to reproductive activities. One possibility, as the nesting habitat occurs as an island in a sea of feeding habitat, is the defense of a territory on the periphery of the nesting habitat plus the feeding area adjacent to the territory. This would seem to be an optimal strategy for increasing one's own potential fitness at the expense of the relative fitness of others, not only by defending resources sufficient for reproduction and feeding but also by preventing access by other individuals to that resource. Results from this study show that peripheral territory holders do not defend adjacent feeding areas, nor do they enjoy higher nesting success (Part C) than central territory holders. There are two possible explanations why peripheral territory holders do not defend adjacent land for use in foraging: (a) they are not capable of defending both nesting and feeding areas, which seems somewhat unlikely, or (b) the food supply is not

defendable as it is not uniformly distributed in space and time around the nesting habitat. It would thus not be adaptive for a peripheral territory holder to defend an area adjacent to the nesting area if the food supply, its distribution and abundance, could not be a priori predicted spatially or temporally.

No evidence was obtained that individual males defended both a nesting territory and a distinct feeding territory (Part A). This would be adaptive if the occurrence of the food supply was not predictable. Also, an individual could not be in two places at the same time, which may be required if intense competition for both types of territory was occurring.

The third option, to defend just a nesting territory, would result if the food supply was not an economically defendable resource. This seems to be the case in the Clay-colored Sparrow.

The Clay-colored Sparrow has been successful in occupying a type of habitat which holds very few other species, and few individuals of these species. Probably less than ten pairs of all these other species nested on both areas combined during either the 1975 or 1976 breeding season, as compared to over seventy pairs per year of Clay-colored Sparrows (Part C). The Clay-colored Sparrow may have evolved from a species of sparrow which held all purpose territories; all other _Spizella_ sparrows which have been studied in depth defend essentially all purpose

territories. Clay-colored Sparrows thus have occupied successfully a particular type of habitat, the extensive stands of _Symphoricarpos occidentalis,_ by a separation of the defense of a courtship/mating/nesting area from that of a food gathering area.

One would predict that, if stabilizing selection (Mayr 1963) is in operation in these sparrows, that territory size which is optimal in terms of reproductive fitness would be the one which is most frequently defended. I found just such an optimal size in both populations of Clay-colored Sparrows (Part C). No evidence was obtained on the heritability of territory size, because of the lack of return of fledglings to the study areas (Part A). It nevertheless appeared as if the birds were indeed maximizing reproductive fitness by preferentially defending territories of a particular size.

Territory size itself within the nesting habitat would be subject to several forces, both ecological and behavioural. In the present study, predation pressure on nests was determined as the major force preventing territories decreasing to a very small size. However, to increase one's relative contribution to future gene pools, it would be adaptive to defend as large a territory as possible. If Clay-colored Sparrows defended as large a territory as other _Spizella_ sparrows, they would thereby exclude many other Clay-colored Sparrows from breeding. I argue that the upper limit to territory size seems to have

been determined by the amount of time and energy devoted to territory defense which in some way influences overall reproductive success when large territories are defended, and by proximate factors such as nest cover and pressure from intruders (Part C).

LITERATURE CITED

Armstrong, E. A. 1973. A Study of Bird Song. Second edition. Dover, New York. 343pp.

Avery, M., and L. W. Oring. 1977. Song dialects in the Bobolink (Dolichonyx oryzivorus). Condor 79:113-116.

Baker, M. C. 1974. Genetic structure of two populations of White-crowned Sparrows with different song dialects. Condor 76:351-356.

Baker, M. C. 1975. Song dialects and genetic differences in White-crowned Sparrows (Zonotrichia leucophrys). Evolution 29:226-241.

Baldwin, S. P., H. C. Oberholser and L. G. Worley. 1931. Measurements of birds. Sci. Publ. Cleveland Mus. Nat. Hist. 1-165.

Banfield, A. W. F. 1974. The Mammals of Canada. Univ. of Toronto Press, Toronto. 438pp.

Barash, D. P. 1974. The evolution of marmot societies: a general theory. Science 185:415-420.

Beer, C. G. 1970. Individual recognition of voice in the social behavior of birds. IN Advances in the Study of Behavior. D. S. Lehrman et al. (eds). Academic Press, New York. Pp.27-74.

Bent, A. C. 1965. Life histories of North American Blackbirds, Orioles, Tanagers, and their allies. U. S. Natl. Mus. Bull. 211. 549pp.

Bent, A. C. 1968. Life histories of North American Cardinals, Grosbeaks, Buntings, Towhees, Finches, Sparrows, and their allies. U. S. Natl. Mus. Bull. 237. 1889pp.

Bertram, B. C. R. 1970. The vocal behaviour of the Indian Hill Mynah, (Gracula religiosa). Anim. Behav. Monogr. 3:79-192.

Best, L. B. 1977a. Nestling biology of the Field Sparrow. Auk 94:308-319.

Best, L. B. 1977b. Territory quality and mating success in the Field Sparrow (Spizella pusilla). Condor 79:192-204.

Betts, M. M. 1955. The food of titmice in oak woodland. J. Anim. Ecol. 24:282-323.

Bird, R. D. 1961. Ecology of the aspen parkland of Western Canada. Can. Dept. Agric., No. 1066, Ottawa.

Borror, D. J. 1961. Songs of finches (Fringillidae) of eastern North America. Ohio J. Sci. 61:161-174.

Brown, J. L. 1975. The Evolution of Behavior. Norton, New York. 761pp.

Brown, J. L., and G. H. Orians. 1970. Spacing patterns in mobile animals. Ann. Rev. Ecol. Syst. 1:239-262.

Bruning, J. L., and B. L. Kintz. 1968. Computational Handbook of Statistics. Scott, Foresman and Co., Illinois. 269pp.

Buckley, F. G., and P. Buckley. 1972. The breeding ecology of Royal Terns, (*Sterna maxima maxima*). Ibis 144:344-359.

Busby, D. G. 1978. Feeding ecology of a dense population of nesting Yellow Warblers. Unpublished M. Sc. thesis, University of Manitoba, Winnipeg. 62pp.

Catchpole, C. K. 1972. A comparative study of territory in the Reed Warbler (*Acrocephalus scirpaceus*) and Sedge Warbler (*A. schoenobaenus*). J. Zool. 166:213-231.

Catchpole, C. K. 1974. Habitat selection and breeding success in the Reed Warbler (*Acrocephalus scirpaceus*). J. Anim. Ecol. 43:363-380.

Catchpole, C. K. 1976. Temporal and sequential organization of song in the Sedge Warbler (*Acrocephalus schoenobaenus*). Behaviour 59:226-246.

Cederholm, G., and J. Ekman. 1976. A removal experiment on Crested Tits *Parus cristatus* and Willow Tits *P. montanus* in the breeding season. Ornis Scand. 7:207-213.

Coulson, J. C. 1966. The influence of the pair-bond and age on the breeding biology of the kittiwake gull *Rissa tridactyla*. J. Anim. Ecol. 35:269-279.

Crook, J. H. 1965. The adaptive significance of avian social organizations. Symp. Zool. Soc. Lond. 14:181-218.

Davis, L. I. 1964a. Voice structure in *Spizella*.

Southwest. Nat. 9:255-296.

Davis, L. I. 1964b. Biological acoustics and the use of the sound spectrograph. Southwest. Nat. 9:118-145.

Delius, J. D. 1965. A population study of Skylarks, Alauda arvensis. Ibis 107:466-491.

Dhondt, A. A. 1966. A method to establish boundaries of bird territories. Le Gerfaut 56:404-408.

Dhondt, A. A., and J. Huble. 1968. Age and territory in the Great Tit (Parus m. major). Ang. Ornith. 3:20-24.

Dittus, W. P. J., and R. E. Lemon. 1969. Effects of song tutoring and acoustic isolation on the song repertoires of Cardinals. Anim. Behav. 17:523-533.

Dobson, C. W., and R. E. Lemon. 1975. Re-examination of the monotony threshold hypothesis in bird song. Nature 257:126-128.

Eberhardt, C., and L. F. Baptista. 1977. Intraspecific and interspecific song mimesis in California song sparrows. Bird-Banding 48:193-205.

Emlen, S. T. 1971a. The role of song in individual recognition in the Indigo Bunting. Z. Tierspychol. 28:241-246.

Emlen, S. T. 1971b. An experimental analysis of the parameters of bird song eliciting species recognition. Behaviour 41:130-171.

Emlen, S. T., and N. J. Demong. 1975. Adaptive significance of synchronized breeding in a colonial

bird: a new hypothesis. Science 188:1029-1031.

Erskine, A. J. 1974 - 1976. The co-operative breeding bird survey in Canada. Can. Wildl. Serv. Progress Notes, Nos. 39 - 41.

Erwin, R. M. 1977. Foraging and breeding adaptations to different food regimes in three seabirds: the Common Tern, *Sterna hirundo*, Royal Tern, *Sterna maxima*, and Black Skimmer, *Rynchops niger*. Ecology 58:389-397.

Evans, R. M. 1970. Imprinting and mobility in young Ring-billed Gulls, *Larus delawarensis*. Anim. Behav. Monogr. 3:193-248.

Falls, J. B. 1969. Functions of territorial song in the White-throated Sparrow. *IN* Bird Vocalizations. R. A. Hinde (ed). Cambridge University Press, Cambridge. 207-232pp.

Fox, G. A. 1961. A contribution to the life history of the Clay-colored Sparrow. Auk 78:220-224.

Fretwell, S. D. 1972. Populations in a Seasonal Environment. University Press, Princeton, New Jersey. 217pp.

Friedmann, H. 1963. Host relations of the parasitic cowbirds. U. S. Natl. Mus. Bull. 233.

Gass, C. L., G. Angehr and J. Centa. 1976. Regulation of food supply by feeding territoriality in tHe Rufous Hummingbird. Can. J. Zool. 54:2046-2054.

Greenwood, P. J., and P. H. Harvey. 1976. The adaptive significance of variation in breeding area fidelity of

the Blackbird (_Turdus merula_). J. Anim. Ecol. 45:887-898.

Hamilton, W. D. 1971. Geometry for the selfish herd. J. Theor. Biol. 31:295-311.

Harris, M. A., and R. E. Lemon. 1972. Songs of Song Sparrows (_Melospiza melodia_): individual variation and dialects. Can. J. Zool. 50:301-309.

Hartshorne, C. 1956. The monotony-threshold in singing birds. Auk 83:176-192.

Hartshorne, C. 1973. Born to Sing. Indiana University Press, Bloomington, Indiana. 304pp.

Heidemann, M. K., and L. W. Oring. 1976. Functional analysis of Spotted Sandpiper (_Actitis macularia_) song. Behaviour 56:181-193.

Hinde, R. A. 1952. The behaviour of the Great Tit (_Parus major_) and some other related species. Behav. Suppl. 2:1-201.

Hinde, R. A. 1956. The biological significance of the territories of birds. Ibis 98:340-369.

Holmes, R. T. 1973. Social behaviour of breeding Western Sandpipers (_Calidris mauri_). Ibis 115: 107-123.

Horn, H. S. 1966. Measurement of 'overlap' in comparative ecological studies. Amer. Nat. 100:419-424.

Horn, H. S. 1968. The adaptive significance of colonial nesting in the Brewer's Blackbird (_Euphagus cyanocephalus_). Ecology 49:682-694.

Howard, H. E. 1920. Territory in Bird Life. Murray, London.

Howard, R. D. 1974. The influence of sexual selection and interspecific competition on Mockingbird (_Mimus polyglottos_) song. Evolution 28:428-438.

Knapton, R. W., and J. R. Krebs. 1974. Settlement patterns, territory size, and breeding density in the Song Sparrow (_Melospiza melodia_). Can. J. Zool. 52:1413-1420.

Krebs, J. R. 1971. Territory and breeding density in the Great Tit _Parus major_. Ecology 52:2-22.

Krebs, J. R. 1977. The significance of song repertoires: the Beau Gests hypothesis. Anim. Behav. 25:475-478.

Kroodsma, D. E. 1974. Song learning, dialects and dispersal in the Bewick's Wren. Z. Tierpsychol. 35:352-380.

Kroodsma, D. E. 1977. Correlates of song organization among North American wrens. Amer. Natur. 111:995-1008.

Kruuk, H. 1964. Predators and anti-predator behaviour of the Black-headed Gull, _Larus ridibundus_ L. Behav. Suppl. 11:1-129.

Lack, D. 1968. Ecological adaptations for breeding in birds. Methuen and Co., London. 409pp.

Lein, M. R. 1972. Territorial and courtship songs of birds. Nature 237:48-49.

Lemon, R. E. 1965. The song repertoire of Cardinals

(Richmondena cardinalis) at London, Ontario. Can. J. Zool. 43:559-569.

Lemon, R. E. 1967. The response of Cardinals to songs of different dialects. Anim. Behav. 15:538-545.

Lemon, R. E. 1975. How birds develop song dialects. Condor 77:386-406.

Marler, P. 1952. Variations of the song of the Chaffinch, Fringilla coelebs. Ibis 94:458-472.

Marler, P., and W. J. Hamilton. 1966. Mechanisms of Animal Behavior. Wiley, New York. 771pp.

Marler, P., and P. Mundinger 1970. Vocal learning in birds. IN Ontogeny of Vertebrate Behavior. Academic Press, London and New York. 389-450pp.

Marler, P., and M. Tamura. 1962. Song 'dialects' in three populations of White-crowned Sparrows. Condor 64:368-377.

Martin, S. G. 1974. Adaptations for polygynous breeding in the Bobolink Dolichonyx oryzivorus. Amer. Zool. 14:109-119.

Mayfield, H. F. 1965. The Brown-headed Cowbird, with old and new hosts. The Living Bird 4:13-28.

Maynard Smith, J. 1974. Territorial behaviour IN Models in Ecology. Cambridge Univ. Press, Cambridge. 125-138.

Mayr, E. 1963. Animal Species and Evolution. Belknap Press, Cambridge, Mass.

McKinney, D. F. 1973. Ecoethological aspects of

reproduction. IN Breeding Biology of Birds. Nat. Acad. Sci., Washington. 6-21.

McLaren, I. A. 1972. Polygyny as the adaptive function of breeding territory in birds. IN Growth by Interssusception. E. S. Deevey (ed). Trans. Conn. Acad. Arts and Sci. 44:191-210.

Milligan, M. M., and J. Verner. 1971. Interpopulational song dialect discrimination in the White-crowned Sparrow. Condor 73:208-213.

Mills, J. A. 1973. The influence of age and pair-bond on the breeding biology of the Red-billed Gull Larus novaehollandiae scopulinus. J. Anim. Ecol. 42:147-162.

Morse, D. H. 1968. A quantitative study of foraging male and female spruce-woods warblers. Ecology 49:779-784.

Morse, D. H. 1970. Territorial and courtship songs of birds. Nature 226:659-661.

Morse, D. H. 1976. Hostile encounters among spruce-woods warblers (Dendroica: Parulidae). Anim. Behav. 24:764-771.

Mundinger, P. C. 1975. Song dialects and colonization in the House Finch Carpodacus mexicanus on the east coast. Condor 77:407-422.

Nice, M. M. 1937. Studies in the life history of the Song Sparrow. Part 1. Trans. Linn. Soc. N. Y. IV. 247pp.

Nottebohm, F. 1969. The song of the Chingolo Zonotrichia

capensis in Argentina: description and evolution of a
system of dialects. Condor 71:299-315.

Nottebohm, F. 1972. The origins of vocal learning. Amer.
Nat. 106:116-140.

Nottebohm, F., and R. K. Selander. 1972. Vocal dialects
and gene frequencies in the Chingolo Sparrow
(Zonotrichia capensis). Condor 74:137-143.

O'Connor, R. J. 1977. Differential growth and body
composition in altricial passerines. Ibis
119:147-166.

Orians, G. H. 1966. Food of nestling Yellow-headed
Blackbirds, Cariboo Parklands, British Columbia.
Condor 68:321-337.

Orians, G. H. 1971. Ecological aspects of behavior. IN
D. S. Farner and J. R. King (eds). Avian Biology
Vol.1. Academic Press, New York. 513-546.

Orians, G. H., and M. F. Willson. 1964. Interspecific
territories of birds. Ecology 45:736-745.

Pelton, J. 1953. Studies of the life-history of
Symphoricarpos occidentalis Hook. in Minnesota.
Ecol. Monogr. 23:17-38.

Perrins, C. M. 1965. Population fluctuations and clutch
size in the Great Tit (Parus major). J. Anim. Ecol.
34:601-647.

Perrins, C. M. 1970. The timing of birds' breeding
seasons. Ibis 112:242-255.

Petrinovich, L., T. Patterson and H. V. S. Peeke.

1976. Reproductive condition and the response of White-crowned Sparrows (Zonotrichia leucophrys nuttalli) to song. Science 191:206-207.

Pitelka, F. A., R. T. Holmes and S. F. MacLean, Jr. 1974. Ecology and evolution of social organization in Arctic sandpipers. Amer. Zool. 14:185-204.

Post, W. 1974. Functional analysis of space-related behavior in the Seaside Sparrow. Ecology 55:564-575.

Potter, P. E. 1972. Territorial behavior in Savannah Sparrows in southeastern Michigan. Wilson Bull. 84:48-59.

Ricklefs, R. E. 1969. An analysis of nesting mortality in birds. Smiths. Contr. Zool. 9:48pp.

Robins, J. D. 1971a. A study of Henslow's Sparrow in Michigan. Wilson Bull. 83:39-48.

Robins, J. D. 1971b. Differential niche utilization in a grassland sparrow. Ecology 52:1065-1070.

Root, R. B. 1967. The niche exploitation pattern of the Blue-gray Gnatcatcher. Ecol. Monogr. 37:317-349.

Rothstein, S. I. 1974. Mechanisms of avian egg recognition: possible learned and innate factors. Auk 91:796-807.

Royama, T. 1970. Factors governing the hunting behaviour and selection of food by the Great Tit (Parus major L.). J. Anim. Ecol. 39:619-668.

Salt, W. R. 1966. A nesting study of Spizella pallida. Auk 83:274-281.

Shiovitz, K. A. 1975. The process of species-specific song recognition by the Indigo Bunting *Passerina cyanea* and its relationship to the organization of avian acoustical behavior. Behaviour 55:128-179.

Smith, C. C. 1968. The adaptive nature of social organization in the genus of tree squirrels *Tamiasciurus*. Ecol. Monogr. 38:31-63.

Smith, R. L. 1974. Ecology and Field Biology. 2nd edition. Harper and Row, New York. 850pp.

Smith, W. J. 1969. Messages of vertebrate communication. Science 165:145-180.

Smith, W. J. 1977. The Behavior of Communicating. Harvard Univ. Press, Cambridge. 545pp.

Snow, D. W. 1956. Territory in the Blackbird *Turdus merula*. Ibis 98:438-447.

Sokal, R. R., and F. J. Rohlf. 1969. Biometry. Freeman and Co., San Francisco. 776pp.

Sowls, L. K. 1948. The Franklin Ground Squirrel *Citellus franklinii* (Sabine), and its relationship to nesting ducks. J. Mammal. 29:113-137.

Thielcke, G. 1969. Geographic variation in bird vocalizations. *IN* Bird Vocalizations. R. A. Hinde (ed). Cambridge Univ. Press. 311-339.

Thompson, W. L. 1970. Song variation in a population of Indigo Buntings. Auk 87:58-71.

Thompson, W. L. 1976. Vocalizations of the Lazuli Bunting. Condor 78:195-207.

Thorpe, W. H. 1968. Perceptual basis for group organization in social vertebrates, especially birds. Nature 220:124-128.

Verner, J. 1976. Complex song repertoire of male Long-billed Marsh-Wrens in eastern Washington. The Living Bird 14:263-300.

Verner, J. 1977. On the adaptive significance of territoriality. Amer. Nat. 111:769-775.

Verner, J., and M. M. Milligan. 1971. Responses of male White-crowned Sparrows to playback of recorded songs. Condor 73:56-64.

Walkinshaw, L. H. 1939. Notes on the nesting of the Clay-colored Sparrow. Wilson Bull. 51:17-21.

Walkinshaw, L. H. 1944. The eastern Chipping Sparrow in Michigan. Wilson Bull. 56:193-205.

Walkinshaw, L. H. 1945. Clay-colored Sparrow notes. Jack-pine Warbler 22:120-131.

Walkinshaw, L. H. 1968. Eastern Field Sparrow. IN A. C. Bent. Life histories of North American Cardinals, Grosbeaks, Buntings, Towhees, Finches, Sparrows, and their allies. U. S. Natl. Mus. Bull. 237. 1217-1235.

Watson, A., and R. Moss. 1970. Dominance, spacing behaviour and aggression in relation to population limitations in vertebrates. IN Animal Populations in relation to their Food Resources. A. Watson (ed) Blackwell, Oxford. 167-218.

Weeden, J. S. 1965. Territorial behavior of the Tree Sparrow. Condor 67:193-209.

Weir, T. R. (ed) 1960. Economic Atlas of Manitoba. Dept. Ind. Comm., Prov. of Man. 39pp.

Welsh, D. A. 1975. Savannah Sparrow breeding and territoriality on a Nova Scotia sand dune beach. Auk 92:235-251.

Wiens, J. A. 1969. An approach to the study of the ecological relationships among grassland birds. Ornithol. Monogr. 8:93pp.

Wiens, J. A. 1973. Interterritorial habitat variation in Grasshopper and Savannah Sparrows. Ecology 54:877-884.

Willing, R. M. 1970. The role of song in the behavior and evolution of three species of spizellid sparrows: sonograph and field playback studies. Unpubl. M.Sc. Thesis, Simon Fraser Univ., Vancouver.

Wilson, E. O. 1975. Sociobiology: the new synthesis. Belknap Press, Cambridge, Mass. 697pp.

Windsor, D., and S. T. Emlen. 1975. Predator-prey interactions and adult and prefledging Bank Swallows and American Kestrels. Condor 77:359-361.

Wood, D. L., and D. S. Wood. 1972. Numerical color specifications for bird identification: iris color and age in fall migrants. Bird-banding 43:182-190.

Wood, M. 1969. A bird bander's guide to determination of age and sex of selected species. Univ. Park, Pa.

State Univ.

Yeaton, R. I., and M. L. Cody. 1974. Competition
release in island Song Sparrow populations. Theor.
Pop. Biol. 5:42-58.

APPENDICES

APPENDIX 1

Morphological and behavioral differences between male and female Clay-colored Sparrows

Wing-chord length.

Figure 1a shows the distribution of wing-chord lengths in 162 adult male and 134 adult female Clay-colored Sparrows caught in May and June on the Manitoba study areas, and initially sexed by the presence of a brood patch or a cloacal protuberance (Wood 1969). Lengths in females ranged from 56 to 62mm, with a peak at 59mm (mean = 59.4mm, standard deviation = 1.2mm), and lengths in males ranged from 60 to 66mm, with a peak at 63mm (mean = 63.0mm, standard deviation = 1.4mm). A similar distribution of wing-chord lengths occurred in 83 adult specimens of known sex obtained from the National Museums of Science, Ottawa, and the Royal Ontario Museum, Toronto. Females peaked at 60mm (mean = 58.7mm, standard deviation = 1.6mm), and males peaked at 63mm (mean = 62.2mm, standard deviation = 1.4mm). Males therefore have longer wings than females, although there is an area of overlap between 59 and 62mm.

A similar bimodal distribution was also obtained from the measurements of the wing-chords of 26 Clay-colored Sparrows caught on two study plots in central Mexico, near Guadalajara (20° 40' latitude, 103° 20' longitude) and near Sanabria (19° 30' latitude, 101° 40' longitude) (Figure 1c); one peak at 59mm and the other at 63mm. Finally, for

200

Figure 1. Measured right wing-chord (after Baldwin, Oberholser and Worley 1931) for three samples of adult Clay-colored Sparrows. 1A shows the distribution of measurements for 134 females (hatched bars) and 162 males (open bars) live-trapped in Manitoba, 1B for 22 female (hatched bars) and 61 male (open bars) museum specimens, and 1C for 26 adults live-trapped in Mexico.
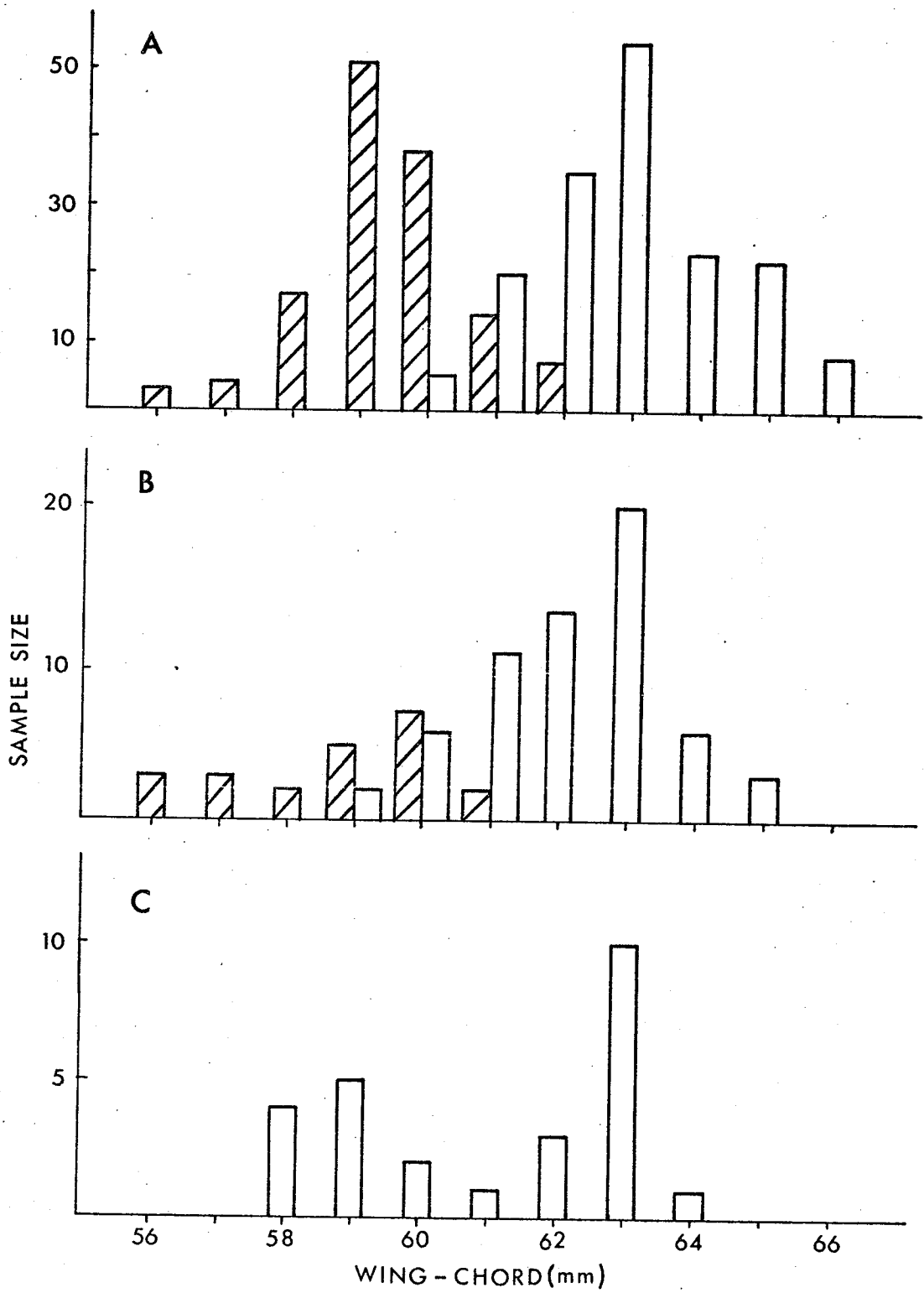
9 immature museum specimens for which the sex was known, the six males ranged from 61 to 63mm (mean = 62.2mm) and the females from 58 to 61mm (mean = 59.3mm).

Superciliary stripe coloration.

During 1974 and 1975, I noticed that the headmarkings, especially the superciliary stripe, of females appeared more buff-colored than those of males. Consequently, I matched the color of the superciliary stripe against Munsell soil color charts (see Wood and Wood 1972), on 70 adults caught in May and early June, 1976, and on 80 adult museum specimens. In 1976, I also matched the color of the breast feathers of 13 immatures caught in August that were banded as nestlings on the study areas in Manitoba, and of 21 adults recaptured in August following the postnuptial molt that had been banded in the previous springs. I took the same comparisons on the 11 immature museum specimens.

The Munsell color chart used for all comparisons on the birds was the hue 10YR, which shows the values 2 (black) to 8 (white) across a chromatic scale to dark yellowish-brown to yellow. The coloration of the superciliary stripe of all sparrows fell along a continuum from white (8/1 and 8/2) and light gray (7/1 and 7/2) through pale brown (8/3, 8/4, 7/3, 7/4) to yellow (8/6, 8/8, 7/6, 7/8).

Males had, on average, whitish superciliary stripes, while those of the females were more pale-brown (Table 1). For statistical analysis, categories were combined (8/1 and 8/2, 8/3 and 8/4), and the differences between males and

Table 1. Superciliary stripe color of adults on the Manitoba study areas (N = 70).

	Chart value / chroma			
	8/1	8/2	8/3	8/4
Males	28	13	1	0
Females	1	6	14	7

females were found to be significant ($X^2 = 37.8$, $P < 0.001$).

The color of the superciliary stripe of three of the 83 adult museum specimens could not be used because of damage to the eye area. In the remaining 80, a trend similar to the field data appears; superciliary white in males, browner in females (Table 2). Again, when categories are combined, the differences between the sexes are significant ($X^2 = 21.1$, $P < 0.01$).

Some behavioral and morphological observations on male and female Clay-colored Sparrows

Observations on males and females in the field on my study areas revealed the following differences in behavior. Only males were known to sing; on no occasion was a known female observed singing during the course of the study. Females are reported to do most of the incubating and brooding of the young (Fox 1961, Bent 1968). Of 78 males caught in the period mid-June to mid-July, and sexed by cloacal protuberance, none had developed a brood patch. Of over 200 flushes of a banded bird of known sex from a nest containing young, only three proved to be males. Often an adult would sit tight and remain motionless on a nest when approached. In all such instances, when the bird was identified by its leg band, it proved to be a female. Fox (1961) gives the proportion of time spent by the female incubating as 81% and brooding of the young as 71%, and by the male 13% and 9% respectively. My observations

Table 2. Superciliary stripe color of adult museum specimens of
Clay-colored Sparrows.

	Chart value / chroma							
	8/1	8/2	8/3	8/4	7/1	7/3	7/4	7/6
Males	8	27	18	4	1	0	0	0
Females	0	0	9	6	0	2	3	2

	Chroma alone			
	1	2	3	4
Males	9	27	18	4
Females	0	0	11	11

essentially agree with these proportions.

Measurements taken on 83 specimens of adult Clay-colored Sparrows of known sex revealed that this species is essentially monomorphic for culmen depth and length, and for tarsometatarsus length (Table 3).

Table 3. Measurements of 83 adult Clay-colored Sparrows of known sex from the National Museums of Canada, Ottawa, and the Royal Ontario Museum, Toronto.

Parameter	Sex	Sample	Range(mm)	Mean	SD
Culmen depth	Male	61	4.2 - 5.6	4.79	0.33
	Female	22	4.4 - 5.4	4.70	0.41
Culmen length	Male	61	8.0 - 9.7	8.80	0.44
	Female	22	8.1 - 9.4	8.72	0.31
Tarsometatarsus	Male	61	15.1 - 18.8	17.01	0.88
	Female	22	15.3 - 19.1	17.23	1.13

APPENDIX 2

The expected values for R versus R and N versus N in the analysis in Table 3 were calculated using the equation

$$C = n(n - 1) / 2$$

which gives the number of possible combinations C of two individuals in a group of size n (Brown 1975:91). Equivalent expected values for R versus N were taken as (R x N) possible pairs.

APPENDIX 3

Bent (1968) lists the following as potential predators on the nests of Clay-colored Sparrows: the mammals _Microtus pennsylvanicus_, _Peromyscus maniculatus_, _Mustela ermina_, _M. frenata_, _M. rixosa_, and _Mephites mephites_, the birds _Lanius ludovicianus_ and _Pica pica_, and the reptile _Thamnophis sirtalis_.

Bent (op. cit.) also mentions other sources of destruction of the nest as fire and trampling by cattle and horses. These factors were not directly responsible for any egg loss or loss of young on my study areas.

APPENDIX 4

Horn's (1966) measure of overlap is the equation:

$$\hat{C}_\lambda = \frac{2 \sum\limits_{i=1}^{S} X_i Y_i}{\sum\limits_{i=1}^{S} X_i^2 + \sum\limits_{i=1}^{S} Y_i^2}$$

This equation is a simplified form of Morisita's (IN Horn 1966) index of overlap which can be used when the sizes of the two samples being compared are equal.

APPENDIX 5

Means and standard deviations for each male in the two analyses given in Tables 2 and 3 in Part B are given below in Tables 4 and 5 respectively.

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Table 4. Comparison of songs from the two main study areas. Each value is the mean of measurements on five songs per bird. Means and standard deviations for all 10 birds combined are given in Table 2 in Part B.

| | STUDY AREA #1 | | | | | | | | | |
| | BIRD # | | | | | | | | | |
Song characteristic	1	2	3	4	5	6	7	8	9	10
Total song length (sec)	1.86 ± 0.08	1.30 ± 0.09	1.52 ± 0.04	1.85 ± 0.06	2.14 ± 0.16	1.97 ± 0.11	1.74 ± 0.09	$1.6? \pm 0.07$	1.77 ± 0.08	1.43 ± 0.12
Length of first buzz (sec)	0.80 ± 0.04	0.77 ± 0.06	0.62 ± 0.09	1.06 ± 0.07	1.14 ± 0.16	0.72 ± 0.06	0.63 ± 0.11	0.63 ± 0.08	0.89 ± 0.12	0.64 ± 0.09
Interbuzz interval (sec $\times 10^{-2}$)	9.3 ± 0.3	9.0 ± 0.2	8.6 ± 0.4	11.6 ± 0.4	10.8 ± 0.6	9.9 ± 0.7	10.4 ± 0.6	9.8 ± 0.2	10.1 ± 0.3	9.2 ± 0.4
Number of syllables/song	174.8 ± 5.2	101.8 ± 4.2	143.6 ± 8.4	185.6 ± 4.8	206.4 ± 9.9	164.8 ± 8.6	66.8 ± 2.4	114.8 ± 6.6	75.8 ± 4.8	99.8 ± 8.8
Number of buzzes/song	3	2	2.8 ± 0.5	2	2	3.2 ± 0.5	3	2	2.8 ± 0.5	3
Number of notes/syllable	2	2	2	2	2	2	6	2	5	2
Number of notes/second	205.6 ± 4.2	166.4 ± 6.6	204.6 ± 2.4	214.7 ± 5.5	203.3 ± 7.6	186.6 ± 4.8	264.4 ± 6.6	157.5 ± 7.6	227.6 ± 4.2	160.3 ± 5.1
Upper frequency limit(khz)	6.5	6.2 ± 0.5	6.4 ± 0.6	6.0	6.6 ± 0.2	6.4 ± 0.3	6.0	5.9 ± 0.2	6.7 ± 0.3	6.6 ± 0.3
Lower frequency limit(khz)	2.0	2.5	2.2 ± 0.3	2.1 ± 0.2	2.2 ± 0.3	2.5	2.0	2.4 ± 0.2	2.5	2.0
FM(ascending)(hz/sec $\times 10^{-2}$)	2.46 ± 0.22	0.98 ± 0.28	1.48 ± 0.16	4.76 ± 0.44	3.44 ± 0.36	1.14 ± 0.21	——	2.66 ± 0.31	——	0.86 ± 0.08
FM(descending)(hz/sec $\times 10^{-2}$)	1.68 ± 0.14	0.76 ± 0.21	0.96 ± 0.24	1.86 ± 0.34	1.62 ± 0.18	1.36 ± 0.24	3.20 ± 0.42	2.74 ± 0.26	2.60 ± 0.14	1.60 ± 0.15

Table 4 (cont.)

| | STUDY AREA #2 | | | | | | | | | |
| | BIRD # | | | | | | | | | |
Song characteristic	1	2	3	4	5	6	7	8	9	10
Total song length (sec)	$1.75^{\pm}0.17$	$1.67^{\pm}0.09$	$1.97^{\pm}0.12$	$1.73^{\pm}0.05$	$1.48^{\pm}0.09$	$1.58^{\pm}0.08$	$1.83^{\pm}0.13$	$2.00^{\pm}0.14$	$1.93^{\pm}0.11$	$1.45^{\pm}0.09$
Length of first buzz (sec)	$0.53^{\pm}0.09$	$0.76^{\pm}0.09$	$0.85^{\pm}0.10$	$0.96^{\pm}0.09$	$0.85^{\pm}0.17$	$1.06^{\pm}0.05$	$1.17^{\pm}0.12$	$0.65^{\pm}0.09$	$0.72^{\pm}0.11$	$0.53^{\pm}0.09$
Interbuzz interval (sec$\times10^{-2}$)	$10.4^{\pm}0.4$	$10.6^{\pm}0.5$	$9.9^{\pm}0.3$	$10.8^{\pm}0.3$	$8.1^{\pm}0.2$	$8.2^{\pm}0.3$	$9.1^{\pm}0.4$	$13.6^{\pm}0.5$	$12.6^{\pm}0.4$	$8.1^{\pm}0.2$
Number of syllables/song	$118.6^{\pm}5.5$	$60.6^{\pm}3.8$	$178.8^{\pm}6.8$	$168.4^{\pm}4.8$	$106.4^{\pm}9.6$	$82.6^{\pm}6.8$	$177.2^{\pm}8.8$	$78.6^{\pm}4.2$	$186.4^{\pm}9.2$	$132.9^{\pm}4.2$
Number of buzzes/song	3	$2.8^{\pm}0.5$	2	2	2	2	$2.2^{\pm}0.5$	3	$3.4^{\pm}0.6$	$3.2^{\pm}0.5$
Number of notes/syllable	2	5	2	2	2	4	2	6	2	2
Number of notes/second	$154.6^{\pm}8.3$	$205.8^{\pm}6.6$	$190.8^{\pm}5.6$	$207.5^{\pm}7.8$	$152.0^{\pm}4.3$	$220.3^{\pm}7.2$	$203.7^{\pm}6.6$	$270.6^{\pm}8.9$	$218.3^{\pm}5.6$	$204.9^{\pm}3.2$
Upper frequency limit(khz)	6.0	$5.9^{\pm}0.2$	$6.4^{\pm}0.3$	6.5	$6.7^{\pm}0.3$	$6.8^{\pm}0.3$	6.0	6.5	$6.6^{\pm}0.2$	$6.4^{\pm}0.3$
Lower frequency limit(khz)	$2.2^{\pm}0.3$	$2.1^{\pm}0.2$	$2.4^{\pm}0.2$	2.0	2.0	2.5	$2.4^{\pm}0.2$	$2.2^{\pm}0.3$	$2.4^{\pm}0.2$	2.0
FM(ascending)(hz/sec$\times10^{-2}$)	$0.66^{\pm}0.14$	—	$0.98^{\pm}0.12$	$3.66^{\pm}0.40$	$2.84^{\pm}0.33$	—	$1.66^{\pm}0.21$	—	$1.88^{\pm}0.18$	$2.06^{\pm}0.19$
FM(descending)(hz/sec$\times10^{-2}$)	$0.78^{\pm}0.10$	$1.44^{\pm}0.20$	$2.66^{\pm}0.08$	$2.14^{\pm}0.16$	$1.88^{\pm}0.14$	$0.66^{\pm}0.04$	$1.84^{\pm}0.14$	$1.80^{\pm}0.16$	$1.98^{\pm}0.14$	$2.14^{\pm}0.16$

Table 5. Comparison of songs between four populations of Clay-colored Sparrows. Each value is the mean of measurements taken on three songs per bird. Four males lacked a FM(ascending) component to the syllable. Means and standard deviations where present for all three birds per study area combined are given in Table 3 in Part B.

Song characteristic	Study Area #1			Study Area #2			Delta			Winnipeg		
	1	2	3	1	2	3	1	2	3	1	2	3
Total song length (sec)	1.30 ± 0.07	1.75 ± 0.08	1.86 ± 0.04	1.67 ± 0.06	1.48 ± 0.04	1.83 ± 0.08	1.96 ± 0.04	1.41 ± 0.06	1.84 ± 0.03	1.58 ± 0.06	2.04 ± 0.14	1.50 ± 0.02
Length of first buzz (sec)	0.73 ± 0.05	0.62 ± 0.08	1.05 ± 0.04	0.74 ± 0.06	0.83 ± 0.10	1.08 ± 0.04	1.14 ± 0.04	0.88 ± 0.11	0.84 ± 0.09	0.98 ± 0.06	1.08 ± 0.10	0.66 ± 0.02
Interbuzz interval (sec x 10^{-2})	9.0 ± 0.2	9.7 ± 0.5	11.7 ± 0.4	10.5 ± 0.4	8.2 ± 0.1	9.0 ± 0.2	10.4 ± 0.3	11.4 ± 0.2	9.8 ± 0.1	10.4 ± 0.4	9.6 ± 0.2	8.4 ± 0.4
Number of syllables/song	101.3 ± 2.5	66.4 ± 1.8	184.4 ± 2.4	60.4 ± 2.4	105.2 ± 4.6	177.4 ± 6.2	166.4 ± 4.0	294.2 ± 6.6	86.6 ± 3.6	121.6 ± 4.4	183.0 ± 0	144.5 ± 0.5
Number of buzzes/song	2	3	2	2.33 ± 0.58	2	2	3	2	2	2	3	3
Number of notes/syllable	2	6	2	5	2	2	2	1	4	2	2	2
Number of notes/second	165.3 ± 4.2	262.3 ± 3.2	215.7 ± 3.2	151.6 ± 2.4	204.2 ± 3.2	201.2 ± 3.2	190.8 ± 4.2	226.4 ± 4.8	199.6 ± 7.5	164.7 ± 4.6	197.6 ± 2.2	215.5 ± 0.5
Upper frequency limit (khz)	6.2 ± 0.3	6.0	6.0	6.0	6.5	6.0	6.5	6.7 ± 0.3	6.5	6.3 ± 0.3	6.0	6.5
Lower frequency limit (khz)	2.5	2.0	2.0	2.2 ± 0.3	2.0	2.2 ± 0.3	2.5	2.3 ± 0.3	2.5	2.2 ± 0.3	2.5	2.5
FM(ascending) (hz/sec x 10^{-2})	0.94 ± 0.14	----	4.68 ± 0.18	----	2.80 ± 0.12	1.64 ± 0.10	1.88 ± 0.12	----	----	0.94 ± 0.06	1.64 ± 0.04	3.62 ± 0.28
FM(descending) (hz/sec x 10^{-2})	0.74 ± 0.18	3.18 ± 0.21	1.78 ± 0.20	1.38 ± 0.14	1.86 ± 0.08	1.82 ± 0.08	0.62 ± 0.08	1.44 ± 0.07	0.84 ± 0.06	1.62 ± 0.04	0.72 ± 0.06	2.68 ± 0.12

APPENDIX 6

Individual differences between the songs of twelve males were analyzed in Table 4 in Part B. The songs of three males were represented in that table; the songs of the remaining nine are given below in Table 6.

Table 6. Songs of nine more Clay-colored Sparrows analyzed in Table 4 in Part B. Each value represents the mean of measurements taken on five songs per bird.

Song characteristic	Bird #								
	1	2	3	4	5	6	7	8	9
Total song length (sec)	1.80 ± 0.12	1.77 ± 0.17	1.83 ± 0.20	1.58 ± 0.10	1.66 ± 0.27	1.78 ± 0.10	1.87 ± 0.06	1.67 ± 0.04	1.74 ± 0.01
Length of first buzz (sec)	0.79 ± 0.09	0.69 ± 0.12	0.57 ± 0.03	0.35 ± 0.04	0.53 ± 0.06	0.54 ± 0.04	1.00 ± 0.05	0.94 ± 0.04	0.39 ± 0.03
Interbuzz interval (sec x 10^{-2})	9.9 ± 0.7	11.8 ± 0.3	11.0 ± 0.4	10.4 ± 0.4	12.9 ± 0.7	11.7 ± 0.3	11.7 ± 0.3	11.7 ± 0.7	11.6 ± 0.7
Number of syllable/song	76.4 ± 4.0	133.4 ± 7.6	171.8 ± 10.8	140.6 ± 14.0	71.4 ± 4.7	164.6 ± 6.3	145.8 ± 5.8	316.0 ± 7.2	140.1 ± 2.9
Number of buzzes/song	2	2.4 ± 0.6	3.4 ± 0.6	3.2 ± 0.5	3	3	1.8 ± 0.5	1.8 ± 0.5	4
Number of notes/syllable	5	1	2	2	2	2	6	1	2
Number of notes/second	230.9 ± 1.8	80.2 ± 3.2	200.8 ± 2.7	203.5 ± 5.7	206.0 ± 5.0	213.3 ± 1.6	240.6 ± 4.6	201.4 ± 2.7	201.2 ± 2.6
Upper frequency limit (khz)	5.4 ± 0.2	5.9 ± 0.2	6.3 ± 0.3	6.6 ± 0.2	6.2 ± 0.3	6.3 ± 0.3	6.4 ± 0.3	6.0 ± 0.3	6.3 ± 0.3
Lower frequency limit (khz)	2.2 ± 0.3	2.2 ± 0.3	2.3 ± 0.3	2.7 ± 0.3	2.3 ± 0.3	2.6 ± 0.2	2.2 ± 0.3	2.3 ± 0.3	2.3 ± 0.3
FM(ascending) (hz/sec x 10^{-2})	—	0.61 ± 0.08	5.97 ± 0.26	—	1.25 ± 0	3.37 ± 0.21	—	—	3.83 ± 0.5
FM(descending) (hz/sec x 10^{-2})	1.47 ± 0.08	0.68 ± 0.08	1.78 ± 0.13	1.27 ± 0.05	0.85 ± 0.10	3.34 ± 0.26	3.34 ± 0.26	4.24 ± 0.48	—

APPENDIX 7

The repertoires of four males in addition to those given in Table 7 in Part B are tabulated below in Table 7.

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Table 7. Comparison of songs delivered from different perches (a – d) for four males. For an explanation of the values and data analysis, see Table 7 in Part B.

Song characteristic	Male # 6				F	P	Male # 3					F	P
	a	b	c	d			a	b	c	d	e		
Total song length (sec)	1.59	1.50	1.59	4.35	204.8	0.001	1.62	1.74	1.24	1.71	1.74	34.6	0.01
Length of first buzz (sec)	0.47	0.40	0.41	0.27	14.9	0.01	0.50	0.51	0.56	0.59	0.56	3.3	ns
Interbuzz interval (sec x 10^{-2})	9.4	10.5	10.3	8.3	12.6	0.01	13.3	13.2	13.3	13.4	13.3	1.9	ns
Number of syllables/song	146.7	141.0	149.3	215.3	9.1	0.01	145.3	150.7	117.7	154.3	153.7	96.1	0.01
Number of buzzes/song	3	3	3	12.3	112.0	0.001	2.8	3	2	3	3	12.0	0.01
Number of notes/syllable	2	2	2	2	—	—*	2	2	2	2	2	—	—*
Number of notes/second	214.4	218.6	216.3	130.7	282.2	0.001	211.9	205.3	211.6	213.4	206.3	0.9	ns
Upper frequency limit (khz)	6.5	6.5	6.7	6.5	1.0	ns	6.5	6.5	6.5	6.5	6.5	—	—*
Lower frequency limit (khz)	2.7	2.7	2.5	2.5	0.7	ns	2.5	2.5	2.5	2.5	2.5	—	—*
FM(ascending) (hz/sec x 10^{-2})	0	0	0	1.26	10.5	0.01	0.78	0.78	0.81	0.85	0.78	1.9	ns
FM(descending) (hz/sec x 10^{-2})	1.25	1.28	1.36	0.67	160.4	0.001	1.25	1.36	1.25	1.25	1.28	2.4	ns

* The values for these characteristics did not vary within song types.

Table 7 (continued)

Song characteristic	Male #4					Male #5				
	a	b	c	F	P	a	b	c	F	P
Total song length (sec)	1.55	2.18	1.42	23.6	0.01	1.84	3.85	1.81	25.5	0.01
Length of first buzz (sec)	0.99	0.71	0.94	12.7	0.01	0.96	0.46	1.02	106.3	0.001
Interbuzz interval (sec x 10^{-2})	8.3	8.3	8.2	0.5	ns	12.0	9.1	11.6	67.0	0.001
Number of syllables/song	108.0	153.3	103.7	30.7	0.001	76.0	240.0	75.6	37.3	0.001
Number of buzzes/song	2	3	2	—	—*	2	6	2.3	48.0	0.001
Number of notes/syllable	2	2	2	—	—*	6	2	6	—	—*
Number of notes/second	147.3	156.6	153.7	2.6	ns	258.7	143.2	246.6	129.2	0.001
Upper frequency limit (khz)	6.7	6.7	6.5	0.5	ns	5.5	5.7	6.0	1.8	ns
Lower frequency limit (khz)	2.0	2.3	2.3	0.5	ns	2.0	2.0	2.0	—	—*
FM(ascending) (Hz/sec x 10^{-2})	1.04	0.91	1.09	2.5	ns	3.4	2.6	3.2	52.4	0.001
FM(descending) (hz/sec x 10^{-2})	1.56	1.64	1.47	3.1	ns	0	0	1.47	15.6	0.01

* The values for these characteristics did not vary within song types.

APPENDIX 8

There was no difficulty in determining the proportion of Symphoricarpos within most of the one metre intercepts, especially when the transect passed over thick clumps of the shrub, when isolated plants were encountered along the transect, and of course when the shrub was absent. It occasionally proved difficult to obtain an absolute measure of the shrub in transition zones, and thus some intercept lengths were arbitrarily judged on the relative amounts of Symphoricarpos within a one metre intercept. This is partially because the vegetational measures were undertaken in early May, when leaf growth was just starting, and thus much of the cover was afforded by the branches themselves. I deliberately carried out vegetation measures at this time, however, as the male Clay-colored Sparrows themselves would be establishing territories over the vegetation in early May, thus I attempted to approximate the real situation.

Where judgements were made on the cover value of Symphoricarpos within an intercept length, attempts were made to be consistent both within and between study areas. However, because of the subjective assessment of some metre intercepts, I used broad categories of relative amounts of Symphoricarpos within an intercept in the analysis.

APPENDIX 9

Total areas covered by cores and cortices within the territories were not equal (Table 8), hence for the purpose of analysis (see Table 4), the expected number of nests in each area were determined from the ratio of cores to cortices (Table 8).

Table 8. Total areas (m^2) of cores and cortices on the two study
areas in 1975 and 1976.

		Total sum of cores (m^2)	Total sum of cortices (m^2)	Predicted ratio cores:cortices
Study Area #1	1975	13,554	12,871	1.05 : 1
	1976	12,367	10,790	1.15 : 1
Study Area #2	1975	13,075	15,570	0.83 : 1
	1976	13,557	17,555	0.77 : 1

APPENDIX 10

Response values for 32 males to experimental playbacks on Study Area #2 are given in Figure 1. None of the four responses measured showed a consistent relationship with territory size.

Figure 1. Comparison of size of territory with four playback responses for 32 males tested on Study Area #2. The responses are: (A) the number of flights, (B) closest approach, (C) latency of response, and (D) percent change in song rate.

NUMBER OF FLIGHTS

CLOSEST APPROACH (cm)

TERRITORY SIZE (m²)