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

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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 *Gymonorhinus 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.

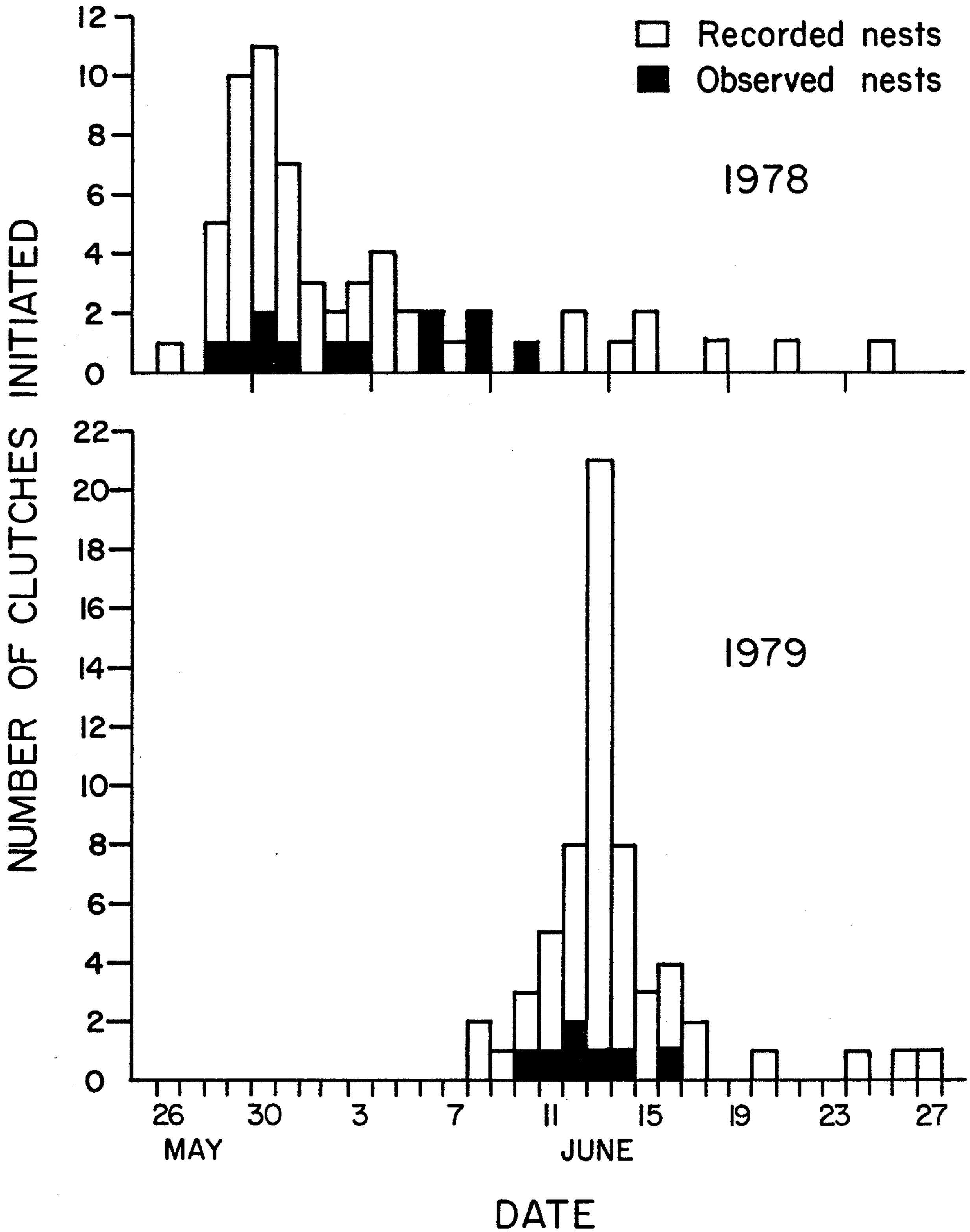
The Yellow Warbler on the Delta Beach Ridge

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°11'N, 98°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.

	Age	
Brood Size	YY[1]	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, $F(3,83) = 0.714$, $p > 0.10$.

Table 4. Feeding rate (Mean±SE) of female Yellow Warblers with broods of 3, 4 and 5 young at 2 and 8 days of age. Sample sizes are the same as in Table 3.

	Brood Size[1,2] and Age					
Time of Day[1,2]	3YY	4YY	5YY	3OY	4OY	5OY
EAM	0.8±0.4	1.3±0.4	1.1±0.7	3.4±0.8	3.4±0.6	5.6±0.7
LAM	1.2±0.5	1.4±0.3	1.2±0.7	3.0±1.1	3.0±0.9	3.3±1.0
EPM	0.4±0.2	1.6±0.7	0.4±0.2	4.5±0.5	3.0±1.1	7.1±0.8
LPM	1.6±0.5	2.3±0.5	0.8±0.4	2.6±0.6	1.3±0.3	6.3±1.2
ALL	1.0±0.2	1.6±0.2	0.9±0.3	3.4±0.2	2.7±0.4	5.6±1.2

[1]Two-way ANOVA of YY: brood size, $F(2,104) = 2.52$, $p < 0.10$; time of day, $F(3,104) = 1.40$, $p > 0.10$.

[2]Two way ANOVA of OY: brood size, $F(2,83) = 11.04$, $p < 0.001$; time of day, $F(3,83) = 2.30$, $p < 0.10$.

Table 5. Mean number (±SE, N in parentheses) of items brought per feeding trip by adult male Yellow Warblers at different times of day. Only feeding trips in which items could be counted are used.

	Brood Size[1,2] and Age					
Time of day[1,2]	3YY	4YY	5YY	3OY	4OY	5OY
EAM	1.1±0.1 (16)	1.3±0.1 (13)	1.1±0.1 (24)	2.3±0.3 (17)	2.8±0.3 (26)	1.7±0.2 (14)
LAM	1.4±0.1 (16)	1.1±0.1 (17)	1.2±0.1 (21)	2.2±0.2 (13)	2.9±0.3 (32)	1.5±0.1 (26)
EPM	1.1±0.1 (19)	1.3±0.1 (12)	1.4±0.1 (24)	1.9±0.2 (27)	2.1±0.2 (39)	1.5±0.2 (21)
LPM	1.2±0.1 (24)	1.3±0.1 (20)	1.3±0.1 (35)	1.5±0.1 (21)	3.0±0.3 (20)	1.5±0.1 (29)
ALL	1.2±0.1 (75)	1.3±0.1 (62)	1.2±0.1 (104)	1.9±0.1 (78)	2.6±0.1 (117)	1.5±0.1 (90)

[1]Two-way ANOVA of YY: brood size, $F(2,229) = 0.77$, $p > 0.10$; time of day, $F(3,229) = 0.76$, $p > 0.10$.

[2]Two-way ANOVA of OY: brood size, $F(2,273) = 30.04$, $p < 0.001$; time of day, $F(3,273) = 3.51$, $p < 0.025$.

Table 6. Mean number (±SE, N in parentheses) of prey items brought per feeding trip by adult female Yellow Warblers at different times of day. Only feeding trips in which items could be counted are used.

	Brood Size[1,2] and Age					
Time of day[1,2]	3YY	4YY	5YY	3OY	4OY	5OY
EAM	1.1±0.1 (7)	1.0±0 (6)	1.0±0 (6)	1.6±0.2 (14)	2.1±0.3 (18)	1.3±0.1 (37)
LAM	1.3±0.2 (11)	1.3±0.2 (10)	(1.0±0 (7)	1.5±0.2 (15)	2.6±0.4 (17)	1.2±0.1 (21)
EPM	1.2±0.2 (5)	1.3±0.2 (12)	1.0±0 (4)	1.6±0.1 (22)	2.1±0.4 (18)	1.1±0.1 (31)
LPM	1.0±0 (6)	1.0±0 (9)	1.0±0 (5)	1.5±0.2 (15)	1.8±0.4 (8)	1.2±0.1 (34)
TOTAL	1.2±0.1 (29)	1.2±0.1 (37)	1.0±0 (22)	1.5±0.1 (66)	2.2±0.2 (61)	1.2±0.1 (123)

[1]Two-way ANOVA of YY: brood size, $F(2,76) = 1.43$, $p > 0.10$; time of day, $F(3,76) = 1.50$, $p > 0.10$.

[2]Two-way ANOVA of OY: brood size, $F(2,238) = 25.91$, $p < 0.001$; time of day, $F(2,238) = 1.74$, $p > 0.10$.

Amongst females feeding 8-day-old young (Table 6) brood size significantly affected the number of items brought per trip, but the time of day did not. Broods of 4 at this age were fed the largest number of items per trip by females.

Table 7 shows the mean number of feeding trips per half hour, the mean number of items per trip and the mean number of items brought per half hour by adult Yellow Warblers to young in the three brood sizes at both ages. Males fed the 2-day-old young more often than females with all brood sizes (broods of 3: $t=8.54$, 94 df; broods of 4: $t=7.97$, 62 df; broods of 5: $t=22.95$, 70 df; $p < 0.01$ in all cases). Male and female parents feeding three 8-day-old young fed the young at equivalent rates ($t=0.68$, 62 df, $p > 0.05$), male parents with broods of four 8-day-old young fed the young more often than the female parents ($t=14.3$, 60 df, $p < 0.01$) and females with five 8-day-old young fed the young more often than their mates ($t=5.33$, 62 df, $p < 0.025$). Both sexes fed 8-day-old young more often than 2-day-old young.

Males with 5 young brought a larger food load per trip than females at both ages of nestlings studied (One-way ANOVA; yy: $F\ (1,124) = 5.39$, $p < 0.025$; OY: $F\ (1,211) = 10.3$, $p < 0.01$). No other significant differences between parents were observed. All parents except females with 5 young increased their load size when feeding older young.

Table 7. Feeding rates and food loads (Mean±SE) of Yellow Warblers parents.

Age and Number of Young	Trips/Half Hour		Items/Trip		Items/Half Hour[4]		
	Males	Females	Males	Females	Males	Females	Total
3YY (48)[1]	1.9±0.2 [2]	1.0±0.2	1.2±0.1	1.2±0.1	2.3±0.1	1.2±0.1	3.5
4YY (32)	2.6±0.2 [2]	1.6±0.2	1.3±0.1	1.2±0.1	3.4±0.1	1.9±0.1	5.3
5YY (36)	3.1±0.3 [3]	0.9±0.3	1.2±0.1 [3]	1.0±0	3.7±0.1	0.9±0.2	4.6
3OY (32)	3.8±0.5	3.4±0.2	1.9±0.1	1.5±0.1	7.2±0.2	5.1±0.1	12.3
4OY (31)	5.2±0.5 [2]	2.7±0.4	2.6±0.1	2.2±0.2	13.5±0.2	5.9±0.2	19.4
5OY (32)	4.2±0.3 [3]	5.6±0.5	1.5±0.1 [2]	1.2±0.1	6.3±0.1	6.7±0.1	13.0

[1]Number of half-hour observation periods in parentheses.

[2]$p < 0.01$ between males and females.

[3]$p < 0.025$ between males and females.

[4]Calculated by multiplying trips/half hour and items/trip. Not statistically analyzed.

When the young were 2 days old, more food items were brought by males than females. Overall, 2-day-old broods of 4 were fed more food items than broods of 5 or 3. When the young were 8 days old, more food items were brought by males to broods of 3 and 4 than by females, while the reverse was true for broods of 5. Overall, broods of 4 were fed more items than broods of 3 or 5 at this age.

Food Items Available and Used

Time of day did not affect the type of prey brought by the parents to the young at both ages (chi-square, $p > 0.05$ in 10 of the 12 cases), therefore observations from all time periods were combined. The number of insects in each group observed being fed by female parents to broods of 3, 4 and 5 young at both ages studied is presented in Table 8. At each age, significant differences in the proportion of each of the 5 insect groups in the diet were observed between brood sizes (YY: $X^2=30.6$, 8 df, $p < 0.005$; OY: $X^2=36.27$, 8 df, $p < 0.005$). At both ages, females with 5 young brought more geometrid larvae, while females with 4 young brought more chironomids and culicids. There were also significant differences in the proportion of items brought by females to broods of 8-day-old young compared to 2-day-old young (broods of 3: $X^2=4.2$, 4 df, ns; broods of 4: $X^2=29.9$, 4 df, $p < 0.005$; broods of 5: $X^2=38.1$, 4 df, $p < 0.005$. More chironomids and culicids and

Table 8. Number of insects in each group observed being fed by female Yellow Warblers to young in three brood sizes at 2 ages.

Insect Group	Brood Size and Age					
	3YY (48)[1]	4YY (52)	5YY (32)	3OY (108)	4OY (82)	5OY (178)
Chironomids and Culicids (I)	22 (67)[2]	26 (60)	1 (5)	68 (76)	117 (82)	95 (66)
Geometrid larvae (II)	8 (24)	15 (35)	18 (82)	10 (11)	6 (4)	34 (23)
Other larvae (III)	1 (3)	0 (0)	0 (0)	2 (2)	1 (1)	1 (1)
Other Diptera (IV)	1 (3)	1 (2)	3 (14)	5 (6)	5 (4)	0 (0)
All other insects (V)	1 (3)	1 (2)	0 (0)	5 (6)	13 (9)	15 (10)
Feeding Trips of Unidentified Prey	19	15	10	42	21	55

[1]Total number of feeding trips observed.

[2]Proportion of all observed prey items

fewer geometrid larvae are fed to the older young in broods of 4 and 5, but females feeding broods of 3 maintain a relatively constant diet throughout.

The number of insects in each group observed being fed by male parents (Table 9) was significantly different between brood sizes at each age (YY: X^2=20.47, 8 df, $p < 0.01$; OY: X^2=103.44, 8 df, $p < 0.005$). Again, broods of 4 were fed more chironomids and culicids, and fewer larvae than expected, while broods of 5 were fed more larvae and fewer chironomids and culicids. The proportion of items in each group brought by males also changed significantly as the nestlings grew older (broods of 3: X^2=34.3, 4 df, $p < 0.005$; broods of 4: X^2=130.5, 4 df, $p < 0.005$; broods of 5: X^2=30.3, 4 df, $p < 0.005$).

Intersexual differences in the proportions of items observed being fed were also significant, except between adults feeding broods of four 2-day-old young. (3YY: X^2= 12.69, 4 df, $p < 0.025$; 4YY: X^2=5.54, 4 df, ns; 5YY: X^2= 10.25, 4 df, $p < 0.05$; 3OY: X^2=13.72, 4 df, $p < 0.01$; 4OY: X^2=10.84, 4 df, $p < 0.05$; 5OY: X^2=11.24, 4 df, $p < 0.025$). Males generally brought a larger proportion of geometrid larvae than females. Females brought more chironomids and culicids.

The composition of the diet of nestlings determined through the observations of prey brought to the young was verified to an extent by the stomach content analyses.

Table 9. Number of insects in each group observed being fed by male Yellow Warblers to young in the three brood sizes at each age

Insect Group	Brood Size and Age					
	3YY (91)[1]	4YY (83)	5YY (111)	3OY (121)	4OY (159)	5OY (134)
I	28 (36)[2]	29 (40)	34 (25)	110 (68)	247 (78)	73 (56)
II	48 (61)	42 (58)	91 (66)	37 (23)	17 (5)	49 (37)
III	2 (3)	0 (0)	2 (1)	8 (5)	2 (1)	3 (2)
IV	0 (0)	1 (1)	5 (4)	1 (1)	1 (0)	1 (1)
V	0 (0)	1 (1)	5 (4)	6 (4)	51 (16)	5 (4)
Feeding trips of Unidentified Prey	16	21	7	43	42	44

[1]Total number of feeding trips observed

[2]Proportion of all observed prey items

Table 10 (see also Appendix I) is a list of the number of insects identified in each group from the nine nestlings collected from each brood size. These results are significantly different from observed proportions of items fed for each brood size, mainly due to differences in the number of insects in groups IV and V present. These insects were usually small, and may have been overlooked during field observations.

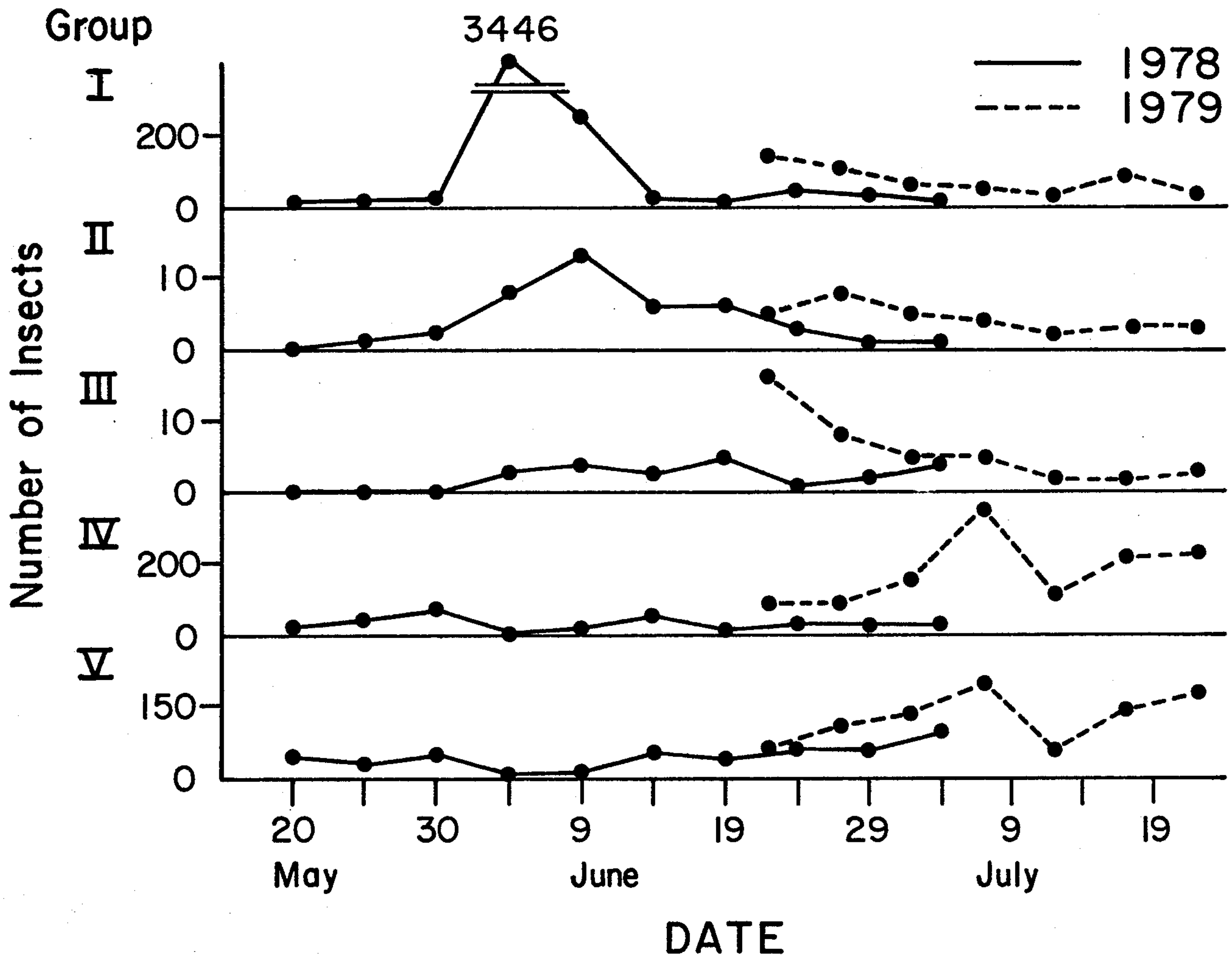
The items fed to the young in the 3 brood sizes were not significantly different (X^2=13.48, 8 df, $p > 0.05$) although they show a trend similar to that of observed feedings.

The number of insects in each of the five groups collected in the sweep net samples is shown in Figure 2. Although the total number of insects varies, the relative importance of each group remains fairly constant throughout the breeding season. Busby and Sealy (1979, Figure 4, p. 1675) present similar results for 1976. Chironomids and culicids (I) was consistently the most abundant group. Chironomids, however, were usually more abundant than culicids. Over 30 species of chironomids have been identified in the Delta Marsh and Lake Manitoba (Tudorancea 1974), each with its own non-random period of emergence (Oliver 1971), accounting for the nearly continuous presence of adult chironomids throughout the breeding season.

Table 10. Total number of insects in each group found in the nine stomachs of 8-day-old Warbler nestlings in each brood size.

Insect Group	Brood Size		
	3	4	5
I	76 (57)[1]	109 (73)	5 (58)
II	28 (21)	17 (11)	21 (17)
III	2 (2)	4 (3)	4 (3)
IV	14 (11)	5 (3)	10 (8)
V	13 (10)	15 (10)	16 (13)

[1]Proportion of all prey items


Group
3446
1978
1979
I
200
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II
10
0
III
10
0
IV
200
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V
150
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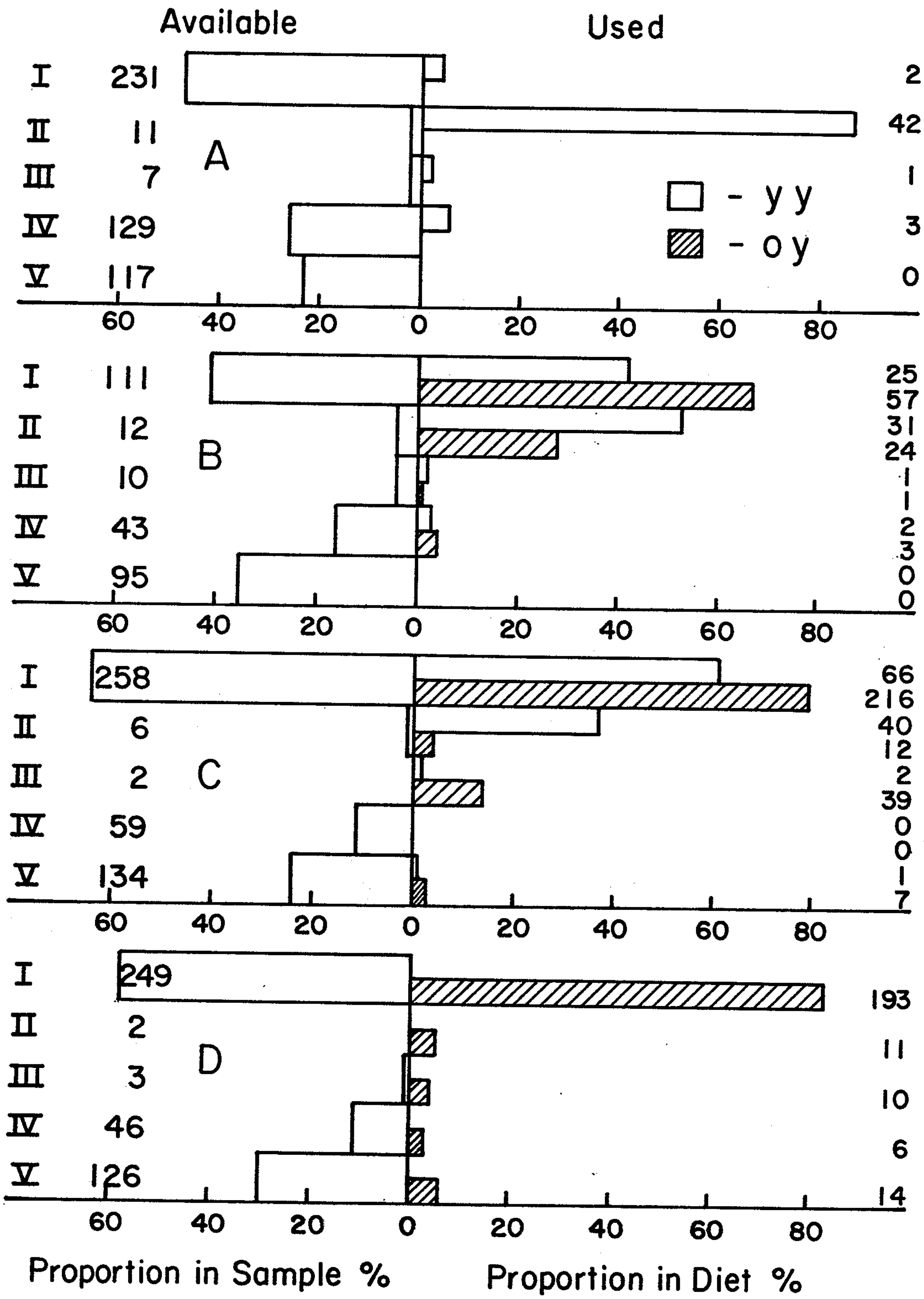
Number of Insects
20
May
30
9
June
19
29
9
July
19
DATE

The prey items fed by parents are compared, in Figures 3 and 4, to prey items available in each sampling period. The relative importance of each insect group is fairly constant. A Wilcoxon sign test was used to compare the proportion available of each group to the observed feeding proportion (by number) of that group and indicated that adult Yellow Warblers select geometrid larvae ($p = 0.0156$) and avoid feeding other larvae ($p = 0.0312$) and all other insects ($p = 0.0156$) when feeding 2-day-old young. Adults feeding 8-day-old young select chironomids and culicids ($p = 0.0078$), geometrid larvae ($p = 0.0078$) and other larvae ($p = 0.0625$), and avoid all other diptera ($p = 0.0156$) and all other insects ($p = 0.078$). Thus, adult Yellow Warblers select particular prey items to feed their nestlings.

Weight and Protein Content of Nestling Food

Items in groups II and III have on the average two and three times the dry weight of the chironomids and culicids (group I) (Table 11).

The weight of an "average" insect fed to a nestling was calculated for adult Yellow Warblers with each brood size at each age by multiplying the number of individual prey items of each group being fed (Tables 8 and 9) by the average weight of insects in that group (Table 11). The results were summed for groups I, II and III, and divided by the total number of insects in the three groups. This estimate, multiplied by the total number of insects brought per half



Available
Used
A
B
C
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□ - y y
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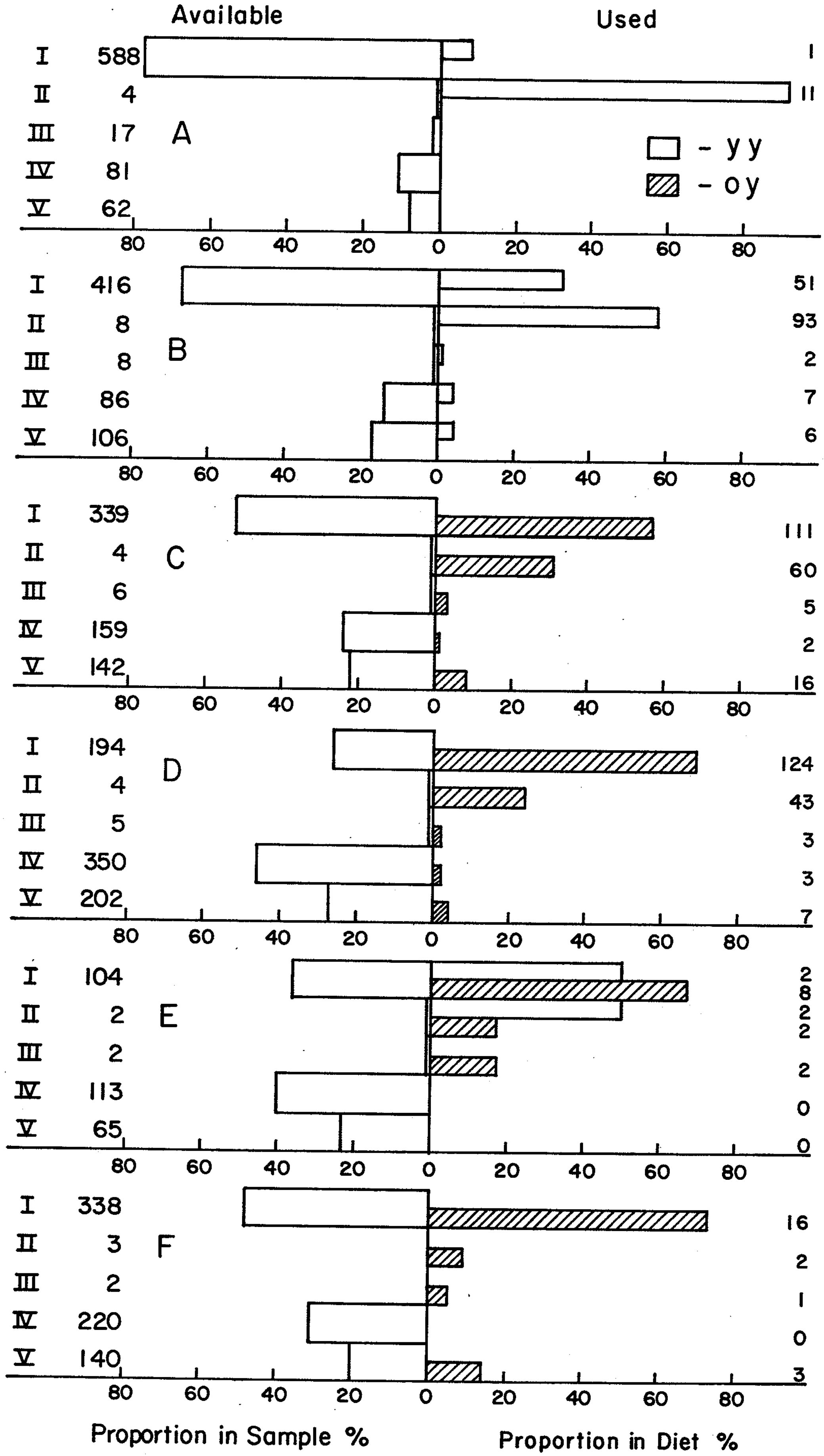
I 231
II 11
III 7
IV 129
V 117
2
42
1
3
0
I 111
II 12
III 10
IV 43
V 95
25
57
31
24
1
1
2
3
0
0
I 258
II 6
III 2
IV 59
V 134
66
216
40
12
2
39
0
0
1
7
I 249
II 2
III 3
IV 46
V 126
193
11
10
6
14
60 40 20 0 20 40 60 80
Proportion in Sample %
Proportion in Diet %


Available
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I 588
II 4
III 17
IV 81
V 62
I 416
II 8
III 8
IV 86
V 106
I 339
II 4
III 6
IV 159
V 142
I 194
II 4
III 5
IV 350
V 202
I 104
II 2
III 2
IV 113
V 65
I 338
II 3
III 2
IV 220
V 140
1
11
51
93
2
7
6
111
60
5
2
16
124
43
3
3
7
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8
2
2
2
0
0
16
2
1
0
3
80 60 40 20 0 20 40 60 80
Proportion in Sample %
Proportion in Diet %

hour (Table 7) yields an estimate of the average weight of food brought per half hour (see Table 12). Since the items observed being fed were biased toward larger prey, the true weight of food brought per half hour was probably smaller. However, since the number of feeding trips in which prey were unidentified was relatively constant (about one-quarter to one-third of the feeding trips, Tables 8 and 9), the values calculated are useful in comparing feeding rates.

Generally, males brought heavier prey items than females. Heavier items were brought to 2-day-old young than to 8-day-old young because a larger proportion of their diet was Lepidoptera larvae. Males feeding 2-day-old young brought more food to larger broods. Females fed 2-day-old young at a rate unrelated to brood size. Overall, larger broods were fed more food than smaller broods at 2 days of age. Females brought more food to larger broods when young in these broods were 8-days-old. Males did not. Overall, at 8 days, broods of 4 were fed more food than broods of 5 or 3.

Other factors apparently are also important. The fat, ash, protein, and water content of insects, as well as their digestibility, possibly affect the proportion of the dry weight that is usable by the nestling. The proportion of dry weight that is protein was determined for the chironomids and larvae (Table 13). Protein content is likely to be the

Table 11. Average dry weight (g) of insects in groups I, II and III.

Group	Number of Insects	Total Dry Weight	Average Weight
I	10,000	30.5446	0.0031
II	47	0.2836	0.0060
III	76	0.6475	0.0085

Table 12. Average dry weight (mg) of insects fed by parent Yellow Warblers to broods of 3, 4 and 5 young at 2 ages.

Brood Size and Age	Average Dry Weight of Average Insect Brought		Average Dry Weight of Food Brought per Half-Hour		
	Males	Females	Males	Females	Total
3YY	5.0	4.0	11.6	4.8	16.4
4YY	4.8	4.2	16.4	7.9	24.3
5YY	5.3	5.9	19.5	5.3	24.8
3OY	4.3	3.6	30.8	18.4	49.2
4OY	3.3	3.3	45.0	19.4	64.4
5OY	4.4	3.9	27.5	26.1	53.7

Table 13. Average protein content (mg) of insects in groups I, II and III.

Group	%Protein	Weight of Protein/Insect
I	59.8	1.9
II	62.6	3.8
III	62.6	5.3

most important component of a nestling's diet, since rapid body growth occurs during this stage of development (Kear 1972).

The average dry weights of the insects were multiplied by the proportion of the weight that is protein, to determine the amount of protein in the insects. The total weight of protein fed to the nestlings by parents at each age and in each brood size was determined using calculations described above (see Table 14). The difference in the total weight of protein brought to broods of 4 and 5 at 5 days of age is smaller than the difference in total dry weight brought to the broods, since the adults feeding broods of 5 fed a larger proportion of Lepidoptera larvae with a higher protein content than adults feeding broods of 4.

Nest Attentiveness of Females

Brood size, but not time of day, affected the total amount of time per half hour that female Yellow Warblers spent brooding 2-day-old young (Table 15). Females with smaller broods spent longer brooding the young than females with larger broods. Female parents with 2-day-old young were equally attentive at the nest and the time of day did not affect this attentiveness. Thus, of the total time spent at or near the nest, females with larger broods spent less timebrooding, and presumably were able to forage near the nest more.

Table 14. Protein content (mg) per average prey item fed to young Yellow Warblers and the protein (mg) fed per half-hour.

Brood Size and Age	Mean Dry Weight of Protein per Average Item		Average Dry Weight of Protein Brought per Half-Hour		
	Males	Females	Males	Females	Total
3YY	3.2	2.5	7.4	3.0	10.4
4YY	3.0	2.2	10.2	4.2	14.4
5YY	3.3	3.7	12.2	3.3	15.5
3OY	2.5	2.2	18.0	11.2	29.2
4OY	2.0	2.0	27.0	11.8	38.8
5OY	2.7	2.4	17.0	16.1	33.1

Table 15. Mean time (±SE, seconds) spent by female Yellow Warblers with 2-day-old young on, near, and away from the nest at four times of day

Distance from Nest	Time of day	Brood Size 3 (43)[1]	4 (31)	5 (36)
Brooding only[2]	EAM	1520±55	1327±75	1134±144
	LAM	1372±61	1515±47	1127±159
	EPM	1396±115	1317±111	1042±195
	LPM	1202±105	1049±132	1051±14
	ALL	1383±44	1310±54	1089±78
Brooding at nest and ≤1m from nest[3]	EAM	1638±31	1602±39	1474±111
	LAM	1579±43	1642±38	1493±90
	EPM	1617±48	1562±98	1610±102
	LPM	1480±84	1315±115	1483±103
	ALL	1583±26	1537±43	1515±50
> 1m but ≤6m[4]	EAM	33±18	11±11	146±90
	LAM	18±12	24±13	59±42
	EPM	0±0	0±0	6±4
	LPM	202±89	124±41	144±75
	ALL	56±22	37±13	89±31
> 6 m (usually out of sight)[5]	EAM	127±30	187±41	180±43
	LAM	203±45	134±37	248±75
	EPM	184±48	238±98	184±102
	LPM	112±31	361±122	173±60
	ALL	158±20	226±41	196±35

[1]Total number of observation periods.

[2]Two-way ANOVA: brood size, $F(2,98) = 7.005$, $p < 0.005$; time of day, $F(3,98) = 2.575$, $p < 0.10$.

[3]Two-way ANOVA: brood size, $F(2,98) = 0.893$, $p > 0.10$; time of day, $F(3,98) = 2.614$, $p < 0.10$.

[4]Two-way ANOVA: brood size, $F(2,98) = 1.229$, $p > 0.10$; time of day, $F(3,98) = 6.391$, $p < 0.001$.

[5]Two-way ANOVA: brood size, $F(2,98) = 1.170$, $p > 0.10$; time of day, $F(3,98) = 0.331$, $p > 0.10$.

The time of day, but not brood size, affected the time spent by females with 2-day-old young > 1 m but ≤ 6 m from the nest. The least amount of time was spent at this distance in the early afternoon time period. Neither the time of day nor brood size affected the time females spent > 6 m from the nest.

The length of a brooding bout increased as brood size increased (Table 16) although the difference is not significant, nor were there differences in the length of a bout due to the time of day. Since females with larger broods have longer brooding bouts, and thus longer periods of non-brooding, they potentially could be more selective of food items to bring to their young than females with smaller broods.

Amongst females attending 8-day-old young, the time of day did not significantly affect the total amouts of time spent at various distances from the nest (Table 17), but brood size did affect this time. Females with broods of 4 spent more time at the nest and less time out of sight than did females with broods of 3 and 5.

Regularity of Male Feedings

The time between feeding visits by males was examined to test the regularity of feeding by males. Five spans of time were chosen, and the results shown as the frequency of observation of each span of time (Table 18). Time of day did not affect the frequency distribution (chi-square)

Table 16. Mean length (±SE, sec.) of brooding period of female Yellow Warblers with 2-day-old broods.

Time of Day[2]	Brood Size[2] 3	4	5
EAM	406±67 (44)[1]	319±51 (33)	464±91 (21)
LAM	318±38 (48)	336±94 (35)	502±80 (20)
EPM	382±60 (33)	411±114 (24)	358±207 (26)
LPM	222±34 (47)	263±39 (25)	589±163 (14)
ALL	326±25 (172)	331±40 (117)	461±78 (81)

[1]Number of brooding bouts in parentheses

[2]Two-way ANOVA: brood size, $F(2,358) = 2.561$, $p < 0.10$; time of day, $F(3,358) = 0.770$, $p > 0.10$.

Table 17. Mean time (±SE, seconds) spent by female Yellow Warblers with 8-day-old young at, near and away from the nest at four times of day.

Distance From Nest	Time of Day	Brood Size 3 (32)[1]	4 (31)	5 (32)
Near or at nest[2]	EAM	589±203	811±172	747±106
	LAM	715±189	806±248	456±90
	EPM	579±91	1387±152	456±81
	LPM	879±122	1134±275	569±123
	ALL	691±78	1030±111	557±50
$>$1m but $\leq$ 6m[3]	EAM	546±253	88±58	139±77
	LAM	570±206	196±82	324±214
	EPM	163±105	19±19	216±82
	LPM	277±126	6±6	126±61
	ALL	389±92	80±29	201±63
$>$6m[4]	EAM	666±247	901±209	914±93
	LAM	513±132	803±215	1019±164
	EPM	1058±85	394±152	1028±116
	LPM	643±135	600±276	1106±135
	ALL	720±85	690±107	1042±63

[1]Total number of observation periods.

[2]Two-way ANOVA: brood size, $F(2,83) = 8.877$, $p < 0.001$; time of day, $F(3,83) = 0.847$, $p > 0.10$.

[3]Two-way ANOVA: brood size, $F(2,83) = 5.407$, $p < 0.01$; time of day, $F(3,83) = 1.998$, $p > 0.10$.

[4]Two-way ANOVA: brood size, $F(2.83) = 5.250$, $p < 0.01$; time of day, $F(3,83) = 0.121$, $p > 0.10$.

Table 18. Frequency of observation of the time periods between consecutive feedings by male Yellow Warblers.

Time of Feedings	Brood Size[1] and Age					
	3YY	4YY	5YY	3OY	4OY	5OY
≤ 2 minutes	9	6	22	16	26	14
≤ 5 minutes	31	17	43	49	66	45
≤10 minutes	28	32	58	36	42	42
≤20 minutes	28	10	20	16	16	22
>20 minutes	11	12	4	6	1	3

[1]Between brood sizes; YY, $X^2 = 27.48$, 8df, $p < 0.05$; OY, $X^2 = 11.86$, 8df, $p > 0.10$.

so results from all times of day were grouped together. Amongst males feeding 2-day-old young, significant differences were observed. Males with 4 young had more long periods ($>$ 20 minutes) between feedings and males with with 5 young had fewer long periods between feedings. Thus, broods of 5 were fed the most regularly by males. There were no significant differences amongst males feeding 8-day-old young.

DISCUSSION

Feeding Rates and Food Loads

Time of Day

Time of day did not usually affect the feeding rate and load size of adult Yellow Warblers feeding their young. Daily variation in the rate adult birds feed their young has been described for many species. Usually, most feeding occurs in the early morning, just after dawn, and at dusk. At mid-day or mid-afternoon, feeding rates are the lowest (Best 1977, Nolan 1978, Pinkowski 1978). These variations are usually due to differences in the activities of the prey species. Many insects are most active in the coolest part of the day, and the diet of some bird species may vary with time of day as well (Walsh 1978). However, in the present study early morning sampling was not done just after dawn, nor was evening sampling done just before sunset. The lack of dietary variation during the day indicates that insect activites were not greatly affecting the foraging success of the birds.

Brood Size and Age

Generally, the adult feeding rate increases with an increase in brood size (Moreau 1947, Lack and Silva 1949, Lack and Lack 1951, Royama 1966, Morehouse and Brewer 1968, Hussell 1972, Best 1977, Walsh 1978). At 8 days of age, the feeding rate of adult Yellow Warblers was greatest in the largest brood size. However, food loads were not the largest (Table 7). At 2 days of age, feeding rate and food load size were greatest for broods of 4.

Other researchers have found no differences in feeding rate with brood size. Pinkowski (1978) found no positive relation between feeding rate and brood size by either male or female Eastern Bluebirds. Seel (1969) found that while the average rate of visiting increased with brood size, there was no significant difference between the rates for broods of 3, 4 and 5 young House Sparrows.

On average, nestlings in larger broods receive fewer feedings per nestling. Royama (1966) suggested that a larger brood size reduces heat loss per nestling, requiring a smaller amount of heat production per nestling because of a more favorable surface/volume ratio. Mertens (1969) and O'Connor (1975a) have confirmed this theory. Dunn (1976) has shown that larger broods are also able to thermoregulate effectively at an earlier age than smaller broods.

Feeding rates have been shown in this study and others to increase as the nestlings get older (Royama 1966, Seel 1969, Gibb and Betts 1970, Nolan 1978, Pinkowski 1978, Walsh 1978). However, males of some species decrease their feeding efforts late in the nesting period. Pinkowski (1978) found that male Eastern Bluebirds often began a second nesting with other females soon after their first brood fledged and before the young were independent. Seel (1969) noticed a decrease in the rate of feeding by male House Sparrows late in the nestling period, and an increase in courtship displaying. This behavior occurred independent of brood size, and therefore could not have been caused by fatigue. In the present study, male Yellow Warblers feeding broods of 5 brought fewer and smaller loads than males with broods of 4 to 8-day-old nestlings. Since the males with broods of 5 fed the young more when they were younger and the females were brooding, they may have become fatigued.

The relative role of males and females in feeding the young varies amongst species. Nolan (1978) found that female Prairie Warblers (Dendroica discolor) assume a slightly larger proportion of the feeding duties. In Field Sparrows, Best (1977) found that this duty is shared nearly equally. On the Delta Beach Ridge, male Yellow Warblers generally assume a greater proportion of the feeding duties.

Males also brought heavier (larger) items to the nest than females. Royama (1966), Morehouse and Brewer (1968) and Gibb and Betts (1970) found that as the feeding rate decreased, the size of items brought increased. Nolan (1978) found that adult Prairie Warblers, in which the young are fed more often by females, brought similar sized food items. As the young grew older, both the feeding rate and the size of items fed increased. Thus, he found no inverse correlation between feeding rate and the size of items fed. Among Yellow Warblers, heavier items were brought by the sex that feeds the young the most often. Within a sex, however, the inverse relation between feeding rate and food size held.

Diet of Nestlings

Busby and Sealy (1979) found the diet of adult Yellow Warblers at Delta was composed mainly of Diptera, particularly chironomids. Studies of the diet of adult Yellow Warblers in other areas have found Lepidoptera larvae, Homoptera and Coleoptera, or Hymenoptera to be the major component of the diet. Adult Yellow Warblers are apparently flexible in their choice of food, and forage opportunistically (Busby and Sealy 1979).

Adult chironomids and culicids, and larval geometrids were the major components of the diet of nestling Yellow Warblers. The proportion of these items in the diet changed with their age. Two-day-old young were fed more geometrid larvae than were eight-day-old nestlings, with corresponding changes in the proportion of chironomids and culicids. Stomach analyses confirmed, to an extent, feeding observations and indicated that chironomids, not culicids, were the most important insect in group I.

Diet and Prey Availability

Generally, adult Yellow Warblers did not feed their nestlings prey in proportion to its availability. They were selective. At both nestling ages, parents fed geometrid larvae in larger proportions than were available. Other studies of passerine nestling feeding have found Lepidoptera larvae to be important components of the diet (Best 1977, Pinkowski 1978). All other larvae and all other insects were under-represented in the diet of 2-day-old nestlings, compared to what was available. When 2-day-old young were fed a geometrid larva, the parents often passed it back and forth between themselves and pulled on it, breaking it into smaller, more manageable pieces that were then fed to the nestlings. Attempts to feed the larva whole to the nestling usually failed. Since other larvae were usually wider and heavier than geometrid larvae (Table 11), they would have required even more processing by the parents before they could be fed to the young. Probably, more effort is required than is practical. Best (1977) found that girth rather than length limited the size of food that young Field Sparrows could ingest. Several studies have shown that the size of food items increases with nestling age, suggesting that the relative size of the nestlings and the food may be important (Gibb and Betts 1970, Best 1977, Nolan 1978, Pinkowski 1978, Walsh 1978). All other insects collected in the insect samples included many hard bodied insects such as Coleoptera, Hymenoptera, and Hemiptera, all of which may have been unsuitable food for young birds.

Chironomids and culicids and all other larvae were selected preferentially for 8 day old young, as well as geometrid larvae. At 8 days of age, the nestlings are nearly adult size, and can swallow larger larvae whole. Chironomids and culicids have soft abdomens that are easily digested and since they are lethargic (Busby 1978) several can be brought to the nest in one foraging trip. However, part of the body is enclosed in a chitinous exoskeleton that is less easily digested than soft bodied insects (Borror et al. 1976). Other Diptera and all other insects were under-represented in the diet, probably because of the large amount of exoskeleton surrounding them, and also because of the observation technique used, as previously discussed.

Given the generalist foraging behavior of adults, the selectivity displayed in obtaining food items for nestlings implies that nestlings may have different food requirements than adults. Growing birds presumably require protein-rich diets, and may need less carbohydrates than active adults (Kear 1972).

Larvae were the favored food items for the nestlings, especially for the 2-day-old young. They are completely soft-bodied, so that the entire insect is easily digested. All the other insects fed were at least partly enclosed in a hard exoskeleton composed of chitin, a nitrogenous polysaccharide $(C_8 H_{13} NO_3)_n$. This substance is very resistant and is insoluble in water, alcohol, dilute acid and alkalis (Borror et al. 1976). The extent of the occurrence of a gastric chitinolytic system in birds is unknown (see Jeauniaux 1961) but it has not been found in all of the few species studied (Ziswiler and Farner 1972), nor has the age been established at which an effective system is present in a developing bird. However, it is reasonable to assume that not all of the protein of a hard-bodied insect is digestible. Thus the difference in the total digestible protein brought per half hour to broods of 4 and 5 8-day-old young is probably smaller than the difference between the values calculated in Table 14.

Since growth rate and the condition of the young were not affected by brood size (Part II), the food brought by parents with 4 young may have been of lower quality, since it was heavier.

Nest Attentiveness, Brooding and Prey Selection

The time spent by a parent at the nest brooding or attending the young will affect its feeding rate and prey selection. The more time it must devote to other parental duties, the less time it has available for feeding the young. This is reflected in the nest attentiveness and brooding times of female Yellow Warblers.

Consistent with Royama's theory that brood size and cooling rate are inversely related, female Yellow Warblers brooded smaller broods of 2-day-old young the most. Walsh (1978) also found that brooding time decreased with increasing brood size in Purple Martins. All females, however, spent most of their time at the nest. Few feedings of the young by the females were observed.

At 8 days of age, the young were better able to thermoregulate, and brooding by the females was not observed. Thus, the females were able to spend more time foraging. Females with broods of 5 young spent the most time away from the nest and also fed the young the most food. Females with 3 and 4 young were out of my sight for nearly equivalent amounts of time. Females with 4 young brought many low quality items, while females with 3 young brought fewer items, but of a higher quality. Thus, while spending similar amounts of time foraging, the females had different foraging strategies.

Male Yellow Warblers attending 2-day-old young were more consistent in feeding broods of 5 young than broods of 4 or 3. At 8 days, no difference in the regularity of feeding was detected between males caring for young in different brood sizes. Thus, prey selectivity was only reflected in male regularity of attendance when the young were 2-days-old.

Parental Investment in Yellow Warblers

The rate of feeding increased with age by parents caring for all brood sizes. Since feeding the young is the most energetically demanding form of parental investment after hatching (Ricklefs 1974), parents increase their investment as the likelihood of reproductive success increases in their present nesting attempt.

At both brood ages studied, female Yellow Warblers invested proportionally in their brood sizes. When the young were 2-days-old, females with 5 young were most selective of the items fed to the young, although the feeding rates were similar amongst the females. With 8 day old broods, females with 5 young brought more, higher quality items to the young than females with smaller broods.

Males with 2-day-old young brought more, higher quality items to broods of 5 young than to broods of 4 or 3. Their feedings were also most evenly spaced at that age, so that the efficiency of food use for the young was probably maximal. Thus, with the 2 day old broods, males apparently increased investment with an increase in brood size. When the young were 8-days-old, males brought more items, of a lower quality, to broods of 4 than 5. The total weight of food brought was largest for broods of 4. However, the relative amount of energy expended to procure the food is the most relevant factor in determining parental investment. Whether it is more energetically demanding to obtain many readily available insects or to obtain fewer, scarcer, higher quality insects is debatable.

PART II.

THE EFFECT OF BROOD SIZE ON THE GROWTH RATE AND CONDITION OF NESTLING YELLOW WARBLERS

INTRODUCTION

The rate of development of altricial birds limits the number of broods that may be produced during the breeding season. Growth, usually measured as an increase in body weight, requires energy that must be budgeted for by the parents. Changes in the growth rate may alter the number of offspring that are raised, and thus affect the fitness of a genotype. Therefore, developmental rate must be influenced by natural selection (Ricklefs 1969, O'Connor 1977). With selection operating through nestling mortality and sibling competition, the growth rates of altricial birds are believed to be the maximum physiologically attainable (Ricklefs 1969, 1973, Werschkul and Jackson 1979).

In species in which adult non-breeding mortality is higher, as has been found in most temperate song birds studied, brood size should be the maximum number that adults can successfully raise, since there is a low probability of future reproductive success (Ricklefs 1977b). There is a potential for an effect of brood size on growth and survival if the adult birds reach an upper limit of feeding rates. Slower growth rates amongst young in larger broods may decrease success by increasing the length of the nestling period and thus the time the young are exposed to predators (Ricklefs 1968b). Alternatively, young may grow at a similar rate, but fledge at a lower weight. Studies by Jarvis (1974), Perrins (1965) and others have suggested that the probability of post-fledging survival is strongly correlated with fledging weight, probably because of the need for independent young to use stored energy during a period of learning to forage for themselves (Crossner 1977). Thus, slower growth rates and lower fledging weights can be detrimental to the young.

Ricklefs (1968b) pointed out that the rates of many developmental processes are closely linked to each other, but largely independent of the nutritional state of the young. Thus, while it is desirable to compare growth rates amongst young in different brood sizes, the condition of the young should also be assessed. This can be done by measuring the proportions of lipid, protein, water and ash in nestlings of the same age, since the relative proportions change during development (see Ricklefs 1967, 1968a, Dunn 1975, Clay *et al.* 1979).

The purpose of Part II of this study was to compare growth rates of Yellow Warblers (*Dendroica petechia*) in broods of 3, 4 and 5 young, and to assess the size and condition of the young just prior to fledging.

METHODS

Growth Rate

Yellow Warbler nestlings in randomly chosen nests were weighed to the nearest 0.1 g between 2030 and 2130 hours (CDT) on a triple beam balance. Nestlings could be weighed until day 6 post-hatching, after which they jumped out of the nest following handling.

Body Components and Measurements

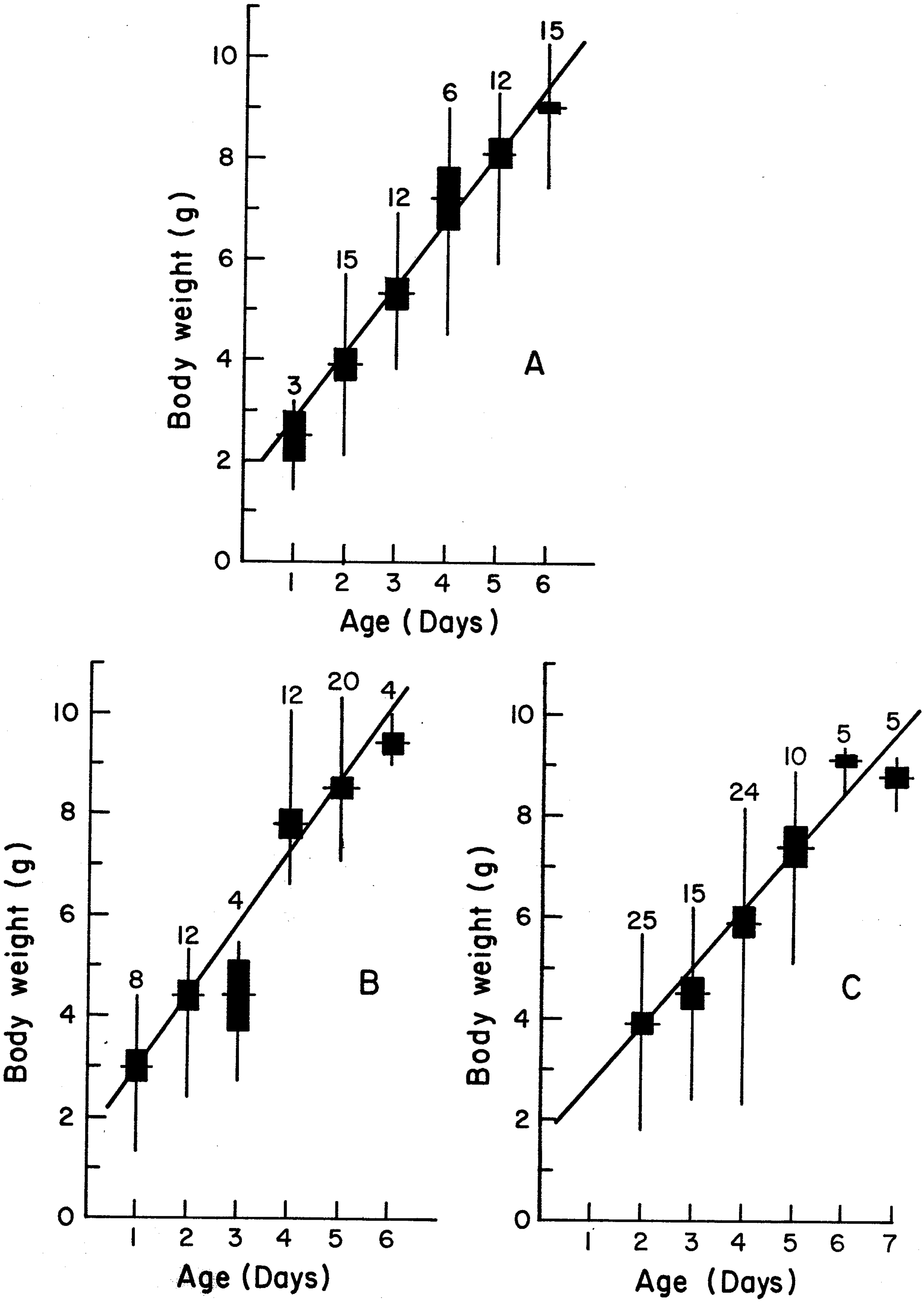
In early July, 1979, 27 eight-day-old nestlings were collected from 9 nests between 1300 and 1400 hours. Three young in 3 broods of 3, 4 and 5 young were taken. The largest three young in the broods of 4 and 5 were selected. After the stomach contents were removed (see Part I), the young were weighed on a Sartorious balance to the nearest 0.1 mg. Measurements, including tarsus length, exposed culmen length, bill height, bill width at commissure, wing chord and total body length (tip of tail to tip of beak) were made with calipers (to nearest 0.1 mm) or a ruler (to nearest 1 mm). The intestines were then removed, stored in 70% alcohol and examined later under a dissecting microscope for the presence of parasites. No parasites were found. The young were then re-weighed, oven dried at 60^{o} for 10 days to constant weight, and stored frozen for several months. The difference in weight before and after drying (wet weight minus dry weight) is the water content. The birds were then re-weighed, and the lipid extracted for 16 hours in petroleum ether (30-60°C) and soaked for 12 hours overnight in the middle of the extraction. The carcasses were re-dried for 8 hours and re-weighed. The difference in weight before and after extraction (dry weight minus lean dry weight) is the lipid content. Later, they were combusted in a muffle furnace at 550°C for 4 hours to determine ash content. Lean dry weight minus ash content estimates the protein content of the nestlings (see Ricklefs 1967).

RESULTS

Growth Rates

Since broods of 3, 4 and 5 young are fed different proportions of food items at different rates on a per nestling basis, these differences might be expected to affect the growth rates of the young. Figure 1 shows the growth rate, measured as change in body weight, of nestlings in broods of 3, 4 and 5 young. There is evidently variation amongst the weights of the nestlings in each brood size at each age, due to both inter- and intra-brood differences. Since the same nestlings were not weighed every day, and the weights shown are means of all nestlings weighed, the curves do not conform exactly in shape to standard growth curves. At only two ages (day 4 and day 5) were there significant differences in the weights of the nestlings (Table 1). In both cases, young in broods of 4 were heavier than young in broods of 3, and young in broods of 5 were the lightest By day 6, the young in all brood sizes were similar in weight again.

The overall growth rates of young in the three brood sizes can be compared using the regression equations provided in Figure 1. A test for the equality of slopes (Sokal and Rohlf 1969) showed no significant difference in the growth rate of the young in the three brood sizes. (One-way ANOVA: $F(2,10) = 1.62$, $p > 0.05$). However, young in broods of 5 apparently grew more slowly (1.12 g/day) than young in broods of 4 (1.39 g/day) or 3 (1.31 g/day).



A
Body weight (g)
0
2
4
6
8
10
Age (Days)
1
2
3
4
5
6
3
15
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B
Body weight (g)
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2
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Age (Days)
1
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C
Body weight (g)
0
2
4
6
8
10
Age (Days)
1
2
3
4
5
6
7
25
15
24
10
5
5

Table 1. Results of one-way ANOVAs between the weights of the young in the 3 brood sizes studied at each age

Age (days)	F	df	p
1	0.698	1,9	ns
2	0.795	2,49	ns
3	1.519	2,28	ns
4	7.82	2,39	$<.01$
5	3.65	2,39	$<.05$
6	1.087	2,21	ns

Size Variation

Body weights are often used to indicate size. However, differences in weight are not always true indicators of size, since weight may fluctuate greatly over short periods. Thus, body measurements are also important in determining size differences.

Body weights and the measurements of tarsus, culmen, wing cord, bill and body length of the 27 collected nestlings are shown in Table 2. There were no significant differences between brood sizes in any measurement (One-way ANOVA), nor was one brood size consistently larger or smaller. Thus, the three largest nestlings in each brood size are apparently of similar size at 8 days of age.

Body Components

Differences in growth may be reflected in differences in gross weight, and also in the relative proportions of the basic body consituents: water, protein, lipid and ash. Differences in the constituents reflect differences in the energy content per gram body weight (Ricklefs 1967).

The weight of water, lipid, ash, and protein in each nestling collected in presented in Appendix II. No significant differences in body components were found between young in the three brood sizes except in ash content (One-way ANOVA: water, $F(2,24) = 0.12$, ns; lipid, $F(2,24) = 0.055$, ns;

Table 2. Weights and measurements (Mean±SE) of collected 8-day-old nestlings in different brood sizes. Degrees of freedom for all ANOVAs are (2,24). No tests were significant.

	Brood Size			
	3	4	5	F
Wet Weight (g)	8.1±0.4	8.0±0.2	7.7±0.1	.623
Dry Weight (g)	2.4±0.1	2.4±0.1	2.3±0.1	.388
Tarsus Length (mm)	18.0±0.4	18.6±0.2	18.5±0.3	1.280
Culmen Length (mm)	8.5±0.3	9.0±0.2	8.8±0.1	1.409
Bill Width (mm)	8.7±0.2	8.9±0.1	8.5±0.2	1.474
Bill Height (mm)	3.0±0.1	3.0±0.1	3.1±0.1	.750
Wing Chord (mm)	36±1	35±1	35±1	.506
Body Length (mm)	67±2	65±1	67±1	.643

ash, $F(2,24) = 5.983$, $p < 0.01$; protein: $F(2,24) = 0.537$, ns). Ash content was greatest in young in broods of 3, and smallest in young in broods of 5. Most commonly, indices of these components are used, which compare the weight of each component to the lean dry weight (Ricklefs 1967). For example, the lipid index is calculated as the weight of lipid extracted divided by the lean dry weight of the bird. Table 3 shows the mean indices of water, lipid, protein and ash of the birds collected from each brood size. Also shown is the mean energy content of the nestlings. This is calculated from the data on the lipid and protein content using thermal equivalents given by King and Farner (1961). One gram of protein and one gram of lipid are equal to 4.2 and 9.5 Kcals of metabolizable energy, respectively. The differences between nestlings in the three brood sizes are not significant. The values are similar to those found by Ricklefs (1967) for nestling Barn Swallows (<u>Hirundo rustica</u>) and Red-winged Blackbirds (<u>Agelaius phoeniceus</u>) at similar stages of development. The stages of development, rather than the absolute age, is important, since the energy index increases during development as a result of decreased water content and an increase in lipid reserves (Ricklefs 1967, 1968a).

Table 3. Indices of major body components (Mean±SE) and energy in nestling Yellow Warblers in different brood sizes.

Index (g/g lean dry weight)	Brood Size 3	Brood Size 4	Brood Size 5
Water	3.07±0.06	3.03±0.06	3.15±0.08
Lipid	0.239±0.042	0.255±0.025	0.275±0.027
Protein	0.880±0.004	0.885±0.002	0.891±0.003
Ash	0.120±0.004	0.115±0.002	0.109±0.003
Energy (Kcal/g)	1.38±0.09	1.44±0.06	1.46±0.06

DISCUSSION

Growth Rates

Brood size apparently does not affect the growth rate of Yellow Warblers. Although there were significant differences in weight at days 4 and 5, by 6 and 8 days of age body weights were essentially the same amongst nestlings in the three brood sizes studied. Nearly equivalent ages of fledging (10.4, 10.5 and 10.6 days for broods of 3, 4 and 5 young, respectively) (Goossen 1978) are an indication that growth rate was not slower in larger broods.

Other studies have also shown that growth rate is not affected by differences in the natural brood size. Best (1977) found no difference in the growth rate of the tarsus in broods of 3 and 4 Field Sparrows (*Spizella pusilla*). Growth, measured by weight, was not affected by brood size in late summer, although in early summer broods of 4 grew faster than broods of 3. Crossner (1977) found little difference in the growth rates of Common Starlings (*Sturnus vulgaris*) in broods of 1 to 6 young, while artificially larger broods grew progressively more slowly. The maximum weight attained followed a similar pattern. Lack and Silva (1949) found no effect of brood size on the weight of European Robins (*Erithacus rubecula*). Royama (1966) found no difference in the size of Great Tits (*Parus major*) at

13 days of age, except in the largest broods, where each young was lighter. Lack (1956) reported that brood size did not affect the weight of young swifts (Apus apus), except in poor summers.

Conversely, some studies have shown an inverse relation between brood size and weight in passerines. Bryant (1978) found that larger broods had a retarded growth rate in House Martins (Delichon urbica). Similar results have been found in nestling Great Tits and Blue Tits (Parus caeruleus) (Gibb 1950, Lack et al. 1957, Perrins 1965). Seel (1970) found that nestling weight decreased with increased brood size in House Sparrows (Passer domesticus), but in European Tree Sparrows (P. montanus) there was no change with brood size. He attributed the difference to differences in food available to the two species. Anderson (1977) studied these two species under conditions of superabundant food and found that fledging weight increased for both species when compared to young raised under "normal" conditions. This supports Seel's suggestion.

The effect of food supply on the clutch size and growth rates of passerines has been examined by O'Connor (1977). When the food supply is both predictable at egg-laying and stable during the nestling period, the number of eggs laid should correspond to the number of young the parents can raise (O'Connor's clutch size adjustment strategy). Because the parents can successfully raise all the young, he predicts that there should be less sibling competition than under other circumstances, and differences among the young within a brood should be minimized. The effects of order of hatching and hatching asynchrony should be slight and growth rate may be moderate rather than the maximum attainable. Since clutch sizes must be increased or decreased by an integral number of eggs, while the available food level is a continuously distributed variable, in any environment the prevailing food levels may correspond to a fractional number of eggs, which cannot be exploited by clutch size variation alone. It is possible to raise an extra nestling in this fraction and by lowering growth rates if the rate is somewhat flexible.

At Delta, the food supply is predictable and fairly stable, due to regular emergences of chironomids (see Part I and Busby 1978). Thus, a clutch adjustment strategy is desirable for breeding adults. The observed growth patterns of the young Yellow Warblers correspond to O'Connor's predictions. Although hatching asynchrony is common in this species (Goossen 1978), variability amongst the young decreased with increasing age. After the first few days, the effect of hatching asynchrony was small. However, Goossen (1978) found that the mean fledging spread of 54 broods was 2.2 days, implying that some of the effects of asynchronous hatch were not completely lost during the nestling period. He argued that it is adaptive for Yellow Warblers to commence incubation prior to the completion of the clutch due to high predation rates on the ridge. Asynchronous hatching and fledging provided a better opportunity for some of the young to survive.

Slopes of the regression lines calculated for the three brood sizes indicate that some variability in growth is possible, as expected by O'Connor's prediction.

Finally, the small amount of nestling loss due to starvation (Goossen 1978) conforms to the expectations of populations using the clutch size adjustment strategy.

No upper limit on feeding rates was apparently reached by parents with smaller broods. If such a limit has been reached, parents with broods of 5 would have had to feed the young at a rate similar to parents with fewer young, and the growth rate or the body composition of the young in the largest broods would have been affected. This was not found. However, rather than increasing the number of items fed per half hour, the parents with 5 young increased the quality of the items fed, so that nutrition, rather than volume of food was maximized. Similarly, Best (1977) found that the frequency of feeding by adult Field Sparrows was not restricted by the adults' capacity to procure food, since the number of feeding trips per nestling was not significantly greater in small broods.

However, Royama (1966) concluded that adult Great Tits could not provide sufficient food to large broods and thus had a limited feeding capacity, the upper limit of which had been reached. He found that large broods were fed mainly dipterans, which he suggested may have been less nutritious food than the lepidopteran larvae fed more frequently to smaller broods.

Body Components

The analysis of lipid, protein, water, and ash composition of the 3 largest nestlings indicates that the nestlings' conditions were unaffected by brood size. Thus, broods of 4 or 5 represented greater potential reproductive success than broods of 3, because of the additional 1 and 2 nestlings, respectively. It is likely that these additional nestlings had a high probability of survival, since by day 6 the mean weights of all young in the different brood sizes were not significantly different (Table 1) and young of all broods on days 6 and 7 showed little weight variation (Figure 1). Thus, the "extra" young in broods of 4 and 5 are likely to be nearly equivalent in contributing to the parents' fitnesses. Goossen (1978) found that the number of young fledged per active and hatched nest increased with an increase in clutch size. Thus, if the young are equivalent in the 3 brood sizes, the parents with larger broods are the most successful.

SUMMARY AND CONCLUSIONS

An inverse relationship between food consumption and brood size has been found in many studies of nestling altricial birds (Lack and Silva 1949, Lack and Lack 1951, Royama 1966, Morehouse and Brewer 1968, Seel 1969, Pinkowski 1978). Royama (1966) proposed that the energy requirements of nestlings changed with brood size. Greater heat loss in small broods is compensated for by the greater amount of food supplied to the nestlings. In a larger brood, less food is needed per chick because of the lower heat loss. Royama found that growth of the young was similar in all but the largest brood sizes of tits, suggesting that the 'extra' food fed to the smaller broods was not being used for growth, but rather for maintenance.

Additionally, he suggested that there is possibly a difference in quality, as well as quantity, of food between broods of different sizes. In his study, he found that nestlings of small or medium-sized broods were fed mainly larval Lepidoptera, while the largest broods were fed adult dipterans frequently, which he believed were possibly less suitable and less nutritious. Thus, adult Great Tits apparently were compensating for the greater heat loss in small broods by feeding higher quality food items.

In this study, Yellow Warblers in broods of 3, 4 and 5 grew at similar rates. The conditions of 8-day-old young also were similar in each brood size. However, the feeding rates and quality of food items fed to the young were influenced by brood size. In this instance, a decrease in the number of food items brought was compensated for by an increase in the quality of food items. At both ages, young in broods of 4 were fed more items/nestling than young in broods of 3. Young in broods of 5 were fed the fewest number of items. The proportion of Lepidoptera larvae in the diet varied in a reverse manner. Young in the broods of 4 were fed the fewest larvae, while young in broods of 5 were fed the most larvae. Thus, selectivity in food items brought is an important mechanism in adjusting parental investment to brood size in Yellow Warblers at Delta.

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APPENDIX I. Stomach contents of 8-day-old Yellow Warbler nestlings, Delta Beach Ridge, Manitoba, 1979.

Nestling Number	Brood Size	Adult Chironomid	Larvae Chironomid	Culicids	Other Diptera	Geometrid Larvae	Other Larvae	Coleoptera	Hemiptera	Adult Lepidoptera	Arachnida	Ephemenoptera	Trichoptera
14-1	3	6	1	3	3	-	-	-	-	-	-	-	-
-2		11	1	-	6	1	-	1	1	-	-	-	-
-3		11	-	-	2	5	-	1	1	-	3	1	1
7-1	3	8	2	1	1	5	1	1	-	-	-	-	-
-2		11	2	-	1	3	-	1	-	-	-	-	-
-3		5	1	-	1	4	-	2	-	-	1	-	-
5-1	3	3	1	-	-	7	-	-	1	-	-	-	-
-2		2	2	-	-	2	-	-	-	-	-	-	-
-3		4	1	-	-	1	-	-	-	-	-	-	-
53-1	4	15	-	4	2	2	-	5	-	-	-	-	-
-2		3	-	-	-	-	-	2	-	1	-	-	-
-3		10	-	-	2	1	-	-	-	-	-	-	-
25-1	4	1	1	-	-	2	-	2	-	-	1	-	-
-2		9	3	6	1	3	-	1	1	-	-	-	-
-3		3	-	-	-	1	-	1	2	-	-	-	-
20-1	4	19	1	2	-	2	-	-	-	-	-	-	-
-2		22	1	-	-	2	4	2	-	-	-	-	-
-3		8	-	1	-	4	-	-	-	-	-	-	-
23-1	5	6	1	-	2	2	-	-	-	-	-	-	-
-2		10	3	8	1	1	4	1	-	-	-	-	-
-3		3	2	-	2	2	-	-	-	-	-	-	-
22-1	5	2	2	5	3	3	-	1	1	-	1	-	-
-2		-	1	-	-	6	-	1	3	-	-	-	-
-3		4	7	6	-	1	-	-	1	-	-	-	-
8-1	5	3	-	-	-	1	-	1	-	-	1	-	-
-2		1	1	1	1	2	-	3	1	-	-	-	-
-3		4	1	-	1	3	-	1	-	-	-	-	-

APPENDIX II. Body components (g) of nestling Yellow Warblers.

Bird	Brood Size	Weight		Water	Lipid	Ash	Protein
		Wet	Dry				
5-1	3	8.09	2.48	5.61	0.65	0.22	1.61
5-2	3	8.58	2.00	6.58	0.12	0.25	1.63
5-3	3	5.08	1.32	3.71	0.05	0.18	1.09
7-1	3	8.51	2.21	6.30	0.24	0.22	1.75
7-2	3	8.81	2.77	6.04	0.70	0.22	1.85
7-3	3	8.84	2.59	6.25	0.55	0.21	1.83
14-1	3	7.91	2.50	5.41	0.63	0.22	1.65
14-2	3	7.94	2.40	5.54	0.57	0.22	1.61
14-3	3	8.13	2.43	5.70	0.58	0.23	1.62
20-1	4	9.15	2.39	6.76	0.19	0.23	1.97
20-2	4	8.22	2.54	5.68	0.54	0.23	1.77
20-3	4	8.51	2.48	6.03	0.55	0.23	1.70
25-1	4	8.33	2.54	5.79	0.59	0.23	1.72
25-2	4	8.18	2.14	6.09	0.36	0.19	1.59
25-3	4	7.73	2.27	5.46	0.56	0.19	1.52
53-1	4	7.24	2.31	4.93	0.56	0.21	1.54
53-2	4	7.05	2.08	4.97	0.42	0.21	1.45
53-3	4	7.69	2.33	5.36	0.47	0.21	1.65
8-1	5	8.03	1.97	6.06	0.25	0.21	1.51
8-2	5	7.82	2.29	6.53	0.41	0.21	1.67
8-3	5	7.91	2.30	5.61	0.51	0.21	1.58
22-1	5	7.54	2.46	5.08	0.67	0.20	1.59
22-2	5	7.48	2.26	5.22	0.66	0.18	1.42
22-3	5	7.88	2.41	5.47	0.52	0.17	1.72
23-1	5	7.35	2.08	5.27	0.43	0.18	1.47
23-2	5	7.39	2.26	5.13	0.47	0.17	1.62
23-3	5	7.74	2.19	5.55	0.42	0.20	1.57