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Parental Care, Growth Rates and Pre-fledging Condition of Yellow Warbler Nestlings in Different Brood Sizes

by

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ABSTRACT

The parental feeding behavior and nest attentiveness of adult Yellow Warblers (*Dendroica petechia*) with broods of 3, 4 and 5 young were studied to determine differences in parental care provided to the young. The growth rate of the young and their size and condition near fledging were assessed to examine the effects of the parental investment provided.

When caring for 2-day-old young, parents increased their investment in larger broods through increasing their foraging rate (males) or increasing the quality of the items brought (both males and females).

Broods of five at 8 days of age were fed more, higher quality food items by females than were smaller broods. Broods of 4 were fed the most food by males, but of a lower quality than the food fed to broods of 3 or 5 young.

Adult Yellow Warblers selected some food items in larger proportions than were available.

Time spent brooding 2-day-old young decreased with an increase in brood size, although female parents were equally attentive at the nest. The attentiveness of female parents to 8-day-old young was related to foraging behavior. Females with broods of 5 brought more, higher quality items to their broods, so that less time was spent at the nest than by females with smaller broods.

Males feeding 2-day-old young fed the young more regularly in broods of 5 than broods of 4, so that fewer long periods (greater than 20 minutes) were observed between feedings. Broods of 3 were fed at an intermediate consistency. At 8 days of age, the evenness of the rate of feeding by male parents was no longer affected by brood size.

The growth rate and condition of the young near fledging were unaffected by brood size.

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INTRODUCTION

The effect of brood size on the nestling feeding rates of parents has been studied in many bird species (European Swifts *Apus apus*: Lack and Lack 1951; European Robins *Erithacus rubecula*; Lack and Silva 1949; 9 species of African birds: Moreau 1947; Eastern Kingbirds *Tyrannus tyrannus*: Morehouse and Brewer 1968; Eastern Bluebirds *Sialia sialis*: Pinkowski 1978; Great Tits *Parus major*: Royama 1966; House Sparrows *Passer domesticus*: Seel 1969; Silky Flycatchers *Phainopepla nitens*: Walsberg 1978). Other workers have examined the prey items brought by the parents but have not related their data to brood size (Piñon Jays *Gymnorhinus cyancephalus*: Bateman and Balda 1973; Yellow-headed Blackbirds *Xanthocephalus xanthocephalus*: Fautin 1941; Tits *Parus* spp.: Gibb and Betts 1963; Purple Martins *Progne subis*: Johnston 1967; Sparrowhawks *Accipiter nisus*: Newton 1978; Eastern Bluebirds: Pinkowski 1978; Great Tits: Royama 1966).

The effect of brood size on the growth rate of nestlings has also been studied in many species (House Martins *Delichon urbica*: Bryant 1978; European starlings *Sturnus vulgaris*: Crossner 1977; Red-winged Blackbirds *Agelaius phoeniceus*: Holcomb and Twiest 1970, 1971; Tits: Lack *et al*. 1957; European Robins: Lack and Silva 1949; House Sparrows: Schifferli 1978, Seel 1970). Other workers have reported growth rates without regard to brood size (Piñon Jays: Bateman and Balda 1973; Great Tits: Harvey *et al*. 1979; European Swifts: Lack and Lack 1951; Blue Tits *Parus caeruleus*, House Martins, House Sparrows: O'Connor 1975b; Tricolored Blackbirds *Agelaius tricolor*, Red-winged Blackbirds: Payne 1969; Eastern Bluebirds: Pinkowski 1975).

The effect of brood size on the feeding rate, prey taken and the growth rate of the young has apparently been determined only in two studies (Field Sparrows *Spizella pusilla*: Best 1977; Purple Martins: Walsh 1978).

The condition of young birds prior to fledging probably affects their survival (Crossner 1977). Body weight is usually correlated with condition, but a more precise method is to ascertain the body composition of the nestlings. This has been done for several species, but without regard to brood size (House Sparrows: Blem 1975; Long-billed Marsh Wrens *Telmatodytes palustris*: Kale 1965; Tricolored and Red-winged Blackbirds: Payne 1969; Barn Swallows *Hirundo rustica* and Red-winged Blackbirds: Ricklefs 1967).

The objective of this study is to determine the effect of brood size on the rate of feeding and the items brought by adult Yellow Warblers *Dendroica petechia* (L.) to nestlings and to relate these results to the growth rates and pre-fledging condition of the young in broods of 3, 4 and 5 young. Part I of this study is an examination of the parental feeding behavior and nest attentiveness of Yellow Warblers with broods of 2- and 8-day-old young. The growth rates of the young and their size and condition at 8 days of age are discussed in Part II.

PART I. PARENTAL CARE IN YELLOW WARBLERS

INTRODUCTION

Parents are classically assumed to allocate energy in such a way as to maximize the number of offspring surviving. It is presumed that natural selection, which operates ultimately through differential reproductive success, has shaped reproductive tactics so that observed reproductive strategies correspond to an optimum that maximizes an individual's lifetime reproductive success, as measured by the number of successful offspring produced by that individual (Williams 1966, Cody 1971, Hirshfield and Tinkle 1975, Stearns 1976, Barash 1977, Ricklefs 1977a, b).

Parental investment has been defined by Trivers (1972; p. 139) as "anything done by the parent for the offspring that increases the offspring's chance of survival while decreasing the parent's ability to invest in other offspring". Parental investment in birds can have many forms: egg-production, incubation and brooding (involving energy loss due to heat expenditure, decreased foraging time, increased susceptibility to predators), nest defense, nest attentiveness, nestling feeding, and nest-site choice (the choice often being a compromise between a site offering more predator protection and a site nearer to better foraging areas) (Trivers 1972, Ricklefs 1977a). Ricklefs (1974) showed that egg production, incubation and feeding the young involve large expenditures of energy, with the latter being the most demanding.

The reproductive strategy of any individual is therefore a balance between the benefits of reproductive effort expressed as increased fecundity, and the costs of reproductive effort in terms of a decreased probability of successful future reproductive attempts (Cody 1971, Wilson 1975). Thus, at any time the reproductive strategy displayed by any individual is a balance between the immediate prospects of reproductive success and the individual's long term future prospects.

A subject of debate has been the mode by which selection has influenced the amount of energy which a parent will invest at any time in a reproductive attempt. Trivers (1972, 1974) and Barash (1975) viewed the probable decision of the parent toward any act from the standpoint of cumulative investment. Previous investment commits one to future investment so that decisions are made to minimize the waste of parental investment. More recently, Dawkins and Carlisle (1976), Boucher (1977) and Maynard Smith (1977) have proposed that the parent's decision should maximize the expected benefits minus the expected costs. Previous investment is important only because of its effect on these expectations. An offspring or a reproductive attempt in which more has been invested is deserving of more present parental investment only because it is going to need less investment in the future (Dawkins and Carlisle 1976). This hypothesis has been supported by Robertson and Biermann (1979).

Overall, the effort required on a per nestling basis decreases with an increase in brood size since some activities, such as incubating and brooding, are required regardless of brood size. Thus, up to a point larger broods more closely maximize the difference between the expected benefit and the expected cost to parent birds in attempting to reproduce, so that more energy should be expended. When broods are too large, parents reach a maximum amount of time and energy that they can invest in reproduction, but it is insufficient to maintain the brood. Loss of some or all of the brood usually occurs (Crossner 1977).

The purpose of Part I of this study was to compare the parental investment, mainly in terms of feeding, given by adult Yellow Warblers Dendroica petechia to broods of 3, 4 and 5 young to determine variation in parental investment after hatching.

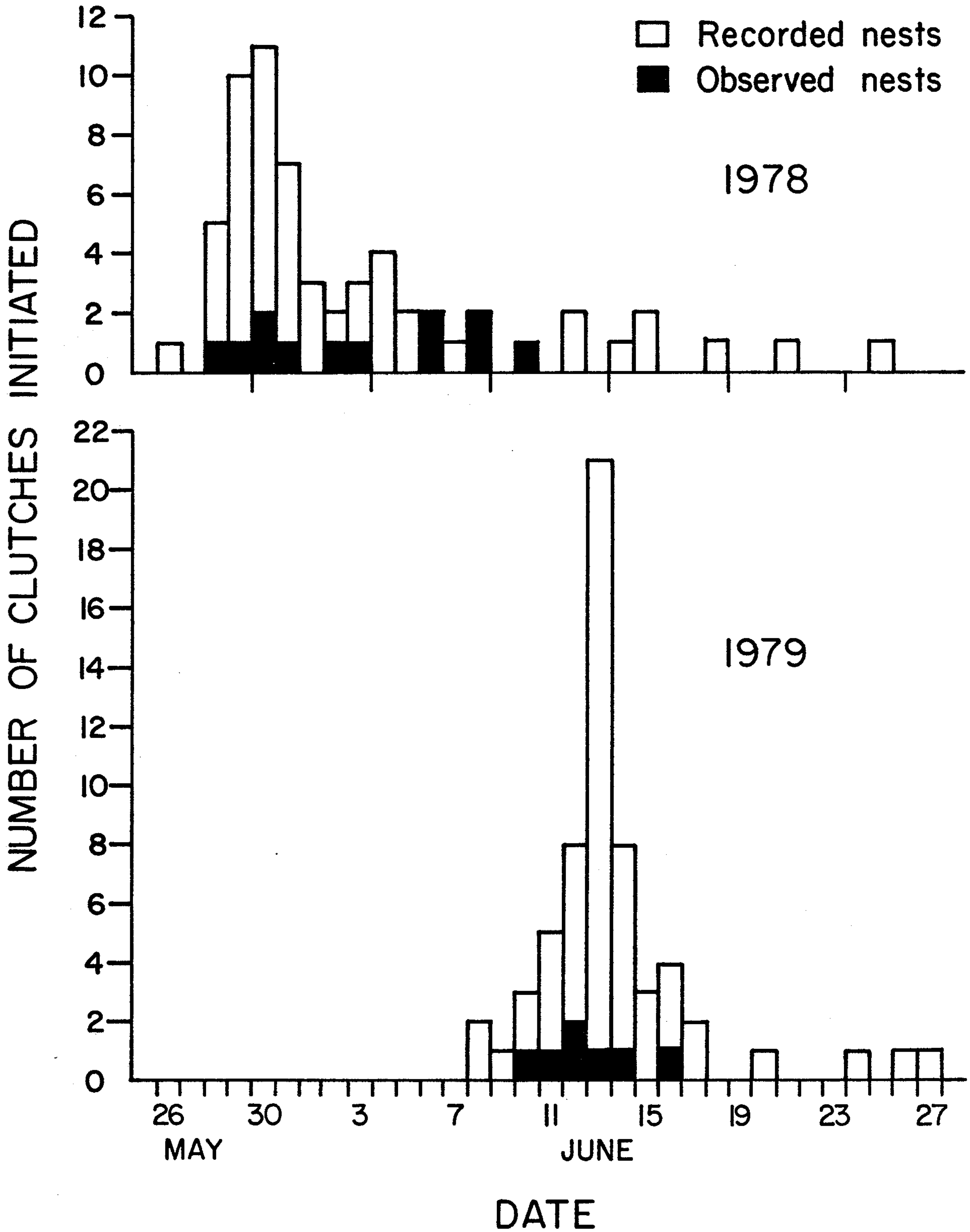
The Yellow Warbler on the Delta Beach Ridge

The Yellow Warbler (Aves: Parulidae) is sexually dichromatic in plumage coloration and pattern. The adult male is bright yellow, usually with prominent chest-nut colored streaks on the breast and abdomen, and the females are a relatively dull yellow, generally with unstreaked breasts (Busby 1978). This plumage dichromatism permitted the parent birds to be sexed when I was observing them at the nest.

Reproductive Biology

The first clutches were initiated on 26 May and 8 June in 1978 and 1979, respectively (Figure 1). In 1979, the late spring considerably decreased the span of time between first and last clutch initiation dates, compared to 1978.

Goossen (1978) comprehensively studied the reproductive biology of Yellow Warblers breeding at Delta. He found the mean clutch size to be 4.5 eggs (range: 3-5 eggs). Usually, one egg was laid per day until the clutch was completed. Only females incubated. The mean interval between laying of the last egg and hatching of the first young was 9.4 days (range: 8-11 days). The nestling period averaged 10.4 days (range 9-13 days) and was slightly longer in larger broods. The average number of fledged young per hatched nest was 2.3 and the average per successful nest(in which at least one young fledged)was 3.3.



Recorded nests
Observed nests
1978
1979
NUMBER OF CLUTCHES INITIATED
0
2
4
6
8
10
12
14
16
18
20
22
26
30
3
7
11
15
19
23
27
MAY
JUNE
DATE

The overall success of active nests (nests in which at least one Yellow Warbler egg was laid) was 47.9%. Predation caused most of the nest failures. Approximately 25% of the nests were parasitized by the Brown-headed Cowbird (Molothrus ater).

Yellow Warblers breed in high numbers on the study area. Between 19.1 and 29.6 pairs/hectare have been reported nesting here (see Goossen 1978 and Hochbaum 1971).

MATERIALS AND METHODS

Habitat

This study was conducted on a portion of the forested beach ridge that separates Lake Manitoba and the Delta Marsh, on the properties of the Portage Country Club and the University of Manitoba Field Station, about 5 km west of Delta, Manitoba ($50^{\circ}11'N$, $98^{\circ}19'W$). The tree vegetation has been described in detail by MacKenzie (1979).

Nest Observations

During the breeding seasons of 1978 and 1979, 139 active Yellow Warbler nests were located. At many of the nests (Table 1) adults were mist-netted and banded with numbered U.S. Fish and Wildlife Service bands in combination with celluloid colored bands to permit individual recognition from a blind. Most of the color-marked birds had been banded in the year observed, but 3 had been banded initially as juveniles the previous year. The age of the birds observed was usually unknown.

Nests were checked and their contents recorded every day during egg-laying and every 3-4 days thereafter. Brown-headed Cowbird eggs were usually removed after the completion of the clutch. Although frequent visits by an observer do not affect nesting success appreciably (see Nolan 1963), nest observations and weighing of young (see Part II) possibly did affect nesting

Table 1. Number of nests at which parental care was observed where the male and female Yellow Warblers were uniquely marked, aluminum banded only or unmarked.

Males \ Females	Colored	Aluminum	Unmarked
Colored	3	1	2
Aluminum	1	1	1
Unmarked	3	2	5

success somewhat. Thus, nest success amongst the Yellow Warblers studied was not determined. Such data are available from Goossen's (1978) detailed study of Yellow Warbler reproductive success on the study area.

Observations were made at 19 (Table 2) nests with broods of 3, 4 and 5 young on day 2 (young young, YY) and day 8 (old young, OY) after hatching of the first chick. Most of the nests observed were less than 2 m above the ground. Observations were made from a blind 1-2 m from the nest at 4 times of the day: 0630-0830 (early morning, EAM), 1000-1200 (late morning, LAM), 1530-1730 (early afternoon, EPM), and 1830-2030 (evening, LPM) (CDT). Wide angle binoculars (7x35 mm) aided observations. In 1978, these observations spanned 12 June to 1 July. In 1979, observations were made from 20 June to 19 July. Parental activities at or near the nest, the distance of the adults from the nest, and the number and identity of prey items fed to the young were recorded on a portable tape recorder and later transcribed. Large insect items that protruded from the parents' bills could be identified easily. Smaller items held entirely between the mandibles or nearly so, were often unidentifiable, so that the items observed being fed were biased toward larger prey. Items brought were identifiable in 864 of 1211 feeding trips observed.

Table 2. Number of nests observed of each brood size at each age.

Brood Size	Age: YY[1]	Age: OY
3	7	4
4	4	4
5	4	3

[1]YY (young young) refers to 2-day-old young, OY (old young) refers to 8-day-old young.

Stomach Contents

In 1979, twenty-seven 8-day-old nestlings were collected and alcohol was injected immediately into their esophagi. The stomach contents were removed within an hour and stored in 70% ethanol. Food items were identified later in the laboratory using a variable power microscope. Intact prey items were few in the samples, but head capsules, thoraxes, wings, occipital rings, and mandibles could be identified to order and often family. This method probably biases results toward insects with harder coverings. Soft parts are more rapidly digested and so do not remain in the stomach as long, so that soft-bodied arthropods such as Lepidoptera larvae may be under-represented by this method. The prey items observed being fed to the young were compared to the prey items in the stomach samples to assess the accuracy of the observations.

Prey Availability

The arthropod fauna of a 100-m portion of the study area was sampled using a standard insect sweep net, in the manner described by Busby and Sealy (1979). This method was found by them to yield representative samples when assessing the availability of arthropods to adult Yellow Warblers at Delta. The fauna was sampled in the morning and evening of every fifth day during the observation periods. The samples were sorted and identified to order or family and grouped into five categories to permit comparison with the prey being fed to young warblers. These groups were: Chironomidae and Culicidae (midges and mosquitoes), Geometridae larvae (inchworms), all other Lepidoptera larvae, all other Diptera, and all other insects (including all other arthropods).

Weight and Protein Composition of Major Food Items

The dry weights (to the nearest 0.1 mg) of the midges, mosquitoes and larvae were determined after being oven-dried at 60°C for one week. The two groups of larvae were then combined and the protein contents of the larvae and the chironomid and culicid samples were determined by the Manitoba Department of Agriculture.

Statistics

Statistical tests used include analysis of variance (ANOVA), chi-square, Student's t-test and Wilcoxon sign rank test. The level of significance used was $p \leq .05$.

RESULTS

Feeding Rates and Prey Items per Feeding Trip

The feeding rate (number of feeding trips per half hour) of males with both 2- and 8-day-old young (Table 3) was significantly affected by brood size, but not by the time of day. Broods of five 2-day-old young were fed more often by males than smaller broods. Males with 8-day-old young fed broods of 4 young more often than broods of 5 or 3.

The time of day and brood size did not significantly affect the feeding rate of females with 2-day-old young (Table 4). Brood size, but not the time of day, affected this rate amongst females feeding 8-day-old young. Broods of five 8-day-old young were fed more often than smaller broods.

The number of items brought per trip was constant throughout the day and did not vary amongst both males (Table 5) and females (Table 6) feeding different brood sizes of 2-day-old young. Both the time of day and brood size significantly affected the number of items brought per trip by male Yellow Warblers to 8-day-old young (Table 5) The largest loads were brought to broods of four 8-day-old young. Loads were generally largest in the early morning and smallest in the late afternoon.

Table 3. Feeding rate (Mean±SE, N in parentheses) per half hour of male Yellow Warblers with broods of 3, 4 and 5 young at 2 and 8 days of age.

	Brood size[2,3] and Age					
Time of Day[2,3]	3YY	4YY	5YY	3OY	4OY	5OY
EAM	1.7±0.5 (12)	2.3±0.5 (8)	3.0±0.6 (9)	3.5±0.7 (8)	4.9±1.0 (8)	4.3±0.9 (8)
LAM	1.7±0.4 (12)	2.3±0.6 (8)	2.4±0.4 (9)	3.9±1.1 (8)	5.1±1.1 (8)	5.0±0.4 (8)
EPM	2.2±0.4 (12)	2.4±0.1 (8)	2.8±0.5 (9)	3.4±1.3 (8)	7.1±1.1 (8)	3.9±0.5 (8)
LPM	2.1±0.4 (12)	3.5±0.6 (8)	4.1±0.6 (9)	4.4±0.9 (8)	3.6±0.6 (7)	3.6±0.2 (8)
ALL	1.9±0.2 (48)	2.6±0.2 (32)	3.1±0.3 (36)	3.8±0.5 (32)	5.2±0.5 (31)	4.2±0.3 (32)

[1]EAM, early morning; LAM, late morning; EPM, early afternoon; LPM, early evening.

[2]Two-way ANOVA of YY: brood size, $F(2,104) = 616$, $p < 0.005$; time of day, $F(3,104) = 2.47$, $p < 0.10$.

[3]Two-way ANOVA of OY: brood size, $F(2,83) = 2.939$, $p < 0.05$; time of day, $F(3,83) = 0.714$, $p > 0.10$.