

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
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Winnipeg, Manitoba

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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.

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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 <u>Diomedea immutabilis</u> | B | P | - | P | Fisher (1969, 1971, 1975) |
| | Sooty Shearwater <u>Puffinus griseus</u> | B | P | - | P | Richdale (1963) |
| | Manx Shearwater <u>P. puffinus</u> | B | P | - | - | de L. Brooke (1978) |
| Pelecaniformes | Northern Gannet <u>Sula bassanus</u> | F | P | - | P | Nelson (1966, 1978) |
| | Brown Pelican <u>Pelecanus occidentalis</u> | F | P | P | P | Blus and Keehey (1978) |
| Ciconiiformes | White Ibis <u>Eudocimus albus</u> | F | P | P | P | Bildstein (1984) |
| Anseriformes | Snow Goose <u>Chen caerulescens</u> | F | P | P | NP | Finney and Cooke (1978) |
| | Mallard <u>Anas platyrhynchos</u> | B | P | P | - | Krapu and Doty (1979) |
| Galliformes | Willow Ptarmigan <u>Lagopus lagopus</u> | F | NP | NP | NP | Hannon and Smith (1984) |

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

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

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

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

where x and t represent age, and 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 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 populations 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.