AGE-RELATED REPRODUCTIVE SUCCESS IN THE YELLOW WARBLER (*Dendroica petechia*)

by

Dawn L. Sutherland

A thesis
presented to the University of Manitoba
in partial fulfillment of the
requirements for the degree of
Master of Science
in
Department of Zoology

Winnipeg, Manitoba

ISBN 0-315-37453-5

AGE-RELATED REPRODUCTIVE SUCCESS IN THE YELLOW WARBLER

(*Dendroica petechia*)

BY

DAWN L. SUTHERLAND

A thesis submitted to the Faculty of Graduate Studies of
the University of Manitoba in partial fulfillment of the requirements
of the degree of

MASTER OF SCIENCE

I hereby declare that I am the sole author of this thesis.

I authorize the University of Manitoba to lend this thesis to other institutions or individuals for the purpose of scholarly research.

Dawn L. Sutherland

I further authorize the University of Manitoba to reproduce this thesis by photocopying or by other means, in total or in part, at the request of other institutions or individuals for the purpose of scholarly research.

Dawn L. Sutherland

The University of Manitoba requires the signatures of all persons using or photocopying this thesis. Please sign below, and give address and date.

ABSTRACT

Age-related reproductive success was investigated in a migratory population of Yellow Warblers (Dendroica petechia). The study was conducted on the forested dune ridge Delta Marsh, Manitoba. Older parents produced significantly more fledglings that returned than did yearling parents. Clutch and brood sizes, were statistically independent of age. Three current hypotheses were tested. The "age-experience" hypothesis was supported the most because reproductive success, in terms of initiation date and post-fledging return was significantly different between age groups. Adult return rate did not differ among age groups once reproductive maturity was reached, which alongside age-related reproductive success did not support the "residual reproductive value" hypothesis. The "anteselection" hypothesis was not supported because there was a gradual increase in reproductive success and the variation in reproductive parameters did not differ in accordance with the predictions of the hypothesis. The variance of clutch size in yearling and older females was heterogeneous; this supported the viewpoint that females laid clutches of different sizes in frequencies according to their age.

Older birds initiated their clutches significantly earlier than yearlings regardless of the zone of the dune ridge forest in which they nested. There was no difference in initiation date of parents that nested in the south zone compared to those parents of the same age that nested in the north zone. Nestlings that fledged earlier than the general population had a greater probability of returning to the dune-ridge forest in the next year. Older birds that nested in the south zone of the ridge forest initiated their clutches earlier than did those yearlings that nested in the south zone. Older females that nested in the north zone initiated their clutches earlier than yearling females in the north zone. Some possible explanations for age-related differences in initiation date were examined.

Parental care differed significantly with age and sex. Older males fed their nestlings more often than did yearling males, and all females. Geometrid larvae were fed most often in the first 4 days post-hatch by all age classes and sexes. Older males fed proportionally more geometrid larvae during the nestling phase than what was available. Chironomids were the most predominant prey item in the last 4 days post-hatch and were fed by parents in proportion to their abundance. The rates of growth in body mass and of the tarsi did not differ in nestlings reared by yearling and older parents.

ACKNOWLEDGEMENTS

I would like to express my sincere gratitude to my supervisor, Dr. S.G. Sealy, for his guidance and support. His enthusiasm and help in the field made this study very rewarding. I would not have been able to collect all the nesting information without the help of Dr. S.G. Sealy and the other co-workers on the study site: Jim Briskie, Liz Hoving, Linda Uin, Eduardo Wilner, Keith Hobson and Gloria Biermann. My thanks to Heidi den Haan, Liz Hoving and Eduardo Wilner for helping with the banding of the fledglings and all co-workers for participating in the banding program. I would like to thank the Field Station Director, Dr. Jennifer Shay, as well as the staff of the University of Manitoba Field Station (Delta Marsh) for providing enjoyable surroundings and help during my stay. I extend my gratitude to the officers of the Portage Country Club for allowing me to conduct part of the work on their property.

Thanks go out to all my friends: Debbie MacLatchy, Val Converse, Irene Labrosse. Odd Bres, Doug Torrance, Liz Hoving, Eduardo Wilner, Keith Hobson, Percy Hebert and Bev Himmick who helped in various ways in the completion of this thesis. Bless the persons who invented aerobics and the bicycle!

I am indebted to my committee members; Dr. Roger Evans, Dr. Brenda Hann and Dr. Terry Galloway. Their comments and criticisms greatly improved this thesis. I would also like to thank Dr. Richard Knapton who provided some useful comments to the final draft of this thesis.

This study was funded by grants from the Manitoba Department of Natural Resouces and the Natural Sciences and Engineering Research Council of Canada (A9556) to S.G. Sealy.

TABLE OF CONTENTS

LIST OF TABLES

GENERAL INTRODUCTION

CHAPTER 1

Table page

LIST OF FIGURES

CHAPTER 2

Figure page

GENERAL INTRODUCTION

Intraspecific variation in clutch size may ultimately occur through selective forces that act over several generations or through proximate factors such as weather, habitat quality, population density and food availability (see Klomp 1970 for review). The time that adults of a migratory species arrive on their breeding grounds may influence clutch size directly. Using records of brood size and post-fledging survival as measures of reproductive success may be more accurate than using clutch size as an estimate of fitness.

The age of an individual may also influence clutch size. The effect of age on reproductive effort can be studied with respect to the proximate factor (physiological mechanism and environment) and/or the ultimate factors (circumstances in life history) that determine the allocation of resources into reproductive tissue versus non-reproductive tissue and activities (Fisher 1930).

The influence of age on reproductive success of birds has been examined in long- and short-lived species. Ricklefs (1974) defined a short-lived species as one whose survivorship is less than 50% to the following year. Cody (1971) characterized short-lived individuals as those which mature early, lay large clutches and have short reproductive spans; long-lived individuals mature later, lay smaller clutch sizes and have longer reproductive spans. Most studies that have examined age-related reproductive effects in birds have been on long-lived species (see Table 1). Ideas that are repeatedly supported in these studies have only recently been applied to short-lived species. Although the number of studies is not as numerous as studies on long-lived species, when more populations of short-lived species are marked and monitored, age-related nesting behaviour will become understood more clearly.

Ricklefs (1974) evaluated reproductive tactics and lifespan and found short-lived species generally breed within the first year. Stearns (1976) argued that short-lived individuals should maximize their reproductive effort in each breeding attempt. Perrins and Moss (1974) recognized that in short-lived species age-related effects may not be apparent because survival is so unpredictable. The literature on short-lived passerines is equivocal as to whether age-related differences in nesting success should be expected. Interpretations have varied depending on whether (1) the sexes were considered separately or as pairs (De Steven 1980), (2) the species was multi-brooded (Smith 1985, Bedard and LaPointe 1985, Ross and MacLaren 1981), or (3) whether nests were open or placed in cavities.

Table 1. A literature review of studies on age-related reproductive success in the Class Aves. Procellariiformes through Charadriiformes are long-lived; Passeriformes are short-lived. (P = age-related reproductive effects were significant, NP = age-related reproductive effects were not found, - = reproductive parameter not studied; F = female, M = male, B = both parents)

Order	Species	Parent	Laying Date	Clutch Size	Brood Size	Source
Procellariiformes	Laysan Albatross *Diomedea immutabilis*	B	P	-	P	Fisher (1969, 1971, 1975)
	Sooty Shearwater *Puffinus griseus*	B	P	-	P	Richdale (1963)
	Manx Shearwater *P. puffinus*	B	P	-	-	de L. Brooke (1978)
Pelecaniformes	Northern Gannet *Sula bassanus*	F	P	-	P	Nelson (1966, (1978)
	Brown Pelican *Pelecanus occidentalis*	F	P	P	P	Blus and Keehey (1978)
Ciconiiformes	White Ibis *Eudocimus albus*	F	P	P	P	Bildstein (1984)
Anseriformes	Snow Goose *Chen caerulescens*	F	P	P	NP	Finney and Cooke (1978)
	Mallard *Anas platyrhynchos*	B	P	P	-	Krapu and Doty (1979)
Galliformes	Willow Ptarmigan *Lagopus lagopus*	F	NP	NP	NP	Hannon and Smith (1984)

Order	Species	Parent	Laying Date	Clutch Size	Brood Size	Source
Gruiformes	American Coot *Fulica americana*	F	P	P	P	Crawford (1980)
Charadriiformes	Artic Skua *Stercorarius parasiticus*	B	P	-	NP	Davis (1976)
	Ring-billed Gull *Larus delawarensis*	B	P	P	P	Haymes and Blokpoel (1980)
	California Gull *L. californicus*	B	P	P	P	Pugesek (1983) Pugesek and Dien (1983)
	Herring Gull *L. argentatus*	B	P	P	P	Davis (1975)
	Red-billed Gull *L. novaehollandiae*	B	P	P	P	Mills (1973)
	Kittiwake Gull *Rissa tridactyla*	B	P	P	P	Coulson and White (1958)
	Sandwich Tern *Sterna sandvicensis*	B	P	P	NP	Veen (1977)
	Roseate Tern *S. dougallii*	F	-	-	P	Nisbet (1978)
	Common Tern *S. hirundo*	B	NP	P	P	Nisbet *et al.* (1984)
	Artic Tern *S. paradisaea*	B	NP	P	P	Coulson and Horobin (1976)

Order	Species	Parent	Laying Date	Clutch size	Brood Size	Source
Charadriiformes	Sooty Tern *S. fuscata*	B	P	-	-	Harrington (1974)
Passeriformes	Tree Swallow *Tachycineta bicolor*	F	P	P	P	De Steven (1978)
	Black-billed Magpie *Pica pica*	B	P	NP	NP	Reese and Kadlec (1985)
	Pied Flycatcher *Ficedula hypoleuca*	B	P	P	P	Harvey *et al.* (1985)
	Great Tit *Parus major*	B	P	P	P	Harvey *et al.* (1979)
	Great Tit *P. major*	F	P	P	NP	Perrins and McCleery (1985)
	Blue Tit *P. caeruleus*	B	P	P	NP	Perrins (1979)
	Eastern Bluebird *Sialia sialis*	B	P	NP	NP	Pinkowski (1977)
	Water Pipit *Anthus spinoletta*	F	P	P	P	Askenmo and Unger (1986)
	Prairie Warbler *Dendroica discolor*	B	-	P	P	Nolan (1978)
	Savannah Sparrow *Passerculus sandwichensis*	B	NP	NP	NP	Bedard and LaPointe (1985)

Order	Species	Parent	Laying Date	Clutch Size	Brood Size	Source
Passeriformes	Ipswich Sparrow *P. s. princeps*	B	P	P	P	Ross (1980a)
	Song Sparrow *Melospiza melodia*	B	P	P	P	Nol and Smith (1987)
	Meadow Bunting *Emberiza croides*	B	-	P	P	Yamagishi (1981)
	Northern Oriole *Icterus galbula*	B	-	P	P	Labedz (1984)
	Red-winged Blackbird *Agelaius phoeniceus*	F	P	P	P	Crawford (1977)
	Yellow-headed Blackbird *Xanthocephalus xanthocephalus*	F	P	P	P	Crawford (1977)
	American Goldfinch *Carduelis tristis*	B	P	P	P	Middleton (1979)

The objectives of the present study are two fold: to contribute further to the understanding of the influence of age on the reproductive success of short-lived birds by documenting the nesting success of a population of Yellow Warblers (<u>Dendroica</u> <u>petechia</u>) of known age and to examine the provision of care by yearling and older parents.

Chapter I

REPRODUCTIVE CHARACTERISTICS IN RELATION TO THE AGE OF FEMALE AND MALE PARENTS

INTRODUCTION

The ability of individuals to reproduce and nurture offspring that survive has been an important consideration in evolutionary ecology. Stearns (1976) defined fit organisms as "...those better represented in the future generations than their relatively unfit competitors." MacArthur and Wilson (1967) found that the reproductive characteristics among populations differed in resource dependency. From their discovery, separate theories to predict age-related reproductive tactics for r- and K-strategists have emerged. Emlen (1970) and Gadgil and Bossert (1970) discuss reproductive tactics in a life-historical sense. They perceived life-history strategies as the optimal allocation of resources distributed among maintenance, growth, and reproduction. Traits that increase fecundity should be pushed to earlier-and-earlier ages until they are opposed by forces such as survival, delayed maturation and self maintenance (Emlen 1970).

Gadgil and Bossert's model (1970) predicts that the value of reproductive effort will continually increase with age.

In the case of the repeated reproducer (as opposed to the "big-bang" strategist), the profit (i.e. the contribution to fitness of the offspring produced at a particular time) relative to the cost of reproduction (in terms of survival and growth) is adjusted at every age such that the overall fitness of life history will be maximized (Gadgil and Bossert 1970). Some crucial considerations with respect to the maximization of fitness over a lifespan are the constraints that limit each reproductive attempt. Lack (1947, 1954) proposed that clutch size has evolved through natural selection to correspond with the largest number of young for which parents can, on average, find food. However, an increase in breeding effort in one breeding attempt may decrease the probability of survival to the next breeding opportunity (Williams 1966). Therefore, a delay in reproducing for the first time may favour the maximization of lifetime reproductive fitness.

Pianka and Parker (1975) addressed age-specific reproductive tactics with respect to reproductive value (V_x), defined by Fisher (1930) as the expectation of all present and future offspring. Reproductive value is calculated by using values of survivorship (l_x) and fecundity (m_x):

$$V_x = m_x + \sum_{t=x+1}^{W} (l_t / l_x)\ m_t \qquad (1)$$

where $\underline{x}$ and $\underline{t}$ represent age, and $\underline{w}$ is the age of last reproduction in a stable population (see Fisher 1930, Pianka and Parker 1975). The two components of reproductive value are the present fecundity, which is the first term in the equation, and the expected future fecundity or 'residual reproductive value' at age $\underline{x}$ (Williams 1966). This equation provides a parameter whereby reproductive strategies are based upon trade-offs between present reproductive effort and future reproductive potential.

In a repeated reproducer, an organism with a high residual reproductive value should invest less in current reproduction than one with a lower expectation of producing offspring in the future (Pianka and Parker 1975). With respect to iteroparous and semelparous strategies, semelparous reproduction results in a residual reproductive value of zero and iteroparous individuals prior to reproductive maturity have a present fecundity value of zero. However, most groups of animals exhibit an intermediate strategy, where survivorship and longevity may constrain reproduction. Thus, in a population where fecundity is greater in older parents the residual reproductive value would be larger in yearling parents than older parents. In this case, survivorship should decrease with age. Ricklefs (1974) compared the age of first reproduction and longevity in birds and found that as the lifespan increased the age of first reproduction was delayed.

Curio (1983) proposed two alternative mechanisms to explain reduced reproductive success in younger parents. First "poor-quality" parents were still present in the yearling cohort and were not eliminated from the population until after their first breeding attempt. Second, younger parents lack the experience which comes with age and repeated breeding. In either case, there is physiological constraint on reproductive success.

I tested three current hypotheses to account for age-related differences in reproductive success. According to the "age hypothesis", younger birds will be less successful simply because they are younger. Fecundity will increase with age and older birds that are breeding for the first time should have greater reproductive success than younger first-time breeders (e.g. Bedard and LaPointe 1985, De Steven 1978). In the "experience hypothesis" older birds breeding for the first time should not be as productive as younger birds that have previous breeding experience. The experience gained from feeding and caring for young is the primary constraint (e.g. Nol and Smith 1987, Harvey *et al*. 1985, Perrins and McCleery 1985). These hypotheses are difficult to test in the dune-ridge population of the Yellow Warbler because second broods are common only in certain years (S.G. Sealy, pers. comm.). I tested these two hypotheses together in what I called the "age-experience" hypothesis, which predicts that older birds will do better than yearlings.

In the "residual reproductive value" hypothesis an organism with a high residual reproductive value is expected to invest less in current reproduction than another organism with a lower expectation of future offspring (Fisher 1930, Emlen 1970, Gadgil and Bossert 1970, Pianka and Parker 1975). In populatioons where age-related reproductive success is present the "residual reproductive value" hypothesis will be indirectly supported if there is a decrease in the probability of return with age (Nol and Smith 1987).

Nol and Smith (1987) referred to the next hypothesis as the "selection hypothesis", but this is misleading because the residual reproductive value hypothesis too is a selection hypothesis. I prefer to call it the ante-selection hypothesis because in this case, selection to remove less competent parents has not had a chance to act prior to the first reproductive attempt, and a greater proportion of "poor" parents will be represented in the younger age cohort (Curio 1983). Therefore, variation in breeding success should be greatest in yearlings.

METHODS AND MATERIALS

Study Area

The study was conducted during the summers of 1985 and 1986 on a 3-km portion of the forested dune ridge that separates Lake Manitoba and the Delta Marsh, Manitoba (see maps in Goossen 1978, Sealy 1980). Additional nesting information from two previous years of nesting (1983 and 1984) was provided by S.G. Sealy. The study included properties of the University of Manitoba Field Station (Delta Marsh) and the Portage Country Club (50°11'N, 98°19'W). Vegetation on the study area was described in MacKenzie (1982) and MacKenzie and Sealy (1981).

Mackenzie (1982) showed quantitatively that a gradient in the overstory vegetation and soil patterns exists from north to south in the dune-ridge forest. Mackenzie and Sealy (1981) found a north-south gradient on the ridge with respect to Eastern and Western Kingbirds (_Tyrannus_ _tyrannus_ and _T_. _verticalis_) nesting distributions relative to vegetation. This observation suggested that the dune-ridge forest represents a habitat that is used non-uniformly by nesting birds, including the Yellow Warbler.

Weather data were obtained from the Environment Canada meteorological station located at the University Field Station. Mean monthly temperatures and total precipitation from 1983 to 1986 are summarized in Table 2. In general, 1983 and 1984 were typical summers for the study area, 1985 was abnormally cool in June and 1986 was a particularly hot summer with heavy rain during one week in July.

Banding Procedures

S. G. Sealy and co-workers have banded and colour marked Yellow Warblers on the study area every year since 1974. This effort has generated a population that contains many known-aged individuals. Mist netting began in mid-May and continued through to mid-or-late August in most summers, except in 1985 when nets were not operated in June through to mid-July. When captured, each warbler was uniquely marked with a standard U.S. Fish and Wildlife Service aluminium band in combination with coloured celluloid bands. Since 1981 S.G. Sealy has banded fledglings with an aluminum band plus a year-specific celluloid band and nestlings at 6-7 days of age with an aluminum band plus a different year-specific celluloid band.

Table 2: Mean maximum and minimum temperatures (°C) and total precipitation (mm) recorded for the summer months of 1983-1986, dune-ridge forest, Delta Marsh, Manitoba.

		Mean temperature(°C)		Total
		Minimum	Maximum	Precipitation (mm)
1983	MAY	1.7	13.2	47.1
	JUN	11.3	22.7	85.8
	JUL	14.8	27.1	62.3
	AUG	14.7	28.3	70.9
1984	MAY	3.9	15.6	29.2
	JUN	11.3	23.6	92.0
	JUL	12.5	26.0	33.4
	AUG	12.8	26.8	42.2
1985	MAY	5.0	18.0	31.5
	JUN	7.3	18.6	55.8
	JUL	10.8	24.5	22.6
	AUG	9.3	20.6	119.5
1986	MAY	11.1	18.8	44.7
	JUN	15.0	21.6	70.4
	JUL	17.2	23.2	209.3
	AUG	14.7	24.0	7.6

Nest Records

Yellow Warbler nests were located by S.G. Sealy and co-workers during the breeding periods of 1983 through 1986 (I was involved in the location of nests during the summers of 1985 and 1986). The colour combinations of those parents that were marked were recorded. I used a taped song periodically in 1985 and 1986 to draw in the male parent for preliminary determination of its band combination; if a banded male responded to the recording, an attempt was made to verify the band combination later.

Nests were numbered with flagging tape and checked every day or every other day until at least one day after laying and then usually every day once hatching began. Clutch initiation was the day the first egg was laid. For nests found during incubation, I back-dated the date of initiation from the day the first young hatched, based on the average period between the last-laid egg and first-hatched egg, which was 10 days (Goossen 1978, Table 9). The incubation period was the period between the date of clutch completion and the last-hatched young. Contents of the nest were recorded on each visit.

An active nest was one that contained at least one egg, a completed nest was one that contained a completed clutch. A nest was recorded as successful if it fledged at least one young. Clutches parasitized by the Brown-headed Cowbird

(*Molothrus ater*) were excluded from all analyses. Only nests initiated prior to the yearly mean within an age group were analysed thus eliminating renests which generally have lower clutch sizes (Goossen 1978, S.G. Sealy, *unpub. data*).

I assumed that nest visitation did not influence the outcome of the nest. Nolan (1963) and Nilsson *et al*. (1985) found little effect of visitation on success; however, Westmoreland and Best (1977) found that standard nest checking procedure affected nesting success and confounded the interpretation of relationships between nest site features and nest outcome. In this study, most nests were visited equally frequently which should have eliminated any bias due to disturbance.

Analyses

Two sample populations were created from the nesting population of known-age individuals; one was of all females of known ages, yearling or older (greater than 2 years), and another was of males of known ages, yearling or older (greater than two years). To remove variation between years each sample population was placed on its own identical comparative axis by setting the mean measurement of reproductive success to zero. This is a standard correctional technique where the observation is subtracted from the within-year mean (x-x) and divided by the within-year standard deviation (see Perrins and McCleery 1985, Nol and Smith 1987). The division by the within-year standard deviation is necessary to correct for the differences in nesting distributions in different years. For example, a year with an extended breeding period would have a greater standard deviation than a year with a condensed breeding season. This procedure allows the data to be pooled from different years. The variation in all measures of reproductive success was not significantly heterogeneous over the years (Box-Scheffe test for homogeneity of variance: Initiation date $F_{3,13}=1.10$, clutch size $F_{3,15}=2.84$, brood size $F_{3,19}=2.84$, $p>0.05$, NS), thus this procedure was justified. Although year-to-year variation may be an important factor to influence reproduction I was interested in the overall effect of age with respect to reproductive success and therefore I removed all year-to-year fluctuations in nesting success.

Once the uncorrected initiation date (in Julian date), clutch size and brood size over the four years of this study were standardized the mean value for each reproductive parameter over the four years was zero (Appendices 1 and 2).

Initiation date, clutch size, and brood size (defined as the number of young present at 6-7 days after hatch) were used as measures of reproductive performance. These features were then separated into age (of adults), habitat and a combined age-habitat category. Chi-square and Kruskal-Wallis statistics were used to examine age-related differences in reproductive success. A two-tailed F-test was used to test for the equality of variance in measures of reproductive success among age groups. Significance tests were two-tailed and a probability less than 0.05 was considered significant (Sokal and Rohlf 1981). Sample sizes were not always equal from one reproductive character to the next because depredation and the effects of weather were ongoing events.

RESULTS

Age and Nest Distribution

The total number of nests found during the study ranged from 280 (in 1983) to 324 (in 1986) (see Appendix 3). Approximately 30% of these nests had one parent that was marked and about half of these marked adults could be assigned an age. An adult was considered older if it had been banded as an adult in a previous year. More accurate ages were obtained from individuals that were banded as nestlings or fledglings in previous years.

The frequency of mated yearling pairs and older pairs did not differ significantly (Table 3: $X^2=3.98$, df=3, $p>0.05$, NS). The expected proportion of age-sex nesting pair combinations varied because older birds were twice as common on the study site than yearling birds. Since there was no significant trend that suggested that pairs were assorted according to age (Table 3), the reproductive success of each

Table 3. The frequency of banded Yellow Warbler pairs nesting in the forested dune ridge, Delta Marsh, Manitoba, 1983-1986.

	YFYM[1]	OFYM[2]	YFOM[3]	OFOM[4]	Total
# pairs	10	11	9	38	68
expected proportions[5]	0.09	0.23	0.18	0.50	
expected frequency	6.12	15.64	12.24	34.00	
X^2	2.46	0.19	0.86	0.47	3.98[6]

[1] YFYM=yearling female-yearling male parents

[2] YFOM=yearling female-older male parents

[3] OFYM=older female-yearling male parents

[4] OFOM=older female-older male parents

[5] all expected proportions calculated using the smallest number of parents of a given age group that nested on the ridge.

[6] $p>0.05$ df=3 NS.

sex of different ages was analysed separately. The banding of nestlings and fledglings revealed that settling patterns in the south and north zones of the ridge were not random (Table 4). Yearling pairs were found in the south zone more frequently than predicted by their relative abundance.

Table 4. The frequency of nesting pairs of Yellow Warblers that completed a clutch in the north and south zones of the forested dune ridge, Delta Marsh, Manitoba 1983-1986.

Ridge zones	YFYM[1]	OFYM[2]	YFOM[3]	OFOM[4]	Total
South:					
# pairs	7	4	9	27	47
expected proportions[5]	0.05	0.17	0.18	0.60	
expected frequency	2.40	8.00	8.00	28.20	
X^2	8.82	2.00	0.13	0.05	11.00[6]
North:					
# pairs	3	2	5	11	21
expected proportions[5]	0.24	0.18	0.32	0.25	
expected frequency	5.04	3.80	6.70	5.30	
X^2	0.83	0.85	0.43	8.24	7.89[6]

[1] YFYM=yearling female-yearling male parent

[2] OFYM=older female-yearling male parents

[3] YFOM=yearling female-older male parents

[4] OFOM=older female-older male parents

[5] all expected proportions calculated by using the smallest number of parents of each age group that nested on the ridge.

[6] $p \leq 0.01$, df=3

Age and Breeding Phenology

Female warblers 2 years old or older initiated their clutches significantly earlier than did yearling females (Table 5: Kruskal-Wallis test $X^2=31.80$, $p\leq0.01$). The variance in initiation dates of yearling and older females did not differ (two-tailed F-test: $F_{44,116}=1.53$, $p>0.05$, NS). When the age of the female was broken into year-classes of only known-age individuals aged to the nearest year, 3-year-olds initiated their clutches the earliest. The mean clutch initiation date of mates of younger males was also significantly later than mates of older males (Table 6: Kruskal-Wallis $X^2=6.06$, $0.01\leq p\leq0.05$). The variance for initiation date in males was homogeneous (two-tailed F-test: $F_{28,68}=1.32$, $p>0.05$ NS).

Age, Breeding Area, and Phenology:

Yearling females that tended nests in the north zone of the ridge forest initiated their clutches later than all other age groups (Table 7: Kruskal-Wallis test: south $X^2=15.8$, north $X^2=14.12$,$p\leq0.01$). Females within the same age group initiated their clutches at about the same time regardless of where they nested (Kruskal-Wallis test by location: yearling $X^2=3.83$, older $X^2=0.74$ $p>0.05$, NS). Mates of older males in the south zone nested significantly earlier than mates of yearling males in the south (Table 8: Kruskal-Wallis test $X^2=5.23$, $0.01\leq p\leq0.05$). Females mated to

Table 5. The corrected mean initiation date, clutch size and brood size for four cohorts of known-age individuals and two age groups of female adult Yellow Warblers, 1983 to 1986. Sample sizes are in parentheses. Figures are mean±S.D.

Age categories	Initiation date[1]	Clutch size	Brood size
Age Cohort: (years)			
1	0.79±1.01 (44)	-0.02±0.81 (52)	-0.09±0.99 (45)
2	-0.14±0.85 (29)	-0.08±1.07 (38)	0.05±0.99 (34)
3	-0.61±0.45 (5)	0.47±0.74 (5)	0.07±1.68 (4)
4+	0.10±0.82 (6)	-0.34±0.93 (6)	-0.27±1.23 (6)
Age Group:			
Yearling	0.79±1.01 (44)	-0.02±0.81 (52)	-0.09±0.99 (45)
Older	-0.29±0.81 (117)	0.02±1.06 (133)	0.04±0.99 (123)

[1] $p \leq 0.01$ (Kruskal-Wallis test)

Table 6. The corrected mean initiation date clutch size and brood size for four cohorts of known-age individuals and two age groups of male Yellow Warblers, 1983 to 1986. Sample sizes are in parentheses. Figures are mean±S.D.

Age categories	Initiation date[1]	Clutch size	Brood size
Age Cohort: (years)			
1	0.43±1.04 (29)	-0.18±1.11 (35)	-0.12±1.10 (34)
2	-0.12±0.86 (11)	0.01±0.88 (15)	0.23±0.71 (13)
3	0.26±0.82 (2)	-0.70±0.03 (2)	0.63 (1)
4	0.84±0.55 (1)	0.18±1.30 (1)	0.63±0.00 (1)
Age Group:			
Yearling	0.43±1.04 (29)	-0.18±1.11 (35)	-0.12±1.10 (34)
Older	-0.18±0.91 (61)	0.08±0.93 (73)	0.06±0.93 (68)

[1] $p \leq 0.01$ (Kruskal-Wallis test)

Table 7. The corrected mean initiation date, clutch size and brood size of the two age groups of female Yellow Warblers in north and south zones of the dune-ridge forest, Delta Marsh, Manitoba, 1983-1986. Sample sizes are in parentheses. Figures are mean±SD.

	Initiation date	Clutch size	Brood size
South:			
Yearling	0.52±0.82[1] (27)	-0.12±0.78 (30)	0.05±1.10 (25)
Older	-0.31±0.86[1] (91)	-0.09±1.07 (103)	0.01±0.97 (96)
North:			
Yearling	1.13±1.17[2] (18)	0.09±0.84 (23)	-0.31±0.82 (21)
Older	-0.22±0.66[2] (26)	0.41±0.94 (29)	0.15±1.11 (26)

[1] $p \leq 0.01$ (Kruskal-Wallis test)
[2] $p \leq 0.01$ (Kruskal-Wallis test)

Table 8. The corrected mean initiation date, clutch size and brood size of two age groups of male Yellow Warblers in north and south zones of the dune-ridge forest, Delta Marsh, Manitoba, 1983-1986. Sample sizes are in parentheses.Figures are mean±S.D.

	Initiation date	Clutch size	Brood size
South			
Yearling	0.41±0.95[1] (17)	-0.44±1.30 (20)	-0.08±1.10 (19)
Older	-0.25±0.90[1] (58)	0.08±0.90 (66)	0.07±0.93 (59)
North			
Yearling	0.45±1.21 (12)	0.17±0.69 (15)	-0.16±1.14 (15)
Older	0.20±0.87 (11)	0.06±1.09 (15)	-0.02±0.95 (14)

[1] $p \leq 0.01$ (Kruskal-Wallis test)

older or yearling males nesting in the north zone initiated their clutches at the same time (Table 8: Kruskal-Wallis test $X^2=0.02$, $p>0.05$, NS). Females mated to males within the same age group initiated their clutches at about the same time regardless of where they nested (Table 8: Kruskal-Wallis test: south $X^2=0.00$, north $X^2=1.95$ $p>0.05$, NS).

Age and Clutch Size

As females aged (up to 3 years), clutch size increased but not significantly (Table 5: Kruskal-Wallis test: $X^2=0.61$, $p>0.05$, NS). The small clutch size in females older than 4 years probably reflects the small sample size. The variance in clutch size between the two female age groups was not equal (two-tailed F-test: $F_{132,52}=1.74$, $0.01\leq p\leq 0.05$). The variation in clutch size was greater for older females than yearling females. The location of the nest in the ridge forest did not affect clutch size. Yearling females laid smaller clutches than older females in both zones of the ridge forest, although this difference was not significant (Table 7: Kruskal-Wallis test: south $X^2=0.16$, north $X^2=1.91$ $p>0.05$, NS). The clutches of females of the same age that nested in the north and south zones of the ridge did not differ significantly (Table 7: Kruskal-Wallis test: yearling $X^2=0.36$, older $X^2=3.16$, $p>0.05$, NS).

There were no significant differences in clutch size between mates of older or yearling males. The number of males older than 2 years was small. The variance in clutch size between yearling and older males did not differ (two-tailed F-test: $F_{34,80}=1.43$, $p>0.05$, NS). The clutch size of the mates of yearling and older males did not differ within a given zone of the ridge (Table 8: Kruskal-Wallis test: south $X^2=2.64$, north $X^2=0.13$, $p>0.05$, NS). The mates of yearling and older males laid clutches of similar size (Table 8: Kruskal-Wallis test: south $X^2=2.64$, north $X^2=0.13$, $p>0.05$, NS). Clutch size did not differ significantly between the mates of males of the same age that nested in separate zones of the ridge (Table 8: Kruskal-Wallis test: yearling $X^2=0.83$, older $X^2=0.09$, $p>0.05$, NS).

Age and Brood Size:

Brood size of yearling and older females did not differ significantly, although it apparently increased in females up to three years of age (Table 5: Kruskal-Wallis test: $X^2=1.26$, $p>0.05$, NS). However, the frequency distribution of brood sizes of yearling and older females was non-random ($X^2=9.79$, $0.01\leq p\leq 0.05$) but this did not cause the variance in brood size of yearling and older females to differ (two-tailed F-test: $F_{122,45}=1.01$, $p>0.05$, NS). Older females generally had small broods (broods of 1-3) or large broods (broods of 5), whereas broods of yearling females were most frequently 4. There was no significant difference in brood size between females of different ages that nested in the same zone of the ridge (Table 7: Kruskal-Wallis test: south $X^2=0.01$, north $X^2=2.08$, $p>0.05$, NS). The number of offspring raised by females of the same age was not influenced by the zone in which they nested (Table 7: Kruskal-Wallis test: yearling $X^2=1.00$, older $X^2=0.34$, $p>0.05$, NS).

The mates of older and younger males successfully raised broods of equal size (Table 6: Kruskal-Wallis test $X^2=0.25$, $p>0.05$, NS). The frequency distribution of brood sizes did not differ between age classes ($X^2=5.10$, $p>0.05$, NS), neither did the variance (two-tailed F-test: $F_{33,72}=1.40$, $p>0.05$, NS). Nests in the north zone were as successful as those in the south zone regardless of the males' age (Table 8: Kruskal-Wallis test: south $X^2=0.02$, north: $X^2=0.03$, $p>0.05$, NS). The males of identical age raised the same number of young regardless of the zone in which they nested (Table 8: Kruskal-Wallis test: yearling $X^2=0.01$, older $X^2=0.10$, $p>0.05$, NS).

Age and Return

Of 527 adults banded from 1982 to 1984, 168 were located during at least one subsequent breeding season. The weighted annual return rate was 49.4% for adults and 24.0% for fledglings, based on an equation of Brownie *et al*. (1978) for mortality estimates:

$$m=100-\Sigma(n_i/N_i)100/\Sigma100(n_i/N_i) \qquad (2)$$

where i is age, n is the number that returned at i, and N is the number banded at i (see Appendix 4). Dispersal is assumed to be minimal and the degree of philopatry is assumed equal in both sexes. This return estimate is comparable to Roberts' (1971) survival estimate of 52.6% for adult Yellow Warblers more than 3 years old in southern Ontario.

The proportion of nestlings that returned from different years did not differ significantly. The return of birds marked as nestlings in their first and subsequent years is recorded in Table 9. The values were calculated using the equation

$$T= n_{ij}/(b_i e_j)10^3 \qquad (3)$$

where, n=the number of individuals of a year class relocated in year j from banding year i, b=the number of yearlings banded in year i and e=the number of birds recaptured from year j (Finney and Cooke 1978).

The estimate of returns in subsequent years was not independent of the year (Table 9). The year class 1983 and 1984 both dropped dramatically after year 1. No significant differences existed between year classes (i.e. individuals of different ages that return in the same year) or between age classes (i.e. individuals of a specific age that return

Table 9. Banding returns of nestling Yellow Warblers in relation to the year banded and estimated year-specific return rates for birds banded as nestlings on the dune-ridge forest, Delta Marsh, Manitoba. The number of nestlings that returned is in parentheses.

Year class[1]	1983	1984	1985
Total banded	356	406	390
Return year[2]			
1984	2.70 (49)	-	-
1985	0.11 (2)	2.46 (40)	-
1986	0.28 (5)	0.49 (8)	2.51 (34)
Total observed	56	48	34

[1] -X^2=2.72, df=1, p>0.05 (chi-square test)

[2] -X^2=5.99, df=2, p>0.05 (chi-square test)

in different years). The number of individuals that returned to the population after their first winter, did not differ.

Nestlings from older parents returned proportionately more often (Table 10 and 11). The zone where a nestling was raised did not have any influence on its return rate (Table 12: $X^2=1.26$, df=1, $p>0.05$, NS). Of the 357 successful nests studied from 1983-1986, 136 fledged young that were recorded later on the study area. The mean initiation date of parents that fledged young that returned was earlier than the initiation date of the population (Table 13: returns:-0.60 ± 0.27, population: -0.45 ± 0.48, $t=2.00$, df=244, $p\leq0.05$). In all years the brood size of parents of nestlings that returned was significantly larger than the population in general. Of the 136 nests which produced returning young, 31 contained more than one fledgling that returned. Therefore, 38.1% of the nests that were successful fledged young that returned the following year, whereas 29.4% fledged one young that returned and 8.7% produced more than one young that returned.

Table 10. Nestling Yellow Warblers reared by female parents of different ages that returned and did not return to the dune-ridge forest, 1984-1986. Expected frequencies are in parentheses.

	Return[1]		Non-returns[2]		
	Yearling	Older[3]	Yearling	Older	
1984	1(2.2)	14(8.6)	9(23.1)	66(56.1)	90
1985	6(4.7)	17(19.1)	51(51.2)	125(144.0)	199
1986	4(4.1)	13(16.3)	58(43.7)	95(105.9)	170
Total	11	44	118	286	459

[1] returns are those individuals that returned to the breeding grounds in subsequent years after banding.

[2] non-returns are those individuals that did not return in subsequent years after banding.

[3] $X^2=1.82$, df=1, $p \le 0.05$ (chi-square test)

Table 11. Nestling Yellow Warblers reared by male parents of different ages that returned and did not return to the dune-ridge forest, 1984-1986. Expected frequencies are in parentheses.

	Returns[1]		Non-returns[2]		
	Yearling	Older[3]	Yearling	Older	
1984	2(7.0)	12(7.0)	14(17.5)	33(34.5)	61
1985	4(2.5)	13(8.9)	38(43.5)	22(22.1)	77
1986	4(5.6)	11(20.1)	54(50.3)	106(99.0)	175
Total	10	36	90	177	313

[1] returns are those individuals who returned to the breeding grounds in subsequent years after banding.

[2] non-returns are those individuals that did not return in subsequent years after banding.

[3] $X^2=28.0$, df=1, $p \leq 0.01$ (chi-square test)

Table 12. Nestling Yellow Warblers reared in different zones of the dune-ridge forest that returned and did not return to the dune-ridge forest, 1984-1986. Expected frequencies are in parentheses.

	Returns[1]		Non-returns[2]		
	North	South[3]	North	South	
1984	9 (10.0)	37 (26.8)	108 (104.2)	204 (217.0)	358
1985	15 (11.2)	29 (30.1)	124 (117.1)	234 (243.6)	402
1986	8 (10.6)	20 (29.2)	103 (113.6)	259 (236.4)	390
Total	32	86	335	697	1150

[1] returns are those individuals who retuned to the breeding grounds in subsequant years after banding.

[2] non-returns are those individuals that did not return in subsequant years after banding.

[3] NS-$p>0.05$ $df=1$ (chi-square test)

Table 13. The mean initiation date (in Julian date), clutch size and brood size of Yellow Warbler parents in which fledglings returned compared to the population mean nesting parameters. Figures are means±S.D. Sample sizes are in parentheses.

	Year	Population	Parents of returns	t	p
Initiation date	1983	166.0±5.6 (79)	162.9±3.2 (23)	3.38	**
	1984	162.7±9.3 (94)	159.3±5.5 (35)	2.55	*
	1985	155.7±7.8 (71)	153.4±4.0 (25)	1.88	NS
Clutch size	1983	4.35±0.64 (100)	4.32±0.56 (23)	0.23	NS
	1984	4.60±0.55 (107)	4.50±0.51 (35)	0.99	NS
	1985	4.33±0.61 (107)	4.52±0.75 (25)	-1.18	NS
Brood size	1983	2.04±1.83 (96)	3.62±0.74 (23)	-6.52	**
	1984	1.81±1.96 (104)	3.78±0.95 (25)	-7.87	**
	1985	2.23±1.85 (100)	3.91±0.90 (25)	-6.51	**

*[1]-p 0.05 (two-tailed t-test)

**[2]-p 0.01 (two-tailed t-test)

DISCUSSION

I evaluated the success of the first nesting attempts in a season by Yellow Warblers to investigate whether yearling parents reared broods as capably as older parents. The age of the parent influenced the date that clutches were initiated and the rate at which young returned to breed in a subsequent year. Initiation date is known to be an important nesting parameter because it influences the survivorship of the offspring (De Steven 1978), the overall seasonal success (Nol and Smith 1987) and/or the possibility of renesting if a first clutch is destroyed (Goossen and Sealy 1982). Yearlings initiated clutches significantly later than did either sex of older parents.

Several explanations may account for the earlier clutch initiation by older parents. First, older males possibly established territories earlier and/or more efficiently. This may have been facilitated by previous knowledge of the habitat or dominance in territorial disputes or both. Studd and Robertson (1985a) examined the time allocated to territory maintenance in relation to the continuous variation in the breeding plumage of male Yellow Warblers in Southern Ontario. They found that males with more brown markings on their breasts were more aggressive towards intruders. Thus these markings provided a reliable badge that signalled social dominance. Older Yellow Warblers may have acquired territories and initiated clutches earlier because they were socially dominant. Others have found different plumage types to facilitate sex- and age-related status signalling (Ketterson 1979, Rowher 1982).

MacKenzie _et al_. (1982) found considerable overlap in nesting habitat between the Yellow Warbler and the Least Flycatcher (_Empidonax minimus_) in the ridge forest. Competition for nesting sites between Least Flycatchers which are more aggressive in territory defense (K.A. Hobson and S.G. Sealy, pers. comm.) and Yellow Warblers may promote spatial segregation of the two species and reduce the availability of south zone nest sites so newly recruited Yellow Warblers are forced to nest in the north zone of the ridge. The prey accessibility and quality may have varied between the north and south zones of the dune-ridge forest (see Goosen and Sealy 1982). A difference in quality would delay the laying dates of individuals that nested in the north zone because more effort would be required to obtain the nutrition necessary for egg production.

Krebs (1971) found that resident Great Tits (_Parus major_) successfully defended their territories against intruders because they were more familiar with the territory and fought harder to keep it. However, in a migratory species early territorial establishment does not necessarily mean these males are the first to acquire mates. Catchpole (1972) found that older _Acrocephalus_ warblers settled on territories earliest but sometimes were not the first to attract mates. Older male Eastern Bluebirds (_Sialia_ sialis) have been observed to reclaim old nesting territories from males that had arrived earlier (Pinkowski 1977). The nest-site tenacity of known-age male and female Yellow Warblers was strong in the present study (see appendix 5). In males, 86% returned to within 200 metres of where they nested in the previous summer. Seventy-eight percent of known-age females nested within 200 metres of where they nested in the previous summer. Strong site tenacity in males of migratory species has been observed in the Willow Ptarmigan Lagopus lagopus, (Hannon 1984), Red-winged Blackbird Agelaius phoeniceus, (Yasukawa 1979) and Prairie Warbler Dendroica discolor, (Nolan 1968). Older birds may be establishing and defending territories more vigorously because of their previous experience.

MacKenzie and Sealy (1981) discovered a 'habitat type' distribution of vegetation between the north and south halves of the ridge (see also MacKenzie 1982). The south zone was characterized by the greater density of small stems which consisted primarily of sandbar willow stems. In the north zone peach-leaved willow stems and a greater density of large stems were most predominant. They found that these distinctions between habitat types were used for nest site selection by Eastern and Western kingbirds. The distribution of nesting pairs of Yellow Warblers on the dune-ridge forest was not random which suggests that there was a difference in quality between the two halves of the ridge forest. However, there were no differences in the initiation date, clutch and brood sizes among individuals of the same age nesting in separate zones of the ridge and the return of nestlings was not affected by the zone in which they were reared. Thus, with respect to the first completed clutches, the location did not affect the initiation date of individuals that nested on the forested dune ridge.

A second possible benefit to initiating as early as possible was that young that fledge early have a greater probability of returning to the study area in subsequent years to breed. Older, female Tree Swallows (Tachycineta bicolor) nest earlier than yearling females (De Steven 1978). Young that fledged late in the season did not return to the breeding area as often as young that fledged early (De Steven 1978). Most Yellow Warbler young that returned in the present study had been raised by older parents. The initiation dates of parents of nestlings that returned were earlier than the general population. Therefore, young that fledged from nests that were initiated early have a greater probability of returning.

The probability of second nesting is increased if initiation of the first clutch is early. In the Song Sparrow (Melospiza melodia), older birds nested earlier and fledged more young than yearling parents but the increased success in the older parents was due to a greater number of nesting attempts within a season rather than more chicks raised per nesting attempt (Nol and Smith 1987). Double-brooded Least Flycatchers on the dune-ridge forest were not the earliest birds to initiate their clutches (Briskie 1985).

Weather conditions at the Delta Marsh are unpredictable. Renesting by Yellow Warblers is common due to destruction of the first nest by predators, wind or rain. Early clutch initiation increases the probability that renesting will be successful if early clutches are destroyed (Goossen and Sealy 1982). On average early nesters lay larger clutches than late nesters (Goossen and Sealy 1982). Therefore, there is a greater probability of fledging more offspring in a first attempt. The mean initiation date of parents that fledged nestlings that returned was earlier than the initiation date of the population. Therefore, on average the probability of return from a nest that was initiated earlier than the population as a whole, is greater.

Fledglings reared by older parents returned significantly more frequently than fledglings reared by yearlings. The greater return rate of fledglings from older parents is support for the age-experience hypothesis in which breeding success will increase with each nesting attempt. Clutch and brood size between age groups that nested in different zones of the ridge did not differ. The probability that nestlings reared on the north and south zones would return was equal. Thus, the proximal effect of habitat (in relation to nesting zone) had no bearing on the reproductive success of the parents. In other words, it was not the location of the nest that caused the difference in reproductive success between age groups of adult Yellow Warblers. Harvey et al. (1985) found that experience promoted age-related differences in the Pied Flycatcher (Ficedula hypoleuca). On the other hand, experience was not an important factor in the reproductive success of the Song Sparrow (Nol and Smith 1987). They suggested that reproductive success in some passerines depended more upon foraging experience and diet. Cosens and Sealy (1986) found that reproductive success of males depended more strongly on repertoire size than on age, although a link between age and repertoire size was drawn. Yearling male Yellow Warblers arrived on the breeding grounds with smaller repertoires (Cosens and Sealy 1986). The males that had small repertoires (i.e. probably yearlings) generally initiated later and fledged fewer young than those males that had large repertoires.

In the ante-selection hypothesis, the nesting parameters of yearlings will vary more than those of older parents. The homogeneity of the variance in most of the nesting parameters of older and younger Yellow Warblers does not support this hypothesis. The inequality of variance in the clutch size of yearling and older female Yellow Warblers was contrary to the predictions of the anteselection hypothesis. Older females had a greater variance in clutch size than yearling females. The variance in Pied Flycatcher reproductive success did not differ (Harvey et al. 1985). Nol and Smith (1987) showed a significant difference between females that nested in the population for a second time and those that did not. In their population of Song Sparrows, as in the Yellow Warbler, success gradually increased with age. Selection against "poor" parents accounted for only some of the reproductive differences between yearling and older birds. The absence of any significant variation in measures of reproduction between older and yearling Yellow Warblers and the incremental increase in nesting success with age does not support this hypothesis.

According to the residual reproductive value hypothesis, the probability of survival will decrease when reproductive effort increases with age. The estimated probability of return in the Yellow Warbler was much less (0.24) for fledglings than older birds (0.48), however, the return rate did not differ after the first year. The residual reproductive value hypothesis assumes that there exists a gradual decrease in survivorship (Gadgil and Bossert 1970). This assumption was not supported by the return rate estimates in the Yellow Warbler. In a migratory species the probability of return may not accurately reflect survival, however, the strong site tenacity Yellow Warblers exhibit suggest that return rate was a reliable estimate (see appendix 5). The different return rates of fledglings compared to adults suggested that there was a greater cost to first-time migrants, however, once a fledgling reached reproductive maturity (i.e., survived the winter and migration to the breeding grounds) the cost of future migrations was equal. Under the residual reproductive value hypothesis the return rate should be correlated with reproductive success. There was no correlation so reproductive effort does not appear to be restrained by yearling Yellow Warblers.

The Yellow Warbler is a relatively short-lived species. On average under 50% of the population breeds more than once (see Greenberg 1980). Life history theory predicts a positive association between longevity and delayed maturation. Perrins and Moss (1974) argued that for a species with over 50% mortality, nesting optimally in every reproductive attempt is essential. In the present study the return rate was equal between reproducing adults in the short-lived Yellow Warbler. This is contrary to most models of age-related reproductive success because it has generally been assumed that the probability of return gradually decreases with age. When the return rate is equal among breeding adults age-related differences in reproductive success will be less pronounced because breeding effort will be essentially equal. In the Yellow Warblers in the dune-ridge forest, age-related differences in reproduction were found in initiation dates and post-fledgling survival. There was a subtle indication that there was a difference in the nesting sites between the two halves of the ridge which enabled the mates of males in the south zone to lay more eggs. Thus, the age and/or experience of Yellow Warbler parents contributed to the reproductive success of a parent.

Chapter II

AGE-RELATED PARENTAL CARE IN THE YELLOW WARBLER

INTRODUCTION

A parent's reproductive effort is assessed not only on the basis of how many young it fledges but also on how much parental care it devotes to each young. There may be a cost to such care in terms of future reproductive attempts. An increase in reproductive effort during one breeding attempt may decrease the probability of survival to the next breeding opportunity (Williams 1966, Gadgil and Bossert 1970). This hypothesis has received indirect support from observations of increased mortality of birds that raised large broods (Kluijver 1970, Nur 1984). Individuals that contribute more parental effort per nestling may have a greater probability of dying, especially if greater reproductive effort was not compensated for by a more favourable habitat, food supply or social status (Bryant 1979). Alternatively, a gradual increase in foraging success with age (i.e. experience) could explain age-specific increases in reproductive output (Dunn 1972). However, if experience is the only component of parental care required for reproductive success, the importance of parental survivorship and the life-history approach would be substantially reduced (Bryant 1979).

In addition, how efficiently parents capture and feed prey to their offspring may ultimately affect the growth and survival of young (e.g. Coulson 1968, 1972; Nisbet 1973; Milne 1974; Perrins and Moss 1974; Jones and Ward 1976). The nestling mass and tarsal length at fledging affects the subsequent survival in the Great Tit (Perrins 1965, Garnett 1981). Therefore, the growth of nestlings of parents of different ages may reflect indirectly the adequacy of the care parents allocate to each of their young.

In this chapter, I evaluate the feeding rates and prey-load sizes of Yellow Warbler parents of different ages in relation to prey that was available during the incubation and nestling stages. The growth of nestlings in nests parented by individuals of different ages was examined to ascertain whether growth was influenced by the age of the parents. In addition, the growth of nestlings in relation to the portion of the dune-ridge forest where the nest was located was compared.

METHODS AND MATERIALS

Nest watches

Incubation watches. Nests containing clutches of 4 or 5 eggs tended by yearling and older parents during incubation were observed for periods of 1 hour, using a 25-power telescope from a blind. All incubation watches occurred from 0630-1100 hr to minimize diurnal effects. Observation periods were not independent between nesting stages because each nest was watched more than once. The frequency with which the males fed their females, and the time the females incubated were recorded on the second and sixth days of incubation (Table 14). The amount of time females incubated was used as a measure of attentiveness and nutritional need.

Nestling period. Nests with broods of 2 to 5 young tended by yearling and older parents were observed for periods of 1 hour when the nestlings were 2, 4, 6, and 8 days old. Observation periods were from 0630-1030 hr, 1200-1600 hr and 1730-2100 hr. Biermann and Sealy (1982) found that the time of day did not affect the rate at which parents fed nestlings, however I avoided any possible diurnal effects on feeding rates by dividing the observation periods proportionately over the day for each nest. Observations were not made during inclement weather (see Kendeigh 1952, Best 1977, Heagy and Best 1983).

For each feeding trip, I recorded the sex of the parent, time, and the order or family of the prey. Prey items were then grouped as: (I) Chironomidae and Culicidae; (II) other Diptera; (III) geometrid larvae; (IV) other larvae; and (V) other arthropods. The number of prey items brought to the nest was determined by counting the number of arthropod abdomens that dangled from the parent's bill. Larger, and hence possibly more visible prey, probably were identified more frequently and accurately than small prey. Larger prey loads were subject to greater errors in estimation.

Table 14. The number of observations at Yellow Warbler nests on the dune-ridge forest, Delta Marsh, in relation to the age of parents, age of brood (days) and brood size. Each hour of observation is from a different nest. Data for 1985 and 1986 are combined.

		Clutch and brood size			
Age of parents	Age (days)	2	3	4	5
Yearling	Incubation				
	2	-	-	7	7
	6	-	-	5	6
	Nestling				
	2	0	2	5	4
	4	0	2	7	3
	6	0	1	8	3
	8	1	2	3	3
Older	Incubation				
	2	-	-	7	11
	6	-	-	6	8
	Nestling				
	2	3	3	5	2
	4	1	2	6	2
	6	2	2	5	2
	8	2	2	4	1
	Total	9	17	43	20

Arthropod sampling

Seasonal fluctuation in arthropod abundance was monitored by sampling every third day from 15 June to 5 July 1985 and 28 May to 6 July 1986. These dates cover the period of the breeding season where all observations were taken. Sampling was conducted on the same transect in the south and north zones of the ridge at approximately 1100 hr. A standard 37-cm wire framed sweep net was swept 10 times through the vegetation at heights of 0.5-3.5 m while walking a transect. Contents of each net were separated by size and order, counted, and then stored in 90% ethanol. I assumed that only prey items at least ≥5 mm long were identified during the feeding observations. By using the insects sampled that were ≥5 mm a more accurate comparison of observed prey loads with sampled availability of prey was accomplished. This method circumvents the size bias on the prey items brought to the nest. Arthropod abundance is ephemeral (Guinan 1985), therefore, a practical time of 1100 hr was chosen to keep day-to-day sampling variance to a minimum. This procedure may have over-estimated prey abundance. Arthropods were sampled after each nest watch, in areas where parents foraged during the nest watches.

Growth rates

Upon hatch (Day 1) the tarsi of nestlings from older and yearling parents were marked individually with a non-toxic felt marker. Only broods of 4 were included in this analysis because growth rates of young are known to differ in broods of different sizes in this population (Biermann and Sealy 1982). Young were measured each day until 6 days post-hatch. In addition, nestlings from nests located in the north and south zones of the ridge with unaged parents were measured to increase the sample size for the comparison of growth between the two sides of the ridge.

Nestlings were handled to induce defecation and then weighed (to 0.1 g) with an Ohaus digital scale. Tarsus was measured (to the nearest 0.1 mm) using calipers. All nestlings in this part of the study were banded after day 6 post-hatch with numbered U.S. Fish and Wildlife Service aluminum bands and coloured celluloid bands that identified them later as birds reared in a particular year.

Analysis of growth

Growth curves were fitted to the harmonic mean mass and harmonic mean tarsus length of nestlings by non-linear regression. Harmonic means were used because sample sizes were not equal (Winkler and Hays 1975). Richards model, was chosen because it provides a close fit for data which may not follow a standard growth curve (Richards 1959). The Richards equation may be written as:

$$\underline{W} = A\ (1 + be^{-kt})^{1/1-m} \qquad (4)$$

where;

$\underline{W}$= size at time t
$\underline{A}$= asymptotic size
$\underline{b}$= time scale
$\underline{k}$= growth rate constant
$\underline{m}$= curve-shape constant

Each of these parameters is discussed in detail in Briskie (1985). Different shapes of the curve are determined by the constant $\underline{m}$. When $\underline{m}=2$ the equation reduces to the familiar Pearl-Verhulst logistic curve. Values of 1 and 2/3 give the Gompertz and von Bertalanffy curves, respectively. The growth rate constant $\underline{k}$, determines the spread of the curve along a time axis. It represents the rate at which a measure of growth, such as mass, changes over time. The time scale constant, $\underline{b}$, reflects the choice of the zero of time.

Since growth measurements were not independent, daily means were used to avoid errors in autocorrelation. Autocorrelation may result because the probability that a measurement of growth increases from $\underline{t}$ to $\underline{t}+ 1$ is related to the original measurement (Zach *et al*. 1984). For example, an underweight nestling at time $\underline{t}$ has a greater than random probability of being underweight at time $\underline{t}+ 1$. A mean value avoids this error because on average some nestlings will weigh more and some will weigh less than the true mean.

The asymptotic mass and tarsal length were obtained from measures taken from mist-netted free-flying young that had fledged at least 20 days earlier. Twenty days was chosen arbitrarily because there is some indication that parental care takes place up to 16 days post-fledge (S.G. Sealy, unpubl. data). The daily harmonic means of mass and tarsal length were fitted by non-linear regression using a procedure outline by Marquardt (1963) and discussed in detail in Briskie (1985). A starting value of m (usually $m=2.00$) was chosen and values of b and k were then selected and fitted until iterations converged or convergence was assumed. Various values of m were substituted until a fit was found that minimized the residual variance. Values of b and k used for comparison were those associated with the best m value. Only curves with the same m value were compared since it is difficult to compare curves with different shapes (Richards 1959). This procedure may create larger residual variance in some instances but the error as a result is negligible compared to errors that result from fitting growth to the nearest standard growth curve (e.g. logistic).

RESULTS

Nest watches and feeding rates

Incubation period. Older females spent less time off the nest than yearling females during the early incubation period although this result was not significant (Table 15: Kruskal-Wallis test: $X^2=0.03$, $p>0.05$, NS). By the sixth day of incubation females of both age classes incubated for almost identical amounts of time. Yearling males fed incubating females twice as often as older males during early incubation; however, in the second half of incubation yearling and older males fed their females at the same rates (Table 15: Kruskal-Wallis test: $X^2=1.64$, $p>0.05$, NS).

Nestling period. The number of prey items that yearling and older females brought to their broods did not differ in relation to the kind of prey item brought to nestlings or the age of the nestlings (Table 16: Kruskal-Wallis test: Diptera $X^2= 1.15$; geometrid larvae $X^2=2.76$; other larvae $X^2=0.23$, all tests NS). Male parents provisioned the nestlings almost exclusively in the first 2 days post-hatch. Over the nestling period older males fed more geometrid larvae than yearling males (Table 17: Kruskal-Wallis test $X^2=7.61$, $0.01\leq p\leq 0.05$). Geometrid larvae were fed by males in disproportionate numbers over the nesting period (Table 17: Kruskal-Wallis test $X^2=7.90$, $0.01\leq p\leq 0.05$).; males provided larvae primarily in the first four days of the nestling period. As the young grew, males switched from

Table 15. The mean (±S.E.) per cent of time spent off the nest, arc sin transformed per cent time spent off the nest by the female and mean number of courtship feeding trips by the male parent in terms of stage of incubation and age of the Yellow Warbler parent on the dune-ridge forest, Delta Marsh, Mainitoba. Data for 1985 and 1986 are combined.

Nesting Stage	Age	% Time female off nest	Arc sin of time off nest	No. of male feeding trips	n
Early Incubation[1]	Older	15.0±3.0	3.4±1.8	1.1±0.3	18
	Yearling	19.2±5.7	3.7±2.4	2.1±0.6	14
Late Incubation[2]	Older	7.9±1.5	2.8±1.2	1.9±1.2	14
	Yearling	9.1±2.3	2.9±1.6	1.4±0.7	8

1-Early Incubation-Day 2
2-Late Incubation-Day 6
3-NS-$p > 0.05$ (Kruskal-Wallis test)

Table 16. The number of identified prey items (prey items/trip/nestling) brought to the nest by yearling (YF) and older (OF) female Yellow Warblers in relation to the age of the brood. Figures are means±S.E. Number of observation periods is given as sample size. Data for 1985 and 1986 are combined.

Age (days)[1]	n	Parent[2]	Prey Items		
			Diptera	Geometrid Larvae	Other
2	11	YF	0.08±0.05	0.02±0.01	0.00±0.00
	13	OF	0.11±0.06	0.04±0.00	0.02±0.02
4	12	YF	0.24±0.14	0.01±0.01	0.01±0.00
	12	OF	0.24±0.10	0.05±0.03	0.00±0.00
6	12	YF	0.14±0.07	0.02±0.01	0.02±0.02
	13	OF	0.52±0.20	0.04±0.02	0.02±0.01
8	9	YF	0.56±0.16	0.01±0.00	0.00±0.00
	9	OF	0.55±0.14	0.01±0.00	0.03±0.09

---

[1] -Kruskal-Wallis test: age of brood: Diptera X^2=17.39, $p<0.05$.
NS-$p>0.05$ for all other prey categories.

[2] -Kruskal-Wallis test: age of parent: NS-$p>0.05$ for all prey categories.

Table 17. The number of identified prey items (prey/trip/nestling) brought to the nest by yearling (YM) and older (OM) male Yellow Warblers in relation to the age of the brood. Figures are means±S.E. Number of observation periods given as sample size. Data for 1985 and 1986 are combined.

Age (days)[1]	n	Parent[2]	Prey Items		
			Diptera	Geometrid Larvae	Other
2	11	YM	0.30±0.18	0.40±0.02	0.00±0.00
	13	OM	0.25±0.09	0.15±0.03	0.01±0.01
4	12	YM	0.15±0.06	0.07±0.02	0.02±0.01
	12	OM	0.61±0.22	0.15±0.04	0.01±0.00
6	12	YM	0.26±0.08	0.06±0.03	0.01±0.01
	13	OM	0.92±0.27	0.03±0.01	0.01±0.01
8	9	YM	0.45±0.09	0.03±0.06	0.02±0.01
	9	OM	0.62±0.12	0.30±0.02	0.07±0.06

[1] -Kruskal-Wallis test: age of brood: Geometrid Larvae $X^2=7.90$, $p<0.05$.
NS-$p>0.05$ for all other prey categories.

[2] -Kruskal-Wallis test: age of parent: Diptera $X^2=4.48$, $p<0.05$.

Geometrid Larvae $X^2=7.61$, $p<0.05$.

Other $X^2=3.03$, $p>0.05$ NS.

Table 18. Mean (±S.E.) number of trips (trips/nestling/hour) in relation to to the age of the parent and the age of the brood. The number of observations is given in parentheses. Data for 1985 and 1986 are combined.

Age (days)[1]	Age of parent[2]			
	YF	OF	YM	OM
2	0.15±0.15 (9)	0.18±0.10 (13)	1.20±0.35 (9)	1.50±0.30 (13)
4	0.65±0.40 (12)	0.50±0.02 (11)	1.05±0.30 (12)	1.95±0.25 (11)
6	0.90±0.50 (12)	1.10±0.40 (12)	1.30±0.45 (12)	1.80±0.50 (12)
8	1.55±0.75 (9)	1.00±0.50 (9)	1.60±0.35 (9)	2.20±0.65 (9)

[1]-Kruskal-Wallis test: age of brood: Female $X^2=23.60$ $p<0.05$.
Male $X^2=1.61$, $p>0.05$ NS.

[2]-Kruskal-Wallis test: age of parent: Female $X^2=0.51$, $p>0.05$ NS.
Male $X^2=6.52$, $p<0.05$.

larvae to chironomids and other Diptera. Older males fed chironomids to their young more often did than yearling males (Table 17: Kruskal-Wallis test $X^2=4.48$, $0.01 \leq p \leq 0.05$). By Day 8 both older and yearling males fed approximately the same number of prey items to their young although older males brought more adult Diptera (primarily chironomids).

Most female parents increased their average number of feeding trips as the nestlings became older (Table 18). Older females made more feeding trips per nestling on the 8th day compared with yearling females. However, overall female feeding rates did not differ significantly. Male parents consistently fed nestlings at a similar rate regardless of the age of the brood. Overall feeding rates were significantly greater for older males than yearling males (Table 18: Kruskal-Wallis test: $X^2=6.53$, $p \leq 0.05$). Older males made more feeding trips to the nest than yearlings after the second day. Males brought greater prey loads to the nest than females, however the differences were not significant (Table 19: Kruskal-Wallis test: $X^2=2.17$, df=1, $p>0.05$, NS). The prey loads did not differ with the age of the parent of either sex or with the age of the brood.

Females in the south zone of the dune-ridge forest fed a similar number of prey items and made the same number of trips compared to females that nested in the north zone (Table 20 and 22). The males of nests located in the south zone of the dune-ridge forest fed their offspring more often than males in the north zone (Table 21: Kruskal-Wallis test: $X^2=4.72$, $0.01 \leq p \leq 0.05$). However, there was no significant difference in the number of prey items brought by males in the south zone compared with males in the north zone (Table 22).

Table 19. Mean (±S.E.) number of prey items brought per trip by yearling and older parents to broods of different ages. The number of observation periods is given in parentheses. Data for 1985 and 1986 are combined.

Age (days)[1]	Age of parent [2]			
	YF	OF	YM	OM
2	1.56±0.09 (9)	2.04±0.04 (25)	1.73±0.03 (45)	1.29±0.01 (68)
4	1.88±0.03 (41)	1.68±0.04 (25)	1.79±0.02 (63)	2.70±0.02 (71)
6	1.56±0.03 (48)	2.05±0.03 (44)	2.31±0.22 (64)	3.54±0.02 (81)
8	1.90±0.03 (49)	2.00±0.02 (45)	2.49±0.03 (57)	3.39±0.02 (80)

[1] -Kruskal-Wallis test: age of brood: X^2=4.71 df=3 p>0.05 NS.

[2] -Kruskal-Wallis test: age of parent: Female X^2=3.01 df=1 p>0.05 NS.

Male X^2=1.33 df=1 p>0.05 NS.

Table 20. The number of identified prey items (prey item/trip/nestling) brought to the nest by female Yellow Warbler parents in the south (SO) and north (NO) zones of the dune-ridge forest, in relation to the age of the brood. Figures are means±S.E. Number of observation periods given as sample size. Data for 1985 and 1986 are combined.

Age (days)	n	Ridge zone where nest placed[1]	Prey Items Diptera	 Geometrid Larvae	 Other
2	16	SO	0.09±0.05	0.03±0.02	0.00±0.00
	8	NO	0.10±0.06	0.03±0.03	0.03±0.03
4	15	SO	0.16±0.05	0.41±0.02	0.00±0.00
	8	NO	0.38±0.22	0.00±0.00	0.00±0.00
6	16	SO	0.44±0.15	0.02±0.01	0.01±0.01
	7	NO	0.06±0.02	0.03±0.02	0.03±0.03
8	9	SO	0.56±0.13	0.00±0.00	0.00±0.00
	3	NO	0.52±0.27	0.01±0.01	0.05±0.05

---

[1] -Kruskal-Wallis test: ridge zone where nest placed: NS-p>0.05 for all prey categories

Table 21. The number of identified prey items (prey item/trip/nestling) brought to the nest by male Yellow Warbler parents in the south (SO) and north (NO) zones of the dune-ridge forest in relation to the age of the brood. Figures are means±S.E. Number of observation periods given as sample size. Data for 1985 and 1986 are combined.

Age (days)	n	Ridge zone where nest placed[1]	Prey Items		
			Diptera	Geometrid Larvae	Other
2	16	SO	0.31±0.08	0.13±0.04	0.00±0.00
	8	NO	0.19±0.10	0.05±0.02	0.00±0.00
4	15	SO	0.42±0.17	0.10±0.03	0.01±0.00
	8	NO	0.26±0.14	0.12±0.05	0.02±0.01
6	16	SO	0.71±0.20	0.05±0.02	0.01±0.00
	8	NO	0.25±0.11	0.04±0.02	0.02±0.01
8	9	SO	0.46±0.11	0.02±0.01	0.01±0.01
	3	NO	0.43±0.23	0.04±0.04	0.04±0.04

[1] -Kruskal-Wallis test: ridge zone where nest placed: NS-$p>0.05$ for all prey categories.

Table 22. Mean (±S.E.) number of trips (trips/nestling/hour) by Yellow Warbler parents in relation to the location of the nest and the age of the brood. Number of observation periods given as sample size. Data for 1985 and 1986 are combined.

Age (days)	n	Ridge zone where[1] nest placed	Sex of parent	
			Female	Male
2	16	SO	0.17±0.08	1.36±0.22
	8	NO	0.26±0.24	1.01±0.29
4	15	SO	0.88±0.26	1.68±0.18
	8	NO	0.51±0.22	1.22±0.36
6	16	SO	1.22±0.32	1.49±0.28
	7	NO	0.65±0.25	1.13±0.35
8	9	SO	1.58±0.42	2.03±0.58
	3	NO	1.09±0.39	1.46±0.32

---

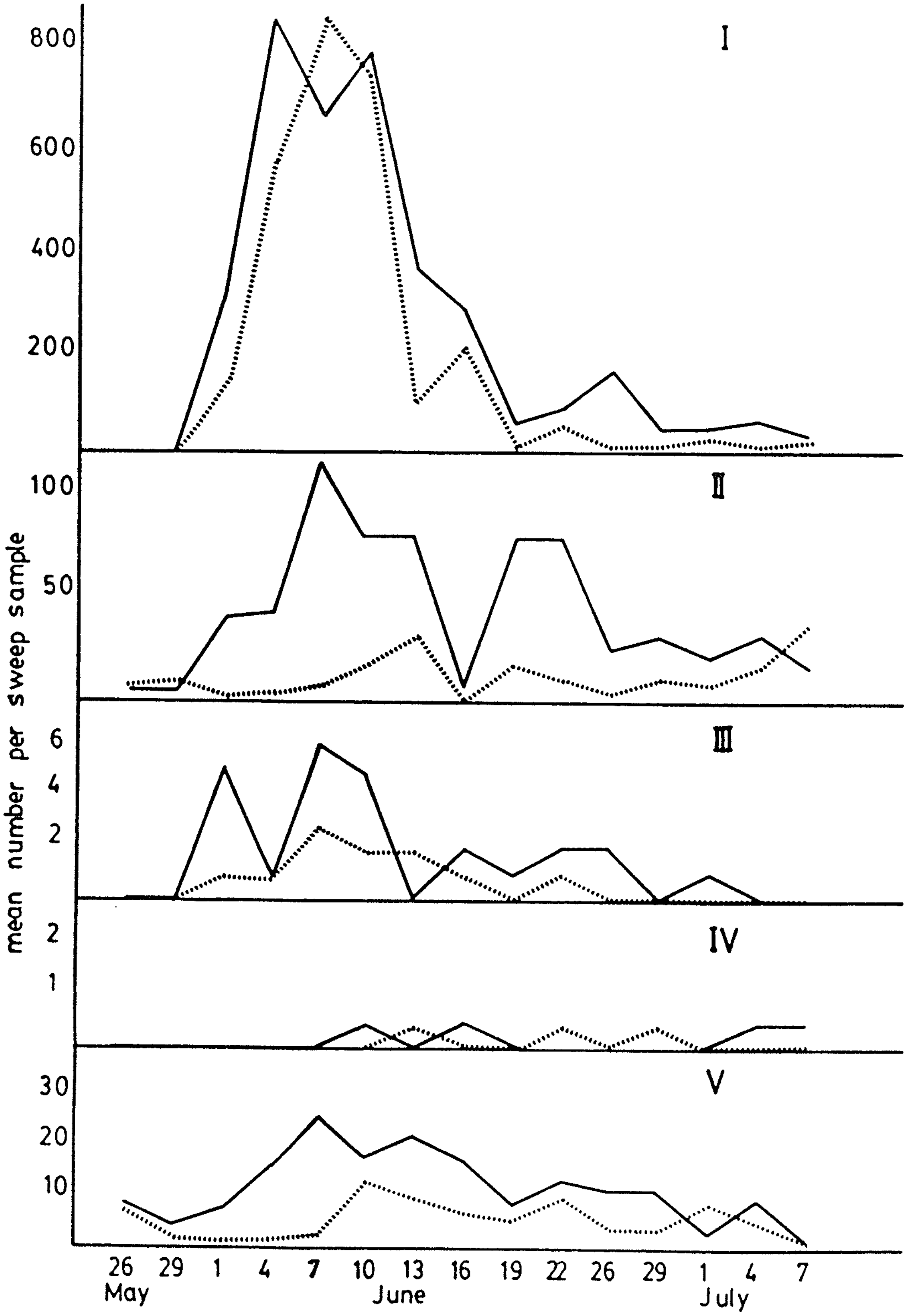
[1]-Kruskal-Wallis test: ridge zone where nest placed: Female NS-$p>0.05$.

Male $X^2=4.72$ $p<0.05$.

Seasonal prey abundance

Chironimids and culicids predominanted throughout the breeding season (Fig. 1). A rather large emergence of chironomids occurred during the early summer and subsequent emergences continued throughout the nesting season in both zones of the ridge. Adult Diptera were more abundant in the south zone for most of the breeding season. Geometrid larvae were more abundant in the south zone. The abundance of the other arthropod groups fluctuated enough on both sides of the ridge that no distinctive trend was apparent.

Figure 1. Mean seasonal arthropod abundance (1985-1986) on the north (broken) and south (solid) zones on the dune ridge. Groups are: (I) chironomids and culicids; (II) Diptera adults; (III) geometrid larvae; (IV) other larvae; and (V) other.



I
II
III
IV
V
800
600
400
200
100
50
6
4
2
2
1
30
20
10
mean number per sweep sample
26
29
1
4
7
10
13
16
19
22
26
29
1
4
7
May
June
July

Prey abundance during nest watches

In general, chironomids were fed most often by male and female parents; on Days 2 and 4 of the nestling period geometrid larvae were also an important food item and fed to young disproportionately to their abundance (Figs. 2 and 3).

Estimates of prey availability from sweep-net samples were compared with prey fed to nestlings using the Wilcoxon match-pair sign test (Seigel 1956). Adults selectively fed nestlings more geometrids than were represented in the sweep-net samples ($T=0$, $p \leq 0.05$). Chironomids and other dipterans were taken in proportion to their relative abundance in sweep-net samples. Lepidopteran larvae and other arthropods were selected in proportions less than what was present in sweep net samples ($T=0$, $p \leq 0.05$).

Older males fed geometrid larvae twice as often to nestlings of 2 days old compared with yearling males (Figs. 2 and 3). Older nestlings were fed predominantly chironomids. Females fed primarily chironomids throughout the nestling stage; on the 2nd and 4th days Diptera and geometrid larvae were fed to the young but these dropped off to residual proportions. There was no significant difference in the type of prey brought to the nest by yearling and older females.

Figure 2. Proportion of arthropods in prey groups I-V in sweep-net samples, and the proportion of arthropods in each group observed being fed to nestling Yellow Warblers on days 2, 4, 6, and 8 of the nestling stage by older males (striped) and females (open). Absolute numbers given on the sides. Arthropod groups same as in Figure 1.

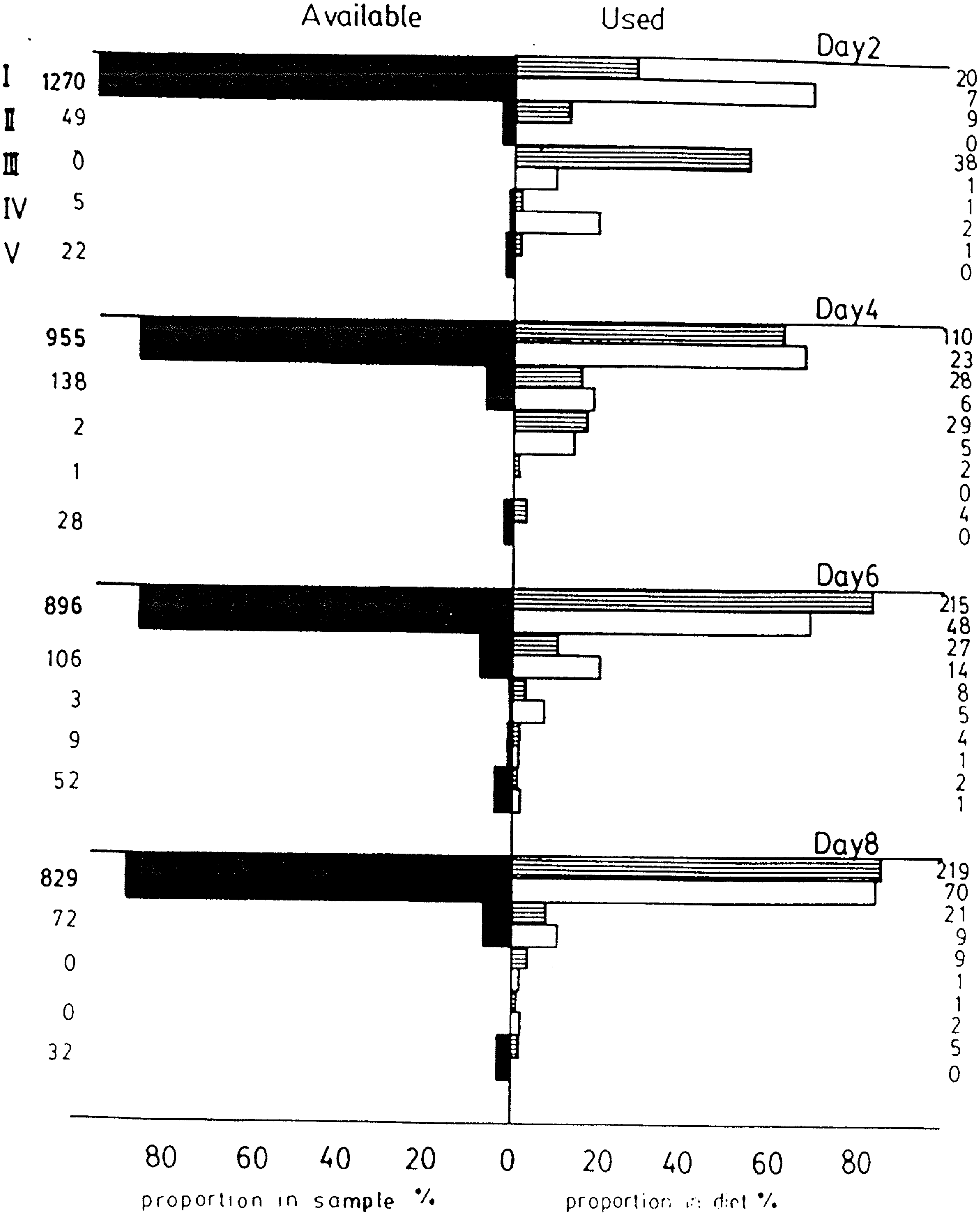
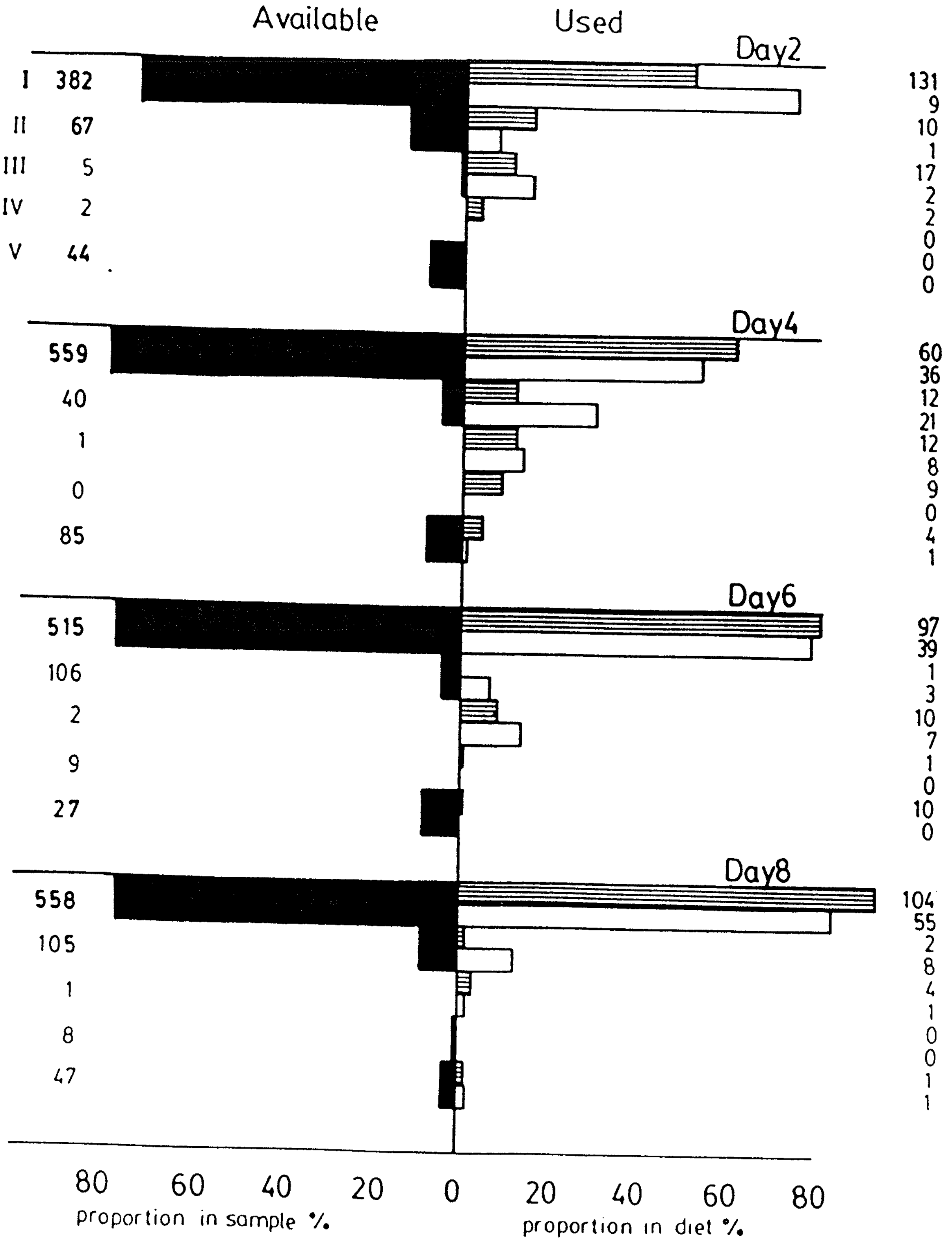

Available
Used
Day2
I
1270
II
49
III
0
IV
5
V
22
20
7
9
0
38
1
1
2
1
0
Day4
955
138
2
1
28
110
23
28
6
29
5
2
0
4
0
Day6
896
106
3
9
52
215
48
27
14
8
5
4
1
2
1
Day8
829
72
0
0
32
219
70
21
9
9
1
1
2
5
0
80
60
40
20
0
20
40
60
80
proportion in sample %
proportion in diet %

Figure 3. Proportion of arthropods in prey group I–V in sweep-net samples, and the proportion of arthropods in each group observed being fed to nestling Yellow Warblers on days 2, 4, 6, and 8 of the nestling period by yearling male (striped) and female (open) parents. Absolute values given on the sides. Arthropods same as in Figure 1.


Available
Used
Day2
I 382
II 67
III 5
IV 2
V 44
131
9
10
1
17
2
2
0
0
0
Day4
559
40
1
0
85
60
36
12
21
12
8
9
0
4
1
Day6
515
106
2
9
27
97
39
1
3
10
7
1
0
10
0
Day8
558
105
1
8
47
104
55
2
8
4
1
0
0
1
1
80
60
40
20
0
20
40
60
80
proportion in sample %
proportion in diet %

Growth rate

The mean mass and tarsal length of nestlings reared by yearling and older parents are summarized in Table 23. The growth rate of nestlings tended by older parents did not differ significantly from those tended by yearling parents (Table 24: Student's T-test, one-way: $T=0.71$, $p>0.05$, $df=5$, NS). The growth rate of the tarsus was identical for nestlings tended by parents of either age class (Table 24: Student's T-test, one-way: $T=0.00$, $p>0.05$, $df=5$, NS). The asymptotic weights of free-flying fledglings caught past 20 days post-hatch did not differ between fledglings rasied by older and yearling parents (older 9.97±0.58 g, $n=36$; yearling 9.87±0.48 g, $n=9$; $t=0.37$, $p>0.05$, NS).

The mean mass and tarsal length of nestlings reared on the south and north zones of the ridge are summarized in Table 25. The mass of nestlings from the south side did not differ significantly from the mass of nestlings reared on the north side (Table 26: Student's T-test one-way: $T=0.00$, $p>0.05$, $df=5$, NS). The tarsal length of nestlings on the south side compared to those on the north side was not significantly different (Table 26: Student's T-test one-way: $T=0.77$, $p>0.05$, $df=5$, NS).

Table 23. Mean mass (g) and mean tarsus length (mm) of nestling Yellow Warblers, in broods of four, in relation to the age of the parents. Figures are means±S.E. Data for 1985 and 1986 are combined.

Parental age		Days since first hatch					
		1	2	3	4	5	6
Yearling	N	14	17	14	8	9	10
	Mass (g)	1.9±0.1	3.1±1.2	4.6±0.3	6.0±0.5	6.3±0.4	7.6±0.5
	Tarsus (mm)	4.7±0.1	6.9±0.1	9.0±0.1	11.0±0.1	11.8±0.1	13.7±0.1
Older	N	17	18	18	14	11	9
	Mass (g)	1.5±0.1	2.5±0.2	4.0±0.2	5.8±0.3	6.9±0.4	7.4±0.6
	Tarsus (mm)	5.4±0.1	7.0±0.1	8.8±0.1	11.0±0.1	12.3±0.1	14.2±0.1

Table 24. Model parameters for growth curves for mass (g) and tarsus length (mm) of nestling Yellow Warblers, from broods of four, in relation to the age of their parents. Figures are parameter estimates±S.E. Data for 1985 and 1986 combined.

Parental age		Model parameters			Residual variance
		m	k	b	
Yearling	Mass (g)	1.9	0.45±0.04	4.91±0.81	0.084
	Tarsus (mm)	2.0	0.50±0.02	4.51±0.36	0.051
Older	Mass (g)	1.9	0.55±0.07	7.82±2.23	0.187
	Tarsus (mm)	2.0	0.50±0.03	4.01±0.42	0.088

Table 25. Mean mass (g) and mean tarsus length (mm) of nestling Yellow Warblers, from broods of four, in relation to the location of the nest on the dune-ridge forest, Delta Marsh, Manitoba. Figures are means±S.E. Data for 1985 and 1986 are combined.

Ridge zone where nest placed		Days since first hatch					
		1	2	3	4	5	6
North	N	23	29	27	20	19	21
	Mass (g)	2.1±0.1	2.9±0.1	4.5±0.2	5.6±0.3	6.7±0.3	7.9±0.4
	Tarsus (mm)	5.1±0.0	6.5±0.0	9.2±0.1	10.1±0.1	12.1±0.4	13.0±0.4
South	N	36	38	34	29	29	25
	Mass (g)	1.8±0.1	2.9±0.1	4.5±0.2	6.0±0.0	7.2±0.2	7.7±0.3
	Tarsus (mm)	5.2±0.0	7.0±0.0	8.9±0.0	10.9±0.0	12.3±0.0	14.0±0.0

Table 26. Model parameters for growth curves for mass (g) and tarsus length (mm) of nestling Yellow Warblers, from broods of four, in relation to the location of the nest on the dune-ridge forest, Delta Marsh, Manitoba. Figures are parameter estimates±S.E.

Ridge zone where nest placed		Model parameters			Residual variance
		m	k	b	
North	Mass (g)	1.9	0.55±0.02	6.95±0.64	0.022
	Tarsus (mm)	2.0	0.45±0.02	4.29±0.35	0.082
South	Mass (g)	1.9	0.55±0.05	7.74±1.42	0.054
	Tarsus (mm)	2.0	0.52±0.03	4.45±0.47	0.087

DISCUSSION

During the incubation period yearling male Yellow Warblers fed their mates as often as did older males. Older males fed their nestlings consistently more often than yearling males throughout the nestling period. Geometrid larvae and adult Diptera were selected by males in disproportionate numbers over the nestling period. Geometrids were fed more frequently in the first four days post hatch. The age of the female did not influence the feeding rate or prey load. The growth of nestlings was not affected by the age of the parents.

In this study reproductive effort was evaluated in two ways: the reproductive success was recorded (Chapter 1) and some aspects of parental care were estimated through feeding rates and prey loads (this Chapter). The feeding rates and prey loads of parent birds were used as measures of the skills of individual parents (Biermann and Sealy 1982, Studd and Robertson 1985b). Several possible reasons have been given to explain age-related differences in feeding rate: foraging ablility (Lack 1954, Perrins and Moss 1974), parental effort (Williams 1966, Gadgil and Bossert 1970), and territory quality (Ralph and Pearson 1971, Cooke and Abraham 1980).

Inexperienced birds may forage less efficiently than older and more experienced individuals. Some studies show that juveniles require more energy and forage longer than adults to obtain an equal quantity of food (Orians 1969, Recher and Recher 1969, Dunn 1972, Groves 1978, Bildstein 1984, Gochfeld and Burger 1984, and Burger and Gochfeld 1986).

Perrins and Moss (1974) proposed that yearling Great Tits may have been inexperienced in procuring food which would cause a delay in laying date. Kallander (1974) found that when Great Tits were provided with extra food they initiated their clutches earlier, which implied that food demand and/or foraging ability constrained laying date. In the Yellow Warbler, yearling females arrived on the breeding grounds weighing significantly less than older females (Biermann and Sealy 1985). These yearling females may have lighter mass because they forage less efficientlly. In the early days of incubation, yearling males fed their females more often; older males fed females more often during late incubation (see Table 15). By the end of incubation there were no differences in mass between females of different age classes (Biermann and Sealy 1985) which excluded the possibility that the difference in mass was a result of morphological differences in development. The greater number of courtship feeding trips during early incubation by yearling males supports the hypothesis that males modified their courtship feeding rates to reflect the nutritional needs of their females.

Lifjeld and Slagsvold (1986) found, in the Pied Flycatcher (Ficedula hypoleuca), some support for the hypothesis that male courtship feeding was important for the nutrition of the female (see also Morris 1986). The age of the males affected the feeding rate in one of the two study seasons. Their study did not support hypotheses that proposed that courtship feeding reliably indicated the quality of the male or was important in establishing and maintaining the pair-bond. Lyon and Montgomerie (1985) assessed the courtship feeding behaviour of Snow Buntings (Plectrophenax niralis) by removing males at the start of incubation. The resulting "early widows" spent more time off the nest (as a result had longer incubation periods) and had lower hatching success. They concluded that courtship feeding was a form of indirect parental care since parents benefited from it. In this regard, male Yellow Warblers of different ages essentially contribute equal amounts of parental care to their mates during different stages of incubation.

One alternative explanation for an age-related difference in feeding rate was that the amount of time and effort devoted to foraging may have influenced the feeding rates. Historically, the assumption of parental investment theory in monogamous birds has been that contributions by each sex to parental care were unequal (Alcock 1974, Alexander 1974). Trivers (1972) predicted that female parents would contribute a similar, maximum amount of parental effort because of their initial large investment in the formation of the gametes. In my study, the age of the female parent did not influence the feeding rate or the number of items brought per trip which does not support the proposal that age and/or experience was a constraint on the maximal amount of parental effort.

Biermann and Sealy (1982) found that the age of the brood influenced the feeding rate in the Yellow Warbler. In their study the parental feeding rates of broods increased as the brood aged. A similar result was found in the present study (Table 19 and 20), that is, feeding rates of female parents increased as their broods became older. This outcome probably resulted from brooding in the first days after hatch which prevented the female from leaving the nest to forage for prey. Thus, female Yellow Warblers contributed similar parental care regardless of age.

Older males fed nestlings consistently more often than yearling males throughtout the nestling stage. In the Yellow Warbler, the ways in which a male can invest in his offspring are more varied than females. The initial investment in the territory, the courtship feeding, and the provisioning of young all contribute to the overall investment. During the nestling period the parental care of the males remained consistent as the brood aged. Thus, parental effort was similar for males throughout the nestling stage.

Differences in the availability of prey in different nest sites of older males was a third alternative explantion for greater feeding rates. The distribution of various prey items did not differ between the north and south zone of the forested dune ridge. Older males fed more geometrids relative to their abundance on the second day than did yearling males. Geometrid larvae are an important component of the nestling diet in Yellow Warblers (Biermann and Sealy 1982, Studd and Robertson 1985b). Geometrid larvae have been found to be distributed disproportionately more in the lower vegetation on the ridge forest where male Yellow Warbler forage more frequently than females (Busby and Sealy 1979). Mackenzie and Sealy (1981) found small stems to be a predominant factor in the south zone nesting sites. The south side nests contained a greater proportion of low vegetation to support geometrid larvae and thus this important food item may be more abundant in the south zone of the dune ridge forest. Males that nested in the south zone made more feeding trips but fed a similar number of prey items to their nestlings compared to those males that nested in the north zone (Table 20 and 21). Both the age of the parent and the availability of prey in a nest site are two independent but important components that determine the feeding rate of a parent.

The growth rate of nestlings may provide an estimate of parental quality. If yearling parents could not raise the same number of young as older parents then the growth rate of offspring from nests of yearling parents would be expected to be reduced (Ricklefs 1969). The growth rate of nestlings from yearling parents was approximately 0.10 less than those raised by older parents, although this result was not significant. The faster growth rate of nestlings from older parents probably reflected the greater number of feeding trips. Ross (1980a) found a similar result in the Ipswich Sparrow (<u>Passerculus sandwichensis princeps</u>) where parental feeding rates were greater in the older sparrows but nevertheless no difference in the growth rate was discovered. Ross and MacLaren (1981) did not find any difference in survivorship in nestlings in relation to the age of their parents.

The probability of survival of young Great Tits is correlated with their mass at fledging (Perrins 1965). In this case the lighter mass of fledglings from older parents would seem maladaptive. In the Yellow Warbler, the asymptotic weights of free-flying fledglings caught past 20 days post-hatch did not differ from fledglings raised by older and yearling parents. Therefore, the difference in mass that existed between nestlings reared by older compared to those raised by yearlings was no longer present just prior to migration.

Ross (1980b) found that the growth rate and the development of the tarsus were affected by habitat. In this case he compared sparse versus dense habitats. He suggested that some of the variation in the greater mass measurements in dense habitat may be attributed to differences in food availability between habitats. Studd and Robertson (1985b) found that growth rate in the Yellow Warbler depended upon feeding rate in some habitats but in other areas there were no such correlations. The growth rates of nestling Yellow Warblers on the ridge did not differ between habitat (the north and south zones). The prey availablity in the south zone did not differ from the north. Thus, the growth rate in the Yellow Warbler was not dependent upon the zone in which a parent nested.

The feeding rates and prey items brought by parents to the nest may affect the survival of their offspring. In the Yellow Warbler, older males brought greater overall numbers of geometrid larvae and Diptera than yearling males. Feeding rate were affected by the age of the parent and the location of the nest, however, the location of the nest had no influence on the return rate of offspring. There was a significant difference in the prey items brought to the nestlings in relation to the age of the parent but this parameter was not significant with respect to the location of the nest. Thus, the return rate of nestlings may be more greatly influenced by the type of prey items brought to the nest that the actual feeding rate.

GENERAL CONCLUSIONS

1. Older parents initiated their clutches earlier and produced more offspring that returned to the dune-ridge forest than yearling parents;

2. the fledglings that returned to the dune-ridge forest were reared by parents that initiated earlier and raised larger broods than the general population;

3. there was no relationship between the return rate of parents and reproductive success;

4. older females had more variable clutch sizes than yearling females, thus there was no difference in the proportion of "poor" parents in each age group;

5. the feeding rate and zone in which a nestling was reared did not affect the probability of its return;

6. the prey items brought to the nestlings may have influenced the probability of return;

7. the feeding behaviour of the female parent was more influenced by the age of the brood;

8. the feeding behaviour of the nale parent was more influenced by the age of the male than by the age of the brood;

9. the growth rate was not affected by the feeding rate or the zone in which a nestling was reared;

10. older parents were more successful because they were older and/or more experienced than yearling parents.

LITERATURE CITED

Alcock, J. 1974. Animal Behavior: an evolutionary approach. Third edition. Sunderland, Massachusetts: Sinauer Associates, Inc.

Alexander, R.D. 1974. The evolution of social behavior. Ann. Rev. Ecol. Syst. 5: 325-383.

Askenmo, C. 1979. Reproductive effort and the return rate of male Pied Flycatchers. Amer. Nat. 114: 748-753.

Askenmo, C., and U. Unger. 1986. How to be double brooded: trends and timing of breeding performance in the Rock Pipit. Ornis Scand. 17: 237-244.

Bedard, J., and G. LaPointe. 1985. Influence of parental age and season on Savannah Sparrow reproductive success. Condor 87: 106-110.

Bedard, J., and M. Meunier. 1983. Parental care in the Savannah Sparrow. Can. J. Zool. 61: 2836-2843.

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

Biermann, G.C., and S.G. Sealy. 1982. Parental feeding of nestling Yellow Warblers in relation to brood size and prey availability. Auk 99: 332-341.

Biermann, G.C., and S.G. Sealy. 1985. Seasonal dynamics of body mass of insectivorous birds breeding on the forested dune ridge, Delta Marsh, Manitoba. Can. J. Zool. 63: 1675-1682.

Bildstein, K.L. 1984. Age-related differences in foraging behavior of White Ibises and the question of deferred maturity. Colonial Waterbirds 7: 25-34.

Blus, L.J., and J.A. Keehey. 1978. Variation in reproductivity with age in the Brown Pelican. Auk 95: 128-134.

Briskie, J.V. 1985. Growth and parental feeding of Least Flycatchers in relation to brood size, hatching order and prey availability. M.Sc. thesis, University of Manitoba, Winnipeg.

Brooke, M. de L. 1978. Some factors affecting the laying date, incubation and breeding success of the Manx Shearwater, Puffinus puffinus. J. Anim. Ecol. 47: 477-495.

Brownie, C., D.R. Anderson, K.P. Burnham and D.S. Robson. 1978. Statistical Inference for Band Recovery Data: A Handbook. United States Department of the Interior Fish and Wildlife Service Resource Publication No. 131.

Bryant, D.M. 1979. Reproductive costs in the House Martin (Delichon urbica). J. Anim. Ecol. 48: 655-675.

Burger, J., and M. Gochfeld. 1986. Age differences in foraging efficiency of American Avocets Recurvirostra americana. Bird Behaviour 6: 66-71.

Busby, D.G., and S.G. Sealy. 1979. Feeding ecology of a population of nesting Yellow Warblers. Can. J. Zool. 57: 1670-1681.

Catchpole, C.K. 1972. A comparative study of territory in the reed warbler (Acrocephalus sciraceus) and the sedge warbler (A. schoenbaenus). J. Zool. (London) 166: 213-231.

Cody, M.L. 1971. Ecological aspects of reproduction. In Avian Biology (Farner and King, eds.). Academic Press, New York. pp. 462-512.

Cooke, F., and K. Abraham. 1980. Habitat and locality selection in Lesser Snow Geese: the role of previous experience. Proc. Int. Ornith. Congr. 17: 998-1004.

Cosens, S.E., and S.G. Sealy. 1986. Age-related variation in repertoire size and repertoire sharing of Yellow Warblers (Dendroica petechia). Can. J. Zool. 64: 1926-1929.

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.

Coulson, J.C. 1968. Difference in quality of birds nesting in the center and on the edges of a colony. Nature, London 217: 478-479.

Coulson, J.C. 1972. The significance of the pair bond in the Kittiwake. Proc. Int. Ornith. Congr. 15: 424-433.

Coulson, J.C., and J. Horobin. 1976. The influence of age on the breeding biology and survival of Artic Terns Sterna paradisea. J. Zool. (London) 178: 2747-2760.

Coulson, J.C., and E. White. 1958. The effect of age on the breeding biology of the Kittiwake Rissa tridactyla. Ibis 100: 40-51.

Coulson, J.C., ad E. White. 1960. The effect of age and density of breeding birds on the time of breeding in the Kittiwake Rissa tridactyla. Ibis 102: 71-86.

Crawford, R.D. 1980. Effects of age on reproduction in American Coots. J. Wildl. Manage. 44: 183-189.

Crawford, R.D. 1977. Breeding biology of year-old and older female Red-winged and Yellow-headed blackbirds. Wilson Bull. 89: 73-80.

Curio, E. 1983. Why do young birds reproduce less well? Ibis 125: 400-404.

Davis, J.W.F. 1975. Age, egg size and breeding success in the Herring Gull Larus argentatus. Ibis 117: 460-473.

Davis, J.W.F. 1976. Breeding success and experience in the Arctic Skua, Stercorarius parasiticus (L.). J. Anim. Ecol. 45: 531-536.

De Steven, D. 1978. The influence of age on the breeding biology of the Tree Swallow Iridoprocne bicolor. Ibis 120: 516-523.

De Steven, D. 1980. Clutch size, breeding success and parental survival in the Tree Swallow (Iridoprocne bicolor). Evol. 34: 278-291.

Dunn, E. 1972. Effect of age on the fishing ability of Sandwich Terns Sterna sandvicensis. Ibis 114: 360-366.

Emlen, J.M. 1970. Age specificity and ecological theory. Ecology 51: 588-601.

Farner, D.S. 1949. Age groups and longevity in the American Robin: comments, further discussion and certain revisions. Wilson Bull. 61: 68-81.

Finney, G., and F. Cooke. 1978. Reproductive habits in the Snow Goose: the influence of female age. Condor 80: 147-158.

Fisher, H.I. 1969. Eggs and egg-laying in the Laysan Albatross, Diomedea immutablilis. Condor 71: 102:112.

Fisher, H.I. 1971. The Laysan Albatross: Its incubation, hatching and associated behaviors. Living Bird 10: 19-78.

Fisher, H.I. 1975. The relationship between deferred breeding and mortality in the Layson Albatross. Auk 92: 433-441.

Fisher, R.A. 1930. The genetical theory of natural selection. Claredon, Oxford.

Gadgil, M., and W.H. Bossert. 1970. Life history consequences of natural selection. Amer. Nat. 104: 1-24.

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

Gochfeld, M., and J. Burger. 1984. Age differences in foraging behaviour of the American Robin (Turdus migratorius). Behaviour 88: 227-239.

Goossen, J.P. 1978. Breeding biology and reproductive success of the Yellow Warbler on the Delta Beach Ridge, Manitoba. M.Sc. thesis, University of Manitoba, Winnipeg.

Goossen, J.P., and S.G. Sealy. 1982. Production of young in a dense nesting population of Yellow Warblers (Dendroica petechia) in Manitoba. Canadian Field-Nat. 96: 186-199.

Greenberg, R. 1980. Demographic aspects of long-distance migration. In Migrant birds in the Neotropics: Ecology, behaviour, distribution and conservation (A. Keast and E. S. Morton, eds.) Smithsonian Inst. Press, Washington, D.C. Pp. 493-504.

Groves, S. 1978. Age-related differences in Ruddy Turnstone foraging and aggressive behaviour. Auk 95: 95-103.

Guinan, D.M. 1985. The diet and foraging behaviour of House Wrens (Troglodytes aedon) and the abundance of invertebrate prey. M.Sc. thesis, University of Manitoba, Winnipeg.

Hannon, S.J. 1984. Factors limiting polygyny in the Willow Ptarmigan. Anim. Behav. 32: 153-161.

Hannon, S.J., and J.N.M. Smith. 1984. Factors influencing age-related reproductive success in the Willow Ptarmigan. Auk 101: 848-854.

Harrington, B.A. 1974. Colony visitation behavior and breeding ages of Sooty Terns (Sterna fuscata). Bird-Banding 45: 115-144.

Harvey, P.H., P.J. Greenwood, C.M. Perrins and A.R. Martin. 1979. Breeding success of Great Tits Parus major in relation to age of male and female parents. Ibis 121: 216-219.

Harvey, P.H., M.J. Stenning and B. Campbell. 1985. Individual variation in seasonal breeding success of Pied Flycatchers (Ficedula hypoleuca). J. Anim. Ecol. 54: 391-398.

Haymes, G.T., and H. Blokpoel. 1980. The influence of age on the breeding biology of Ring-billed Gulls. Wilson Bull. 92: 221-228.

Heagy, P.A., and L.B. Best. 1983. Factors affecting feeding and brooding of Brown Thrasher nestlings. Wilson Bull. 95: 297-303.

Jones, P.J., and P. Ward. 1976. The level of reserve protein as the proximate factor controlling the timing of breeding and clutch size in the Red-billed Quelea (Quelea quelea). Ibis 118: 547-574.

Kallander, H. 1974. Advancement of laying date of Great Tits by the provision of food. Ibis 116: 365-367.

Kendeigh. S.C. 1952. Parental care and its evolution in birds. Illinois Biol. Monogr. 22: 1-356.

Ketterson, E.D. 1979. Status signalling in Dark-eyed Juncos. Auk 96: 94-99.

Klomp, H. 1970. The determination of clutch size in birds: a review. Ardea 58: 1-124.

Kluijver, H.N. 1970. Regulation of numbers in populations of Great Tits (Parus m. major). In Dynamics of Numbers in Populations (P.J. der Boer and G.R. Gradwell, eds.). Proceedings of the Advanced Study Institute, (Oosterbeck) the Netherlands, 1970. Pp. 507-523.

Krapu, G.L., and H.A. Doty. 1979. Age-related aspects of Mallard reproduction. Wildfowl 30: 35-39.

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

Labedz, T.E. 1984. Age and reproductive success in Northern Orioles. Wilson Bull. 96: 303-305.

Lack, D. 1947. The significance of clutch-size. Ibis 89: 302-352.

Lack, D. 1954. The Natural Regulation of Animal Numbers. Claredon Press, Oxford.

Lifjeld, J., and T. Slagsvold. 1986. The function of courtship feeding during incubation in the Pied Flycatcher Ficedula hypoleuca. Anim. Behav. 34: 1441-1453.

Lyon, B.E., and R.D. Montgomerie. 1985. Incubation feeding in Snow Buntings: Female manipulation or indirect male parental care? Behav. Ecol. Sociobiol. 17: 279-284.

MacArthur, R.H., and E.O. Wilson. 1967. Theory of Island Biogeography. Princeton Univ. Press, Priceton.

MacKenzie, D.I. 1982. The dune ridge forest, Delta Marsh, Manitoba: overstory vegetation and soil patterns. Can. Field-Nat. 96: 61-68.

MacKenzie, D.I., and S.G. Sealy. 1981. Nest site selection in Eastern and Western kingbirds: a multivariate approach. Condor 83: 310-321.

MacKenzie, D.I., S.G. Sealy, and G.D. Sutherland. 1982. Nest site characteristics of the avian community in the dune-ridge forest, Delta Marsh, Manitoba: a multivariate analysis. Can. J. Zool. 60: 2212-2223.

Marqualdt, D.W. 1963. An algorithm for least squares estimation on non-linear parameters. J. Soc. Ind. Appl. Math. 2: 431-441.

Middleton, A. 1979. Influence of age and habitat on reproduction by the American Goldfinch. Ecology 60: 418-432.

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-

Milne, H. 1974. Breeding numbers and reproductive rate of eiders at the sands of Fovie National Reserve, Scotland. Ibis 116: 135-154.

Morris, R.D. 1986. Seasonal differences in courtship feeding rates of male Common Terns. Can. J. Zool. 64: 501-507.

Nelson, J.B. 1966. The breeding biology of the Gannet Sula bassana on the Bass Rock, Scotland. Ibis 108: 584-626.

Nelson. J.B. 1978. The Gannet. Vermillion , North Dakota, Buteo.

Nilsson, S.G., G. Bjorkman, P. Forslund and J. Hoglund. 1985. Egg predation in forest bird communities on islands and mainland. Oecologia (Berl.) 66: 511-515.

Nisbet, I.C.T. 1973. Courtship feeding, egg-size and breeding success in Common Terns. Nature (London) 241: 141-142.

Nisbet, I.C.T. 1978. Dependence of fledging success on egg size, parental performance and egg composition among Common and Roseate Terns, Sterna hirundo and S. dougallii. Ibis 120: 207-214.

Nisbet, I.C.T., J.M. Winchell and A.E. Heise. 1984. Influence of age on the breeding biology of Common Terns. Colonial Waterbirds 7: 117-126.

Nol, E., and J.N.M. Smith. (1987). The effects of age and breeding experience on seasonal reproductive success in the Song Sparrow. J. Anim. Ecol. 56: 301-314.

Nolan, V., Jr. 1963. Reproductive success of birds in a deciduous scrub habitat. Ecology 44: 305-313.

Nolan, V., Jr. 1978. The ecology and behavior of the Prairie Warbler (Dendroica discolor). Ornith. Monogr. No. 26. Publ. A.O.U.

Nur, N. 1984. The consequences of brood size for breeding Blue Tits. II. Nestling weight, offspring survival and optimal brood size. J. Anim. Ecol. 53: 497-517.

Orians, G.H. 1969. Age and hunting success in the Brown Pelican (Pelecanus occidentalis). Anim. Behav. 17: 316-319.

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

Perrins, C.M. 1979. British Tits. Collins. London.

Perrins, C.M., and R.H. McCleery. 1985. The effect of age and pair bond on the breeding success of Great Tits, Parus major. Ibis 127: 306-315.

Perrins, C.M., and D. Moss. 1974. Survival of young Great Tits in relation of age of female parent. Ibis 116: 220-224.

Pianka, E.R., and W.S. Parker. 1975. Age-specific reproductive tactics. Amer. Nat. 109: 453-464.

Pinkowski, B.C. 1977. Breeding adaptations in the Eastern Bluebird. Condor 79: 289-302.

Pugesek, B.H. 1980. Increased reproductive effort with age in the California Gull (Larus californicus). Science 212: 822-823.

Pugesek, B.H., and K.L. Dien. 1983. A multivariate study of the relationship of parental age to reproductive success in California Gulls. Ecology 64: 829-839.

Ralph, C.J., and C.A. Pearson. 1971. Correlation of age, size of territory, plumage, and breeding success in the White-crowned Sparrow. Condor 73: 77-80.

Recher, H.F., and J.A. Recher. 1969. Comparative foraging efficiency of adult and immature Little Blue Herons (Florida caerulea). Anim. Behav. 17: 320-322.

Reese, K.P., and J.A. Kadlec. 1985. Influence of high density and parental age on the habitat selection and reproduction of Black-billed Magpies. Condor 87: 96-105.

Richards, F.J. 1959. A flexible growth function for empirical use. J. Exp. Bot. 10: 290-300.

Richdale, L.E. 1949. The effect of age on laying dates, size of eggs and size of clutch in the Yellow-eyed Penguin. Wilson Bull 61: 91-106.

Richdale, L.E. 1963. Biology of the Sooty Shearwater Puffinus griseus. Proc. Zool. Soc. (Lond.) 141: 1-117.

Ricklefs, R.E. 1969. Preliminary models for growth rates of altricial birds. Ecology 50: 1031-1039.

Ricklefs, R.E. 1974. Energetics of reproduction in birds. In Avian Energetics. (R.A. Paynter, ed.). Publ. Nuttall Ornithol. Club, No. 15. Pp. 152-292.

Roberts, J.L. 1971. Survival among some North American wood warblers. Bird-Banding 42: 165-184.

Rohwer, S. 1982. The evolution of reliable and unreliable badges of fighting ability. Amer. Zool. 22: 531-546.

Ross, H.A. 1980a. The reproductive rates of yearling and older Ipswich Sparrows Passerculus sandwichensis princeps. Can. J. Zool. 58: 1557-1563.

Ross, H.A. 1980b. Growth of nestling Ipswich Sparrows in relation to season, habitat brood size and parental age. Auk 97: 721-732.

Ross, H.A., and I.A. MacLaren. 1981. Lack of differential survival among young Ipswich Sparrows. Auk 98: 495-502.

Ryder, J.P. 1980. The influence of age on the breeding biology of colonial nesting seabirds. In Behaviour of Marine Animals: Current Perspectives in Research, Vol. 4. J. Burger, B.L. Olla and H.E. Winn (eds.). Plenum Press: New York. Pp. 153-168.

Sealy, S.G. 1980. Breeding biology of Orchard Orioles in a new population in Manitoba. Can. Field-Nat. 94: 154-158.

Seigal, S. 1956. Non-parametric statistics for the behavioural sciences. McGraw-Hill, New York.

Smith, J.N.M. 1985. Determinants of lifetime reproductive success. In Reproductive Success (Clutton-Brock, ed.). Chicago University Press, Chicago Ill.

Sokal, R.R., and F.J. Rohlf. 1981. Biometry. W.H. Freeman and Company, San Francisco.

Stearns, S.C. 1976. Life-history tactics: a review of the ideas. Quart. Rev. Biol. 51: 3-47.

Studd, M.V., and R.J. Robertson. 1985a. Evidence for reliable badges of status in territorial Yellow Warblers (Dendroica petechia). Anim. Behav. 33: 1102-1113.

Studd, M.V., and R.J. Robertson. 1985b. Sexual selection and variation in reproductive strategy in male Yellow Warblers (Dendroica petechia). Behav. Ecol. Sociobiol. 17: 101-109.

Trivers, R.L. 1972. Parental investment and sexual selection. In Sexual Selection and the Descent of Man (B. Campbell, ed.). Aldine Publishing Co., Chicago.

Veen, J. 1977. Functional and causal aspects of nest distribution in colonies of the Sandwich Tern (Sterna s. sandvicensis Lath.). Behaviour Suppl. 20.

Westmoreland, D., and L.B. Best. 1985. The effect of disturbance on Mourning Dove nesting success. Auk 102: 774-780.

Williams, G.C. 1966. Natural selection, the costs of reproduction and a refinement of Lack's principle. Amer. Nat. 100: 687-690.

Winkler, R.L., and W.L. Hays. 1975. Statistics: probability, inference and decision. Holt, Reinhart and Winston, New York.

Yamagishi, S. 1981. Effects of parent's age class on breeding success of the Meadow Bunting. Nihon Seitai Gakkaishi 31: 117-119.

Yasukawa, K. 1981. Male quality and female choice in the Red-winged Blackbird (Aegelaius phoeniceus). Ecology 62: 922-929.

Zach, R., Y. Liner, G. Rigby and K. Mayoh. 1984. Growth curve analysis of birds: the Richards model and procedural problems. Can. J. Zool. 62: 2429-2435.

Appendix 1. The mean initiation date in Julian date clutch size and brood size for female and male Yellow Warblers from 1983 to 1986 (mean±S.D.). All data from nests where at least one parent was of known age are combined.

Breeding parameters	1983	1984	1985	1986
Female:				
Initiation date	163.46±1.83	157.05±2.07	152.55±2.35	152.93±1.98
Clutch size	4.24±0.75	4.53±0.64	4.38±0.59	4.47±0.82
Brood size	2.14±2.00	1.49±2.00	2.44±1.94	2.71±1.82
Male:				
Initiation date	163.07±2.60	157.84±2.19	152.82±2.59	152.76±1.48
Clutch size	4.18±0.73	4.45±0.85	4.40±0.55	4.45±0.67
Brood size	2.56±1.90	1.61±2.04	2.85±1.83	3.23±1.31

Appendix 2. The corrected mean initiation date (in Julian date), clutch size and brood size for female and male Yellow Warblers that nested on the forested dune ridge, Delta Marsh, Manitoba 1983-1986. Figures are means±S.D.

Breeding parameters	1983	1984	1985	1986
Female:				
Initiation date	0.00±1.00	0.00±1.00	0.00±1.00	0.00±1.00
Clutch size	0.01±1.00	0.00±1.00	0.01±1.00	0.01±1.00
Brood size	0.00±1.00	0.00±1.00	0.01±1.00	0.00±1.00
Male:				
Initiation date	0.00±1.00	0.01±1.00	0.00±1.00	0.00±1.00
Clutch size	0.00±1.00	0.00±1.00	0.00±1.00	0.01±1.00
Brood size	0.00±1.00	0.00±1.00	0.00±1.00	0.00±1.00

Appendix 3. Nesting success of the Yellow Warbler.

	1983	1984	1985	1986
No. clutches recorded	280	365	307	324
No. clutches completed	137	143	127	171
No. clutches successful	96	89	83	96
Percent successful	70.1	62.2	65.5	56.1
Clutch initiation period (C.I.P)	JUN8 -JUL4	JUN1 -JUL7	MAY27 -JUL8	MAY27 -JUN28
Duration of C.I.P (days)	26	36	42	32
Period with 50% of clutches initiated (days)	5	8	8	5
No. lost to predation	30	47	34	27
Lost to predation (%)	21.9	32.9	26.8	15.8
No. lost to parasitism	1	1	0	1
Lost to parasitism (%)	0.7	0.7	0.0	0.7

Appendix 4. Recovery data for Yellow Warblers banded as adults and those banded as nestlings 1982-1985.

A.Adults

Year banded	Number banded	Year of recovery						Row total
		1	2	3	4	5	6	
1982	51	25	40	2	5	2	1	75
1983	163	35	10	17	1	2	0	65
1984	313	11	8	5	4	0	0	25
Column total		71	58	24	10	4	1	

B.Nestlings

Year banded	Number banded	Year of recovery						Row total
		1	2	3	4	5	6	
1982	264	6	8	3	0	0	0	17
1983	356	49	2	5	-	-	-	51
1984	406	40	8	-	-	-	-	40
1985	390	34	-	-	-	-	-	34
Column total		112	25	9	0	0	0	

Appendix 5. The number of male and female Yellow Warblers that returned to nest in a subsequant year in relation to the age at the time of nesting, ridge zone in which the warbler nested and dispersal distance in the preceeding year.

	Age	Ridge zone First year	Ridge zone Second year	n	Average distance (m)
Female	YF	south	south	1	0.0± 0.00
	YF	north	north	1	900.0
	OF	south	south	4	20.0± 44.7
	OF	south	north	1	0.0
	OF	north	south	2	60.0± 84.9
	OF	north	north	1	50.0
Male	YM	south	south	1	0.0
	YM	south	north	1	0.0
	OM	south	south	5	20.0± 44.7