Apportionment of Parental Investment in Breeding American Robins

by

Eduardo M. Wilner

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

Winnipeg, Manitoba

ISBN 0-315-48118-8

APPORTIONMENT OF PARENTAL INVESTMENT IN BREEDING AMERICAN ROBINS

BY

EDUARDO M. WILNER

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

MASTER OF SCIENCE

To my parents, Sabina and David, and of course, to Gabriela.

Your reviewer believes that certain lowly organized animals have been generated spontaneously (that is, without pre-existing parents) during each geological period in slimy ooze. A mass of mud with matter decaying and undergoing complex chemical changes is a fine hiding-place for obscurity of ideas.

Charles Darwin,1863.

ABSTRACT

The apportionment of parental investment during the incubation, nestling, and fledgling periods were studied in a population of American Robins (*Turdus migratorius*) breeding at Delta Marsh, Manitoba. Only females incubated and brooded. Total incubation time did not change significantly with embryo age but incubation constancy increased significantly from day 4 on. Both males and females spent little time perched at or near the nest. Male and female perch activity was similar. Brooding males decreased their perching time with nestling age. Brooding activity decreased significantly with nestling age. Females were more involved in forms of defence that did not require leaving the nest and the contrary counted for the males. Males did not feed either their incubating or brooding mates. Considering all food items fed to nestlings, males delivered higher percentages for almost every prey type. Male robins fed the nestlings both more and more often than females. Feeding effort increased significantly with nestling age when considering both the female alone and the pair combined; male effort was more constant. Male feeding remained greater than the female's for the first two thirds of the nestling period and then equalled the female's in the last. Feeding effort per nestling did not change with brood size. Nestlings in late broods received less brooding time and more (non-significant) food than nestlings in early ones. This difference was due to a significant decrease in brooding activity and a (non-significant) increase in feeding by the female. Males and females fed and defended early brood young equally, but females defended and fed late brood young more than did males.

ACKNOWLEDGEMENTS

I would like to extend special thanks to my supervisor, Dr. S. G. Sealy. His permanent assistance, availability, and encouragement, made this study possible. I would also like to extend my gratitude to my committee members; Dr. R. M. Evans, Dr. W. Guenter, and Dr. T. J. Wiens. Their comments and criticisms greatly improved this thesis.

Dr. R. W. Knapton provided invaluable insights throughout every stage of this work and I am grateful. I am also thankful to L. Needen and R. Balshaw who assisted extensively in the computer handling of my data and proved to have an unlimited supply of patience.

My appreciation is also extended to the staff of the University Field Station (Delta Marsh) for providing enjoyable surroundings and significant help during my stay. The officers of the Portage Country Club kindly allowed me to conduct part of my research on their property and I am thankful.

I am indebted to Coleen Barber, Ron Bazin, Jim Briskie, Bill Dheil-Johnes, Percy Hebert, Keith Hobson, Liz Hoving, Sandra Lee, Alex McIlraith, and Dawn Sutherland for their technical help and foremost their friendship.

More than anybody else, I have to thank my wife, Gabriela Osswald. Not only as my best friend but also as my best critic and field assistant, her support extended to every aspect of this whole experience and at its root made it possible.

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

LIST OF TABLES

LIST OF FIGURES

GENERAL INTRODUCTION

The origin of different strategies for males and females during reproduction has haunted the literature at least since Darwin's (1904, p. 227) discussion of sexual selection:

> "We are naturally led to enquire why the male, in so many and such distinct classes, has become more eager than the female, so that he searches for her, and plays the more active part in courtship. It would be no advantage and some loss of power if each sex searched for the other; but why should the male almost always be the seeker?"

The most recent and influential attempt to address the question of sexual strategies was that of Trivers (1972) who developed the theory of Parental Investment (PI), derived mainly from Bateman's (1948) discussion of sexual selection in *Drosophila* and sexual differences in its post-zygotic energy investment, and Williams' (1966) ideas on the origin of sex. Trivers defined PI (p. 139) as:

> "Any investment by the parent in an individual offspring that increases the offspring's chance of surviving (and hence reproductive success) at the cost of the parent's ability to invest in other offspring."

The differential ability of the sexes to allocate their PI was for Trivers the most relevant variable causing sexual differences. He generalized that the sex with the higher PI (usually the female), becomes the limiting factor for the reproductive success (RS, measured as the number of offsprings produced by the individual [Grafen 1982]) of the sex with the lower PI (usually the male). Consequently, males should compete for access to females, be promiscuous, and be less choosy; females, on the other hand, should be choosy and invest heavily in each mating.

For Trivers, this initial difference in investment (large versus small gametes) had important evolutionary consequences. Reproductive mistakes in females should be more strongly selected against than reproductive mistakes made by males. This argument was (selection wise) reasonable because females invest proportionally more units of their limited PI every time they breed, so greater RS is not achieved by maximizing the **number** of copulations (as in males) but by maximizing the **ratio** between copulation and successful breeding.

Trivers then approached the problem of mate desertion. It was basically here where the relative amounts of investment were analyzed in a new **retrospective** context. Though he argued that investment decisions are based on the maximization of RS, he also reasoned that it is the amount of cumulative past investment in a given breeding attempt that determines the correct decision. In other words, a parent would maximize its RS if its investment is based on decisions on how to avoid wasting what has already been invested. Dawkins and Carlisle (1976) termed this the "Concorde Fallacy". In fact, selection should strongly select against such behavior: a mate that bases its investment decisions on their impact on future RS should on average be fitter than that one that bases them on avoiding wastage of past investment. It is one thing to select against wasteful individuals (with respect to PI), and quite another to select for individuals that make reproductive decisions in order to save crumbling past investment, the latter evolutionary reasoning being fallacious. Hence, the typical female was selected to be a wise investor, the typical male, to combine this quality with that of a wise gambler; neither of them was selected to save, as a prime priority, collapsing previous investment.

Partly based on Dawkins and Carlisle's criticism (1976), Maynard Smith (1977, 1982) derived his "prospective" analysis of PI, contrasting with Trivers' above-mentioned retrospective component. In Maynard Smith's model, Trivers' PI theory was modified in two ways. First (after Dawkins and Carlisle), an organism was considered not to be locked into a certain pattern of future PI based on its past investment. On the contrary, Maynard Smith argued that selection should favor those individuals that allocate their PI in such a way as to maximize their future RS, and not those that behave according to past investment. A hypothetical male, for instance, should desert his mate (regardless of how much PI has been invested up to that point), only if by doing so he increases his future RS, i.e., if his deserted mate is able to raise single-handedly a given proportion of the original clutch and, in addition, his chances of re-mating and fledging new young are good. Adaptive behavior in the prospective model is not determined by its connection with past investment, but by its positive repercussion on future RS.

Maynard Smith's second modification involving game theory likewise constituted a major departure from Trivers' model: the choice of game theory as the proper tool of analysis formally addressed the fact that the behavior of one sex should be considered optimal **only** if it is adaptively based on the behavior of the other.

To sum up, PI theory at its present stage provides us with at least one important answer regarding sexual strategies, namely that the basic pattern of investment by the two sexes can be predicted provided specific information is available, such as the effect of post-zygotic care on the female's ability to produce eggs, the availability of fertilizable females to mate with after the male deserts a mate, the efficiency of mono- versus biparental care, etc. In other words, we can predict the sex that is more likely to provide care, the one more likely to desert, and so on. But what happens when at least some sort of biparental investment is required? Furthermore, given the combinations of sexual PI patterns that are (at least theoretically) available to a mated pair, what determines the role and the pattern of contribution that each sex actually adopts? Unfortunately, no theory has yet been developed that predicts such patterns (Oring 1982, Mock 1983, Breitwisch et al. 1986).

Theoretical developments in the natural sciences require extensive natural history information as a starting point. To develop a theory of PI apportionment we need quantitative data on apportionment schedules in the first place. However, few such schedules have been reported (Breitwisch et al. 1986). It is my goal here to quantify in detail the apportionment of PI in the American Robin *(Turdus migratorius)*, a migratory passerine bird, and to interpret the results against the background of current PI theory.

The population studied on the forested dune ridge Delta Marsh, Manitoba, was suited for this research for at least two reasons. First, it was seasonally monogamous. Monogamy should provide particularly interesting information regarding schedules of PI apportionment, since care by both parents is generally seen as mandatory (Williams 1966, Lack 1968, Orians 1969, Emlen & Oring 1977, Wittenberger and Tilson 1980, Oring 1982, Mock 1983, Leffelaar & Robertson 1986, but see also Greenlaw & Post 1985). Second, robins are double-brooded (Howe 1898, Howell 1942, Bent 1964, Martin 1973, this study), that is, pairs rear two broods per year that differ in their timing and immediate reproductive futures (i. e. the early first brood is followed by another reproductive attempt while the second one is not). Double-brooding then, presents an interesting natural setting in which to explore the effect of these two variables on apportionment patterns of PI between mates.

The general structure of this thesis is as follows: The observed patterns of apportionment for both sexes were quantified during the incubation (Chapter 1) and nestling (Chapter 2) periods, respectively. In addition, information collected opportunistically during the post-nestling period is quantified also in Chapter 2. Finally , the data gathered for the entire breeding season were pooled and the overall picture of PI apportionment is discussed. Monogamy in this population is thus interpreted in terms of the prospective analysis of PI.

CHAPTER 1

THE INCUBATION PERIOD

INTRODUCTION

Most studies of patterns of nest attentiveness during the incubation period have investigated what factors affect incubation behavior or how they do so, thus basically agreeing that the interaction of factors such as weather, food availability, lipid reserves of incubating adults, predation, and mate's behavior should strongly affect this behavior (e. g. Drent 1973, White and Kinney 1974, Cartar & Montgomerie 1987, Thompson & Raveling 1987). Nevertheless, the question **why** this behavior is sexually divided in the first place has seldom been addressed.

The incubation period is generally believed to be energetically inexpensive. Nevertheless, its importance for the study of sexual PI apportionment lies in the characteristic division of labor that takes place during this period. Within the 42 passerine families reviewed by Kendeigh (1952), in only 3 families are the males involved in a greater share of incubation duties, in 7 males do not incubate at all, in 17 females incubate more, and in the remaining 15 families both sexes incubate equally. Similarly, White and Kinney (1974) argued that, in most passerines, incubation is done solely by the female, whereas the role of the male probably is to guard and sometimes feed its mate. The existence of such role-dividing trends in incubation duties begs for an explanation. Still, most studies that deal with PI apportionment schedules ignore the incubation period and deal exclusively with the (more energetically demanding) nestling period, e. g. Royama 1966, Breitwisch et. al. 1986, Grundel 1987, Leffelaar and Robertson; but see also Røskaft 1983, and Greenberg and Gradwohl 1983.

My objective in this Chapter was to study how American Robins apportion their PI during the incubation period. The information available for this species is vague and sometimes even contradictory. Howe (1898) reported that females incubate alone, but that males sit on the nest, though for periods no longer than 3 min. Howell (1942), on the other hand, argued that females incubate unassisted but cited McClanahan (in Howell 1942) who stated that both sexes incubate. Males were reported to feed the incubating female occasionally (Forbush, cited in Howell 1942), and commonly (McClanahan cited in Howell 1942). Females have generally been noted to be the aggressor in nest defense (Howell 1942). Although only the females develop brood patches (personal observation) this is, as Skutch (1957) pointed out, a poor indicator of incubation roles in passerines.

In this chapter, I present the quantitative results of incubation and perching schedules of the sexes in robins. I determine whether or not male robins incubate at all, and whether they feed their mates at the nest. In addition, and based on the nature and number of instances of nest defense observed, I attempt to determine each sex's involvement in nest defense. Finally, the different PI patterns of apportionment thus obtained will be discussed in the light of Maynard Smith's PI prospective analysis (1977, 1982).

METHODS

During 1986 and 1987 a population of American Robins breeding on the forested dune ridge, Delta Marsh, Manitoba, was studied throughout the breeding season. The study portion of the ridge forest extended approximately 3 km from the Assiniboine River Diversion west to Cram Creek, on the properties of the University of Manitoba Field Station and Portage Country Club (50º 11' N, 98º 19' W). MacKenzie (1982) has described the vegetation of this site.

Robins were captured with mist nets through Dr. S. G. Sealy's ongoing banding program at the field station (covering most of the study area) and by netting specific individuals. The captured birds were individually banded with an aluminum band plus one or more colored plastic bands.

Males and females were distinguished by subtle differences in their coloration: males' underparts were slightly brighter, their upper mandibles were yellow while the females' were yellow-brown and darker overall, and the males' napes were usually darker. All nests were tended by pairs with at least one parent banded. Unbanded birds were recognized individually by their characteristic facial plumage. The patterns of the discontinuous eye ring, dark spots on the white gular and jugular regions, and extent of pigment on both upper and lower mandibles varied in this population.

Nests were checked every day at around 1800 hr to determine the clutch-initiation date. Nests found during the egg-laying period were checked similarly until their clutches were completed. Since robins generally lay one egg every 24 hours (Howe 1898, Howell 1942, Bent 1964, this study), the clutch-initiation date was calculated by back-dating. The observation schedule for the incubation period was established by assigning the clutch-initiation date as "day= 0"; subsequently on every second day until hatching, a 60-min observation bout took place between 1700 and 2000 hr. Thus, each observation day is symbolized by a number starting at 0, the clutch initiation date. Data were not collected during inclement weather. A total of 18 nests (9 of clutch size 3, 9 of 4) was watched on different days, all in 1987, on an average of 3.3 times each (SD= 1.4). The sample size for each day is given in Table 1.

Nests were observed from sheltered locations or blinds set approximately 15 to 25 m away. A 20X-40X spotting scope was focused on the nest, and behaviors performed by the "focal adult/s" (at the nest or within 2 m of it) were recorded to the nearest second as timed with two digital stopwatches. It is important to stress that only those behaviors that happened within 2 m of the nest were recorded.

The following variables were defined on the basis of the interpretation of previous behavioral observations. **Incubating**: characterized by the puffing-up of breast and belly feathers (presumably to expose the brood patch), and "accommodation" movements that resulted in the incubating bird sinking deep into the nest cup. **Feeding**: the male arrives at the nest with a load of prey that is fed to its mate. **Perching**: the bird perches either on the rim of the nest, or within 2 m of it (considered a form of nest guarding). **Alarm**

Calling: short, loud, and high-pitched call, typically accompanied by mobbing displays as described in Shedd (1982). **Distress Chirping**: short, low, high-pitched squeal, with no other obvious mobbing display. **Chasing**: darting close to and following a would-be predator, usually also uttering alarm calls.

All natural-occurring instances of nest defense, i. e. when a would-be predator was mobbed or chased with vocalizations uttered, were recorded. Although the small sample size obtained was not suited for extensive analysis, the data were informative and gave an index of the actual rate of encounters with would-be predators and the consequent division of labor between the defending parents.

Statistics

Analysis of variance (ANOVA), chi-square, Spearman rank correlation test, and Wilcoxon matched-pairs signed-ranks test, were used to analyze the data. The level of significance adopted was $p < 0.05$.

Table 1

Number of American Robin nests, with different brood sizes, observed for each of the six observation days (see text) of the incubation period.

	Number of Nests Observed		
	Brood Size		
Observation Day	3	4	Both
2	4	4	8
4	5	4	9
6	4	7	11
8	3	8	11
10	6	8	14
12	3	3	6

RESULTS

Breeding Chronology

The incubation period was defined as the date of clutch initiation to the hatching of the first egg. It averaged 12.1 days in 1986 (SD= 0.9, N=13), 13.5 days in 1987 (SD= 0.9, N=15), and 12.8 days for the two years combined. The combined data for the two years, including the 10 nests whose clutch initiation dates were estimated by back-dating, indicate that more than 50% of the total number of clutches were initiated by 31 May. The average clutch size (at completion) was 3.5 (SD=0.7), and 3.2 (SD=1.0) in 1986 and 1987, respectively. Clutch size for both years was 3.3 eggs.

Although American red squirrels (*Tamiasciurus hudsonicus*), believed to be the main predator of robin nests, were removed from the study area, predation was high in 1987. Fifty-four percent (19 out of 35) of all nests initiated were preyed upon, compared with only one nest (out of 13) in 1986. Seventy-eight percent of all predations in 1987 occurred before hatching, resulting in only 36.6% of all eggs laid (N=114) hatching.

This high incidence of predation forced many pairs to renest. For easier analysis, the breeding season was arbitrarily partitioned into 5-day intervals. Clutch initiation appeared to be bimodal in 1986, and trimodal 1987 (basically due to renesting, Fig.1). The first peak in both cases was the greater and lasted longer than the second one. In 1986, it extended from 11 to 21 May and in 1987 from 7 to 21 May. The second peak lasted from 10 to 20 June in 1986. In 1987 there were two smaller peaks, the first extending from 5 to 10 June,

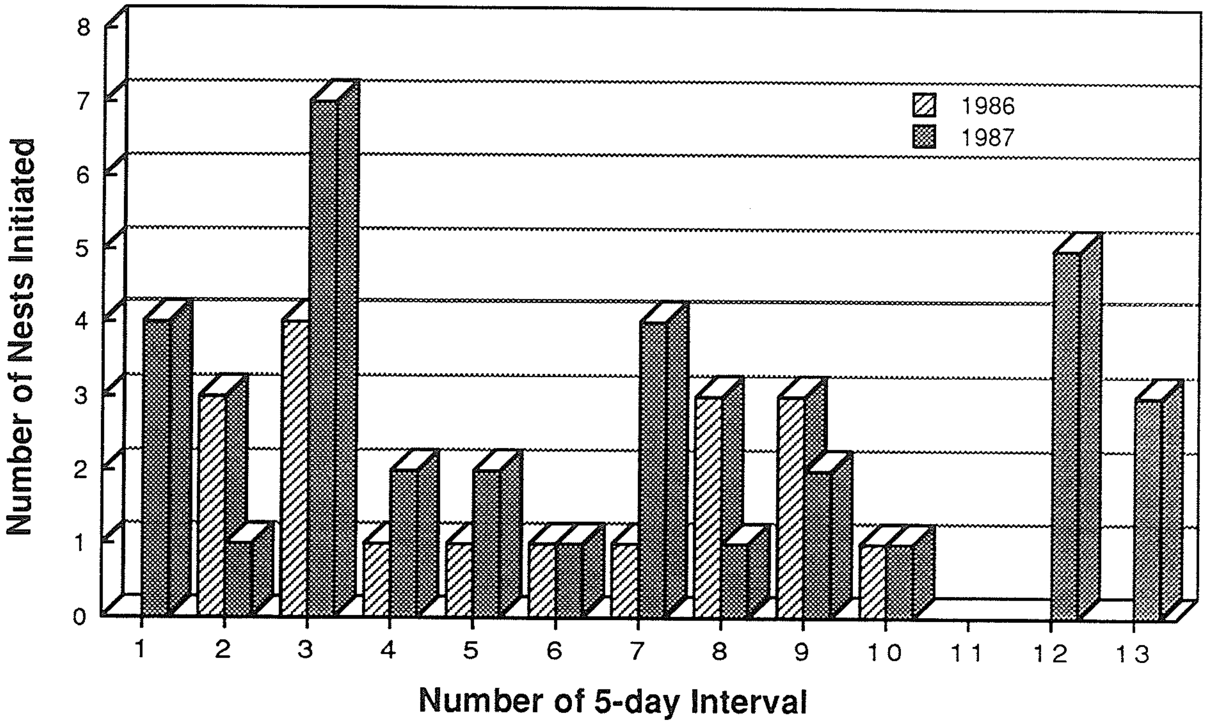

Figure 1. Clutch initiations in each 5-day interval. Interval number 1 started on 11 May, number 13 on 10 July.

the second from 5 to 10 July.

At least 14 identified pairs nested in 1986, and 10 in 1987. If we include the nests where the parents were not positively identified (either because of early nest predation, or because their nest was too high and thus not studied), two more pairs probably bred in the first year, and eight more in the second. Three pairs in 1986 and 7 in 1987 were known to have attempted a second brood. Though most of these nests were built within approximately 50 m of the first ones, the late season foliage may have reduced the number of second nests discovered. The temporal relation between these broods and the first ones is depicted in Fig.2 for the two years.

Overall apportionment of care

The two variables of nest attentiveness measured in this period were incubation and perching. The total time spent in each behavior was recorded and analyzed statistically. The number of incubation bouts, i.e. the number of uninterrupted incubation events per observation session, was also analyzed.

Only females incubated. Males rarely perched on the edge of the nest, and only a few times stood inside the nest cup. These events might explain what some previous authors reported as occasional male incubation bouts. Since this behavior only superficially resembles incubation behavior, I recorded it as perching.

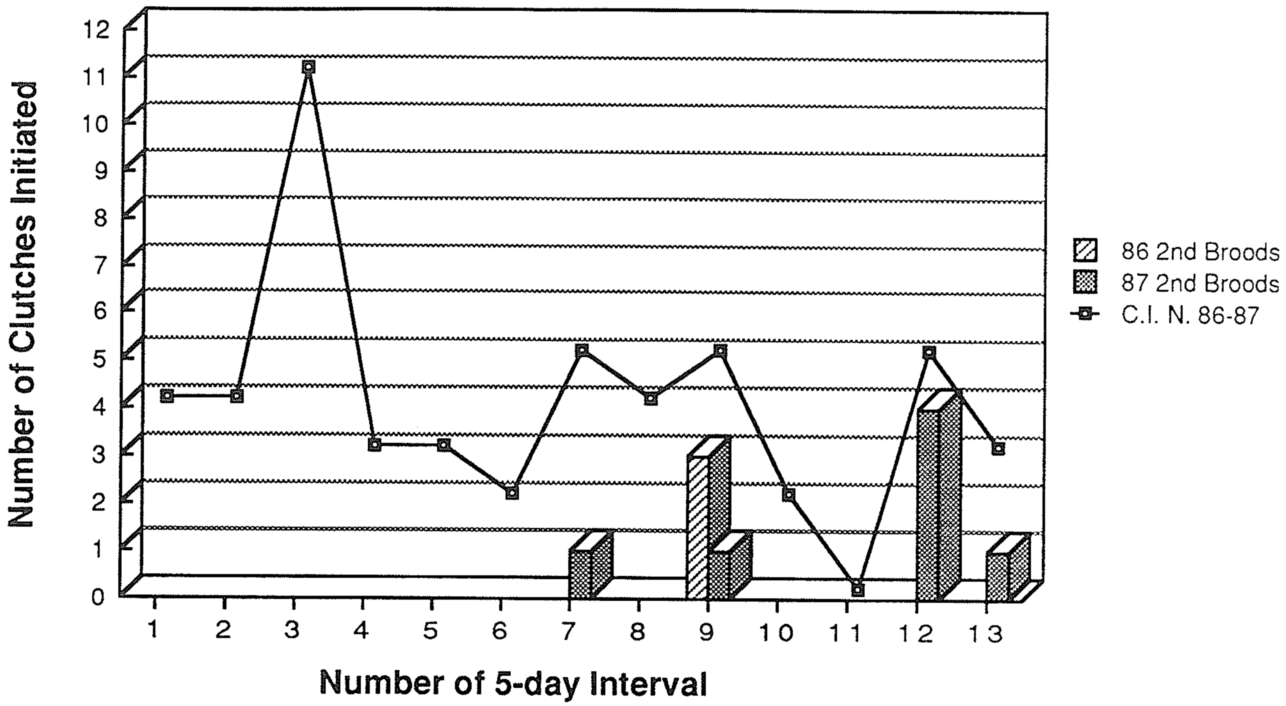

Figure 2. Number of second broods initiated in 1986 and 1987, together with the total number of broods initiated (in both years), in each 5-day interval. Interval number 1 started on 11 May, and number 13 on 10 July. C.I.N. 86-87: total number of nests initiated, both years combined.

I observed a male only once feeding his incubating mate. On one other occasion (on day 6 and while the mate was on an incubation recess), a male brought a small larva (a load usually destined for the youngest nestlings) to its nest. He performed the usual nestling feeding movements, but ate the larva himself after a few seconds. Both males and females perched near or at the nest for short periods, but in the case of the females this behavior merely preceded the resumption of incubation.

Incubation behavior and clutch age

Females incubated an average of 50.5 min each hour (SD= 4.6 min). There was no significant correlation between each day's incubation rate and clutch age (Spearman rank correlation test: $r_s= 0.2$; $P > 0.05$) (Fig. 3). Incubation bouts averaged 2.5 per hour (SD= 0.3) and their duration increased with clutch age (see below). As shown in Fig. 4 the number of incubation bouts decreased after a small peak on day 4. This negative correlation with clutch age was significant from this peak through the end of the incubation period (Spearman rank correlation test: $r_s= -1$; $P < 0.05$).

Perch behavior and clutch age

Male robins perched an average of 2.2 min (SD= 1.4 min) per hour of observation, and females 0.6 min (SD= 0.6 min, Table 2). Male and female daily perch activity was not significantly different (Wilcoxon matched-pairs signed-rank test, $T(6)= 1$, $p > 0.05$). Neither male nor female perching rate was correlated with clutch age (Spearman rank

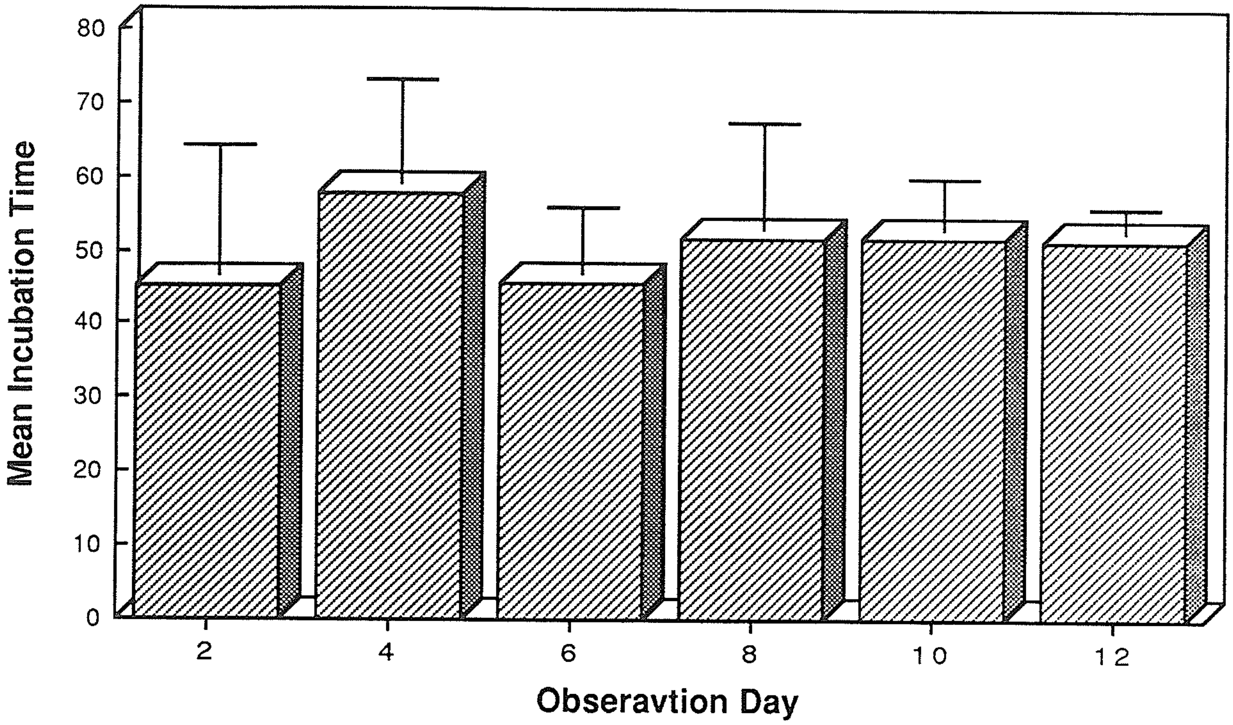

Figure 3. Mean total incubation time (min) per observation hour for each observation day in the incubation period. Vertical "T"= SD.

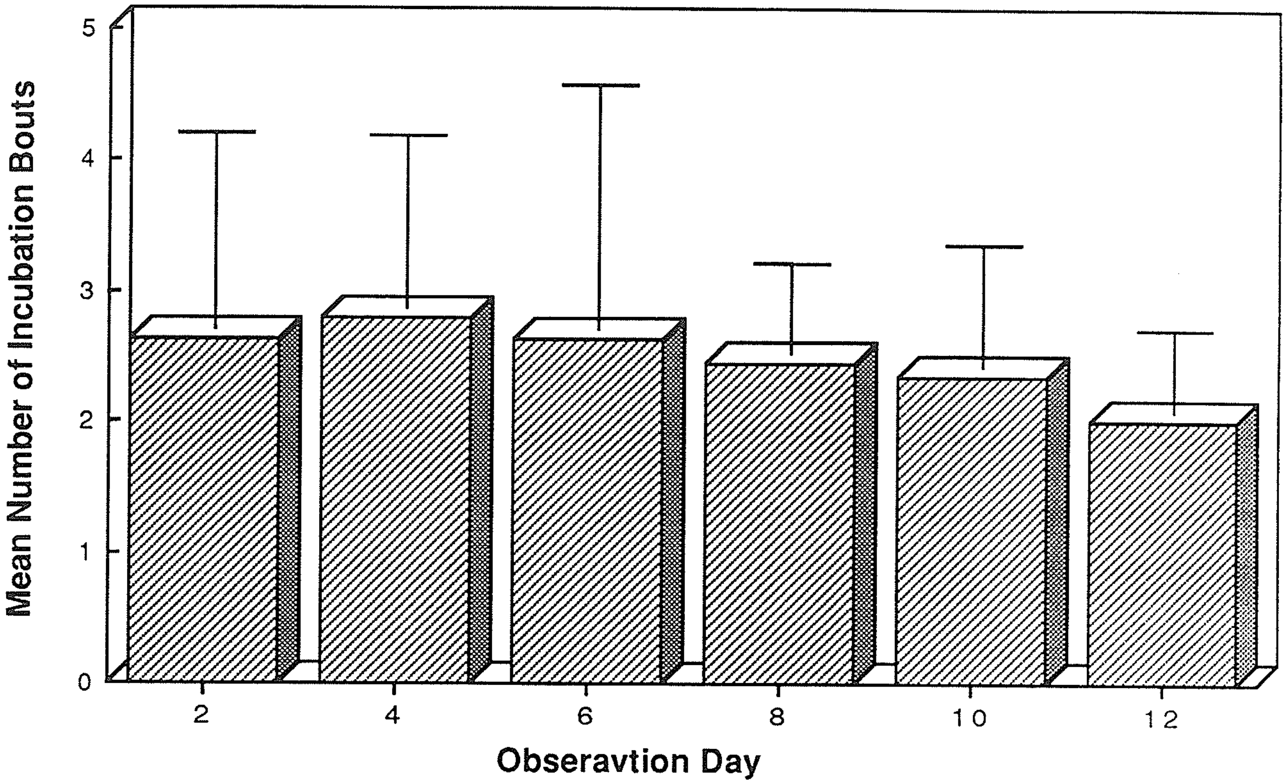

Figure 4. Mean number of incubation bouts (see text) per observation hour for each day in the incubation period.

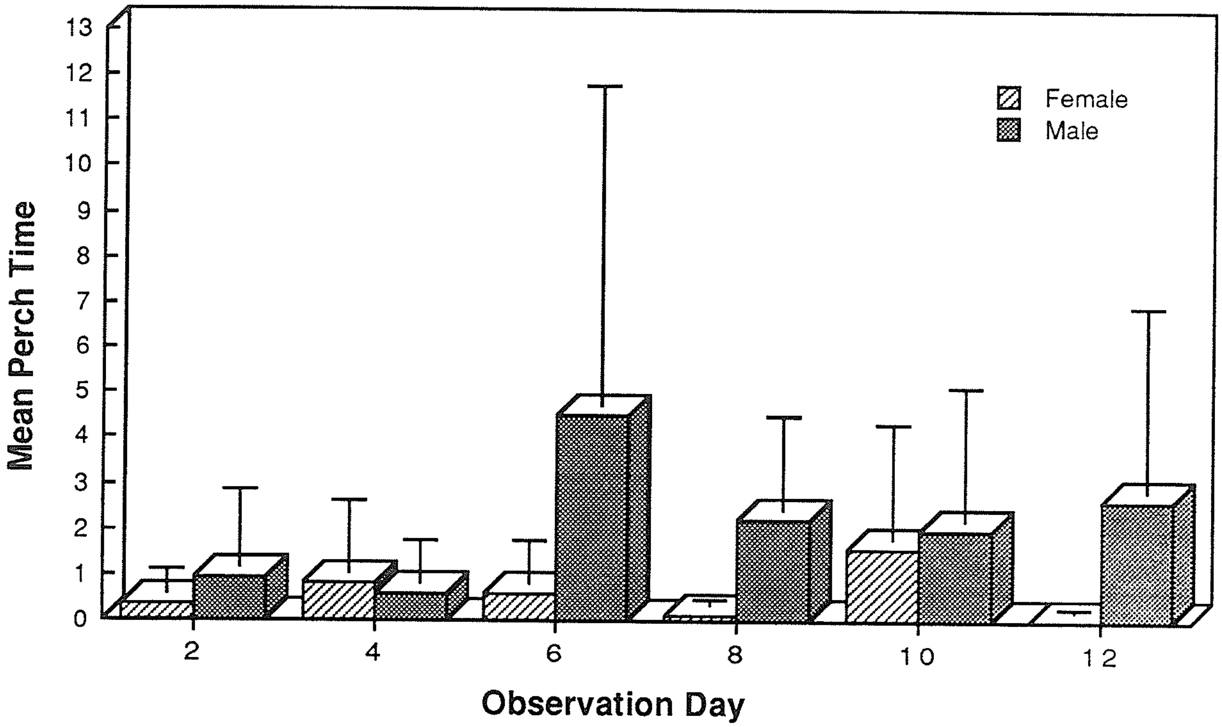

Figure 5. Mean total perch time (min) per observation hour for each day in the incubation period.

Table 2

Mean daily adult time spent perched by the nest per hour of observation (brood size 3 and 4 combined).

	Mean Total Perch Time (min)	
Observation Day	Male	Female
2	1.0	0.4
4	0.6	0.8
6	4.7	0.6
8	2.2	0.1
10	2.0	1.6
12	2.6	0.0

correlation test: $r_s = 0.543$ for the male, and $r_s = -0.257$ for the female; $P > 0.05$) (Fig. 5).

Nest defense

Seven instances of nest defense were recorded in this period. All involved vocalizations, all were recorded at different nests, and all were recorded on different days. Six were performed by females, and one by a male.

DISCUSSION

The observations obtained during the incubation period of the American Robin reveal clearly that direct care of the clutch is female-biased. Only the female robins incubated. Total incubation time did not vary significantly throughout the incubation period, but incubation constancy increased as incubation progressed. Both males and females spent little time perched by the nest. Male robins did not feed their incubating females.

American Robins follow the attendance pattern that White and Kinney (1974) called "secondary mode" incubation, where the females do most (or all) of the incubation, and are not fed by their mates. These authors argued that this mode is the most common among passerine birds. Secondary mode incubators present a sophisticated nest structure (in insulation terms), and the mean egg temperature is maintained by the female's attentiveness.

Drent (1973) noted that the incubating parent performs a dual role; it incubates and guards the nest simultaneously. This was shown conclusively in the Herring Gull (*Larus argentatus*, Baerends et al. 1970) and Pink-footed Goose (*Anser brachyrhyncus*, Inglis 1977) where the authors found significant positive correlations between the number of incubation interruptions and predation rates. This role is further supported in the robin, as the female uttered, almost exclusively, all alarm calls recorded. Furthermore, the bright blue color of robin eggs may render them quite noticeable when the (relatively) cryptic female is not covering them. Oniki (1985) noted that among nests and eggs of

Amazonian passerines, blue eggs were significantly associated with semi-open, sunny and bushy nesting sites. She argued (p. 544) that blue eggs imitate "spots of light on green leaves against a dark background" and are hence camouflaged from would-be predators. Although her reasoning is appealing, this camouflage strategy would only work on sunny days or (and this specifically for the the Delta population) after the thick spring foliage has developed. On the contrary (and to the eggs' disadvantage), the eggs probably would be noticeable on cloudy or early spring days. This puzzle does not refute the "egg-camouflage" hypothesis, but renders it secondary to the behavior of the incubating parent. This new "incubating parent-camouflage" hypothesis seems to be further supported first by the fact that females are more cryptically colored than males (see Methods). Secondly, when the two forms of female nest attentiveness (incubation and perch) are compared, the former seems to be more conspicuous than the latter. In fact, perching in females appeared to be shorter than in males and seem to be an event that briefly preceded the resumption of incubation. The cryptic female possibly minimizes such conspicuous behaviors, but nevertheless perches albeit briefly to avoid damaging the nest contents, as might result from landing directly in the incubation position.

My method probably underestimated the male's investment during this period. Basically, the single male PI component that I measured was the time spent near the nest. In addition, and as mentioned before, the measurement itself was biased towards those perches that I could see from my vantage point. Still, perch behavior was the sole investment that males apparently contributed during this period. As with incubation, it could be argued that a perched parent is also a guarding parent (of the nest, the mate, or both). The fact that male perching seemed to be synchronized with female recesses (personal observation) further supports this hypothesis. This conclusion was also reached by Slack (1976) and Verbeek (1970) who reported the same kind of synchronization in Gray Catbirds (*Dumetella carolinensis*) and Water Pipits (*Anthus spinoletta*), respectively. In robins (this study) and catbirds (Slack 1976) the presence of the guarding male was associated with the occurrence of a number of defense events.

The incubation phase is believed to be the one with the lowest energy expenditure of the three stages considered in this study (Biedenweg 1983, Bryant and Westerterp 1980). Interestingly, Biedenweg (1983) found that female Northen Mockingbirds (*Mimus polyglottos*), with incubation roles similar to the robin, expended less energy than their mates during the incubation period. This low expenditure was related to the long time spent in the insulated nest and the consequent low metabolic heat required. Bryant and Westerterp (1980) reported a similar finding for the House Martin (*Delichon urbica*), although both parents incubate in this species.

Although the female might have less time to forage (Jones 1987), she also expends less energy thermoregulating. If Jones (1987) is correct, adults would be expected to be heavier during the stages that cost less in terms of energy expended (excluding perhaps the pre-laying stage, see Bryant and Westerterp 1980). Thus, Biermann and Sealy's (1985) weight measurements of some insectivorous passerine species at

Delta Marsh throughout the breeding season support the interpretation presented above. Although the sample sizes for robins were small and temporally incomplete, the heaviest females were recorded generally during the incubation period.

If this interpretation is correct, then it is not surprising that male robins do not feed their incubating females, furthermore being themselves involved with almost twice as much the nestling feeding effort of their mates. As Krebs (1970) showed for the Great and Blue Tits (*Parus major* and *P. caeruleus*), the females are fed at different rates, but both in daily quantities and a temporal pattern that enables the laying females to produce one egg daily. The importance of "courtship" feeding in this species was evident, as Krebs reported, because female tits did not have enough time each day to collect sufficient food to maintain their own weight. Clearly, this activity is to the advantage of both sexes. Lyon and Montgomerie (1985) reached similar conclusions based on their finding that female RS decreased when male Snow Buntings (*Plectrophenax nivalis*) were removed. That courtship feeding is not as crucial for female robins seems to be implied by Biermann and Sealy's (1985) weight measurements. If this inference is correct, then there should be no need for courtship feeding to evolve in this species. The results from the present study suggest that the main attentive role of the male during incubation is to guard the nest when the female recesses from incubation. The females, on the other hand, and probably as a result of their basic role as incubators, seem to have a more consistent role in nest defense.

CHAPTER 2

THE NESTLING AND FLEDGLING PERIOD

INTRODUCTION

Biparental PI is generally believed to be necessary in monogamous species (Williams 1966, Lack 1968, Orians 1969, Emlen & Oring 1977, Wittenberger and Tilson 1980, Oring 1982, Mock 1983, Leffelaar & Robertson 1986, but see Greenlaw & Post 1985). Because the nestling period is considered to be the most energetically demanding (basically because of feeding effort) for breeding parent birds (King 1973, Ricklefs 1974, Skutch 1976, Bryant & Westerterp 1980, Biedenweg 1983), sexual PI apportionment patterns in this stage should yield particularly important information to help understand PI apportionment in general.

Although feeding effort might be the most rigorous estimator of total PI in nestlings in terms of energy spent, other forms of PI, such as brooding and nest defense, are probably also costly although not necessarily in energetic terms. Although brooding per se is not a costly activity (Bryant and Westerterp 1980), Jones (though dealing with incubation, 1987) pointed out that there are indirect costs, for example, the decrease in time available for foraging. This cost is further increased if we assume that brooding parents also guard their nests (see Drent 1973). Nest defense, like brooding, is not energetically expensive but it is risky. If a parent is killed while defending its brood, the cost of such behavior will be dramatic in terms of this parent's RS but may be negligible with regard to the kilojoules it spent. In short, and since we know that brooding and nest defense are in fact differentially allocated between mates in different bird species (Kendeigh 1952), they should not be ignored when overall schedules of PI apportionment are studied.

Double-brooded species should be expected to have evolved adaptive patterns of PI allocation between the two broods that maximize the number of young fledged per season. Early and first broods are equivalent (regarding their chances of being followed by the next brood) thus, like Royama (1966), both are referred to as "early"; similarly, "late" broods include second and late broods. In double-brooded species, early broods could be characterized as those that are generally followed by another breeding attempt while the opposite would count for the late ones. In early broods PI should be allocated in such a way as to maximize not only the number of young to be fledged in this attempt, but also the number that will come from the forthcoming one. Thus, double-brooded species offer the uncommon setting where, without manipulation, pairs are subjected to two different breeding contexts between which the best strategy of PI allocation probably differs. We should expect then that comparing PI patterns in early and late broods should be particularly enlightening. In fact, nestling feeding rates (Seel 1966), intensities of male nestling defense (Curio et al. 1985), and different parent-fledgling associations (Snow 1958, Keller 1979, Smith and Roff 1979, Harper 1985) have been reported to differ between first and second broods. Nevertheless, such comparisons are few, and genarally both broods have been merged to create larger sample sizes (e. g. Breitwisch et al. 1986).

It is not surprising that most information on PI after hatching pertains to the nestling period, although some authors believe that care after fledging demands even more (Royama 1966, Skutch 1976, Morehouse & Brewer 1968, Drent & Daan 1980, but see Pinkowski 1977). Although data on the post-fledging period are more difficult to obtain, their relevance is obvious, especially in double-brooded species where the fledging period of the first brood often overlaps incubation of the second.

In this chapter, I quantify the apportionment schedules of three components of PI for robins at Delta: feeding effort, nest attentiveness (brooding and nearby perching), and defense. These components were studied (except for nest attentiveness in the fledgling period) in both nestling and fledgling periods, and their patterns were compared in early and late broods. Based on the information obtained and that of other studies, hypotheses to explain male and female PI apportionment in this species are presented. The underlying theoretical framework is basically that of Maynard Smith's PI prospective analysis (1977, 1982).

METHODS

The nestling period

The observation procedures and materials were basically the same as those outlined in Chapter 1, except that observation bouts were 90-min long and took place between 0530 and 1130 hr. Each observation day is given a number, starting at hatching day or "day= 0".

Thirty-two nests were watched in 1986 and 1987 (all brood sizes combined), (Table 3). Each nest was subjected to an average of 4.5 observation bouts (SD= 1.5). Three nests could be observed per day, and these were chosen randomly, first from the available nests with brood sizes of 3 and 4, and when 3 of these nests were not available, from nests with other brood sizes as well. The effect of brood size *per se* was not my objective, hence broods of 3 and 4 young were favored because they were more common, and thus gave a larger sample. Except when indicated otherwise, analyses were performed on these two brood sizes. All broods were divided into "early" or "late", depending on whether they hatched before or after 5 June, the approximate mid-season date for both summers.

Behavioral classes observed and recorded

The following variables were defined on the basis of the interpretation of previous behavioral observations. **Brooding**: characterized by the puffing-up of breast and belly feathers (presumably to expose the brood patch), and accommodation

Table 3

Brood sizes of nests observed on each of the six observation days (see text) in the nestling period, 1986 and 1987 combined.

	Brood Size				
Day	1	2	3	4	5
2	2	5	10	8	1
4	3	5	13	6	1
6	3	3	14	8	1
8	1	5	9	8	1
10	1	4	8	7	1
12	1	3	7	5	1

movements over the nest cup; **Feeding**: the parent arrives at the nest with a load of prey that it feeds to the nestlings; **Perching**: the bird perches either on the rim of the nest, or within 2 m of it;

Alarm Calling: short, loud, and high-pitched calls, typically accompanied by mobbing displays as described in Shedd (1982); **Distress Chirping**: short, low, high-pitched squeals, with no other obvious mobbing display; and **Chasing**: darting close to and following the would-be predator, usually also uttering alarm calls.

A new set of feeding variables was recorded in addition to those mentioned in Chapter 1: "**feeding**" (a feeding trip), and its subsets "**prey type**" and "**prey load**". Variable prey type refers to the kind of food item delivered, and prey load refers to its size or amount. The major types delivered (e.g. fruit, damselfly, spider, etc., with finer degrees of resolution attempted whenever possible) were individually identified and counted. Earthworms were easily identified but usually were brought in a number of dangling loops. Furthermore, as with larvae, worms were noticeably of different sizes. Midges, though generally nearly uniform in size, sometimes were brought in quantities so large that individuals could not be counted. To record this variation meaningfully, I used the following standarized unit of measurement.

The length and width of the of the bills of male and female robins are essentially the same (Power 1974, Swihart and Johnson 1986). Thus lengths of worms and larvae were measured in units of bill length (BLU) and width in units of bill depth (BDU). The actual average values of bill depth and length were recalculated from each sex's average in Power's study (1974). In addition, the beaks of 3 females and 3 males of the ridge forest population that were measured fell within Power's SD intervals. Thus one BLU was set at 13.5 mm, and one BDU at 5.2 mm. Length in the field was estimated with a resolution not smaller than 0.5 BLU. Widths of worms and larvae were ranked 0.5 BDU, 1 BDU, and 1.5 BDU. Counts of individual midges were based on the number of heads and abdomens sticking out of the parent's bill. However, the often-delivered large loads of midges sometimes precluded individual counts. Nevertheless, a few counts were possible when adults remained motionless for brief periods before feeding. Thus, observed loads were ranked according to 5 fixed counts depending on their size: 6, 8, 10, 15, and 20 midges. Individual midges were counted absolutely in smaller loads.

All prey types and their different standarized sizes were eventually converted to mg of dry-weight. These were obtained from Guinan's (1985) previous arthropod sampling and weighing on the same study site. Dry-weights for prey types that Guinan did not measure were obtained by his procedures.

To test for sexual differences, minor prey types and the different sizes of the major prey types were combined into broader prey categories: "midge", "worm" (including all sizes of earthworms), "larvae" (including all sizes of larvae), "insect" (including unknown insects and all other minor insect prey), and "fruit". To test for correlation between nestling age and prey type delivered, only the most common prey categories were used, i. e., those prey types that were brought more than 10% of the times, namely, worms, midges, and larvae. Their absolute combined dry-weight totals (all nests, all brood sizes) on each observation day were combined, and the corresponding percentage was derived for each type.

Since dry-weight delivery rates are usually favored over feeding rates as better estimators of parental feeding effort (e. g., Royama 1966, Grundel 1987), all prey types were eventually pooled and converted into two major dry-weight categories: animal and fruit. Male and female contributions were then transformed to mg of dry animal or fruit delivered * nestling^{-1} * 90 min^{-1}. For both years and all brood sizes combined, 2.9% of the total dry-weight delivered was fruit; sexual delivery patterns for fruit were basically the same as those observed in all other food items (see results, Table 7). Hence, for all further analyses the variable "dry-weight" was not subdivided. The division seemed only to increase the complexity of the analysis, but not its ability to resolve sexual differences.

The fledging period

These data, in contrast to the two other periods, were recorded opportunistically. I visited the vicinity of the nest nearly every day after fledging. With luck, a young was spotted when no adults were around, and in these cases I waited hidden for the arrival of the parent/s with food, and recorded their sex. In most cases, the adult robins spotted me first, and mobbed me. On these occasions, the sex of the adult/s was recorded, and the behavior was catalogued as "defense". If the parent robin was carrying food, the event was recorded as "feeding". On these occasions, if the young were not found I assumed their nearby presence on the basis of the adults' behavior. This method yielded 109 observations on 23 nests in the two years, each nest thus providing an average sample of 4.7 observations (SD= 4.2).

RESULTS

Brooding period parameters

The brooding period was defined as the date of the first hatching to the fledging of the first young. It averaged 13.4 days (13.5 days, SD= 1.3, N= 17 in 1986; 13.4 days in 1987, SD= 0.9, N= 17). The earliest hatching date was on 20 May 1987 (29 May 1986), and the latest was 17 July 1987 (7 July 1986). The mean clutch size at hatching was 3.4 eggs (3.5 eggs, SD= 0.7, N= 20 in 1986; 3.3 eggs, SD= 0.8, N= 22, in 1987). Two hatching peaks were evident (see Fig. 6). The first and more pronounced extended from 29 May to 10 June 1986, and from 5 June to 24 June 1987. The second lasted from 25 June to 4 July in 1986, and in 1987, from 15 July to 24 July. The pattern of fledging was similar (Fig. 7). The earliest fledging was 12 June 1986 and 1 June 1987, and the latest 19 July 1986 and 29 July 1987. The average brood size at fledging was 3.2 in 1986 (SD= 0.7, N= 19), and 2.9 in 1987 (SD= 0.9, N= 20).

No nests were preyed upon during this stage in 1986 but in 1987, 2 nests were partially and 2 were completely preyed upon. Six clutches (both years combined) contained unhatched eggs. Three nests contained 2 unhatched eggs, and the other 4 nests contained single unhatched eggs. The parents did not remove unhatched eggs.

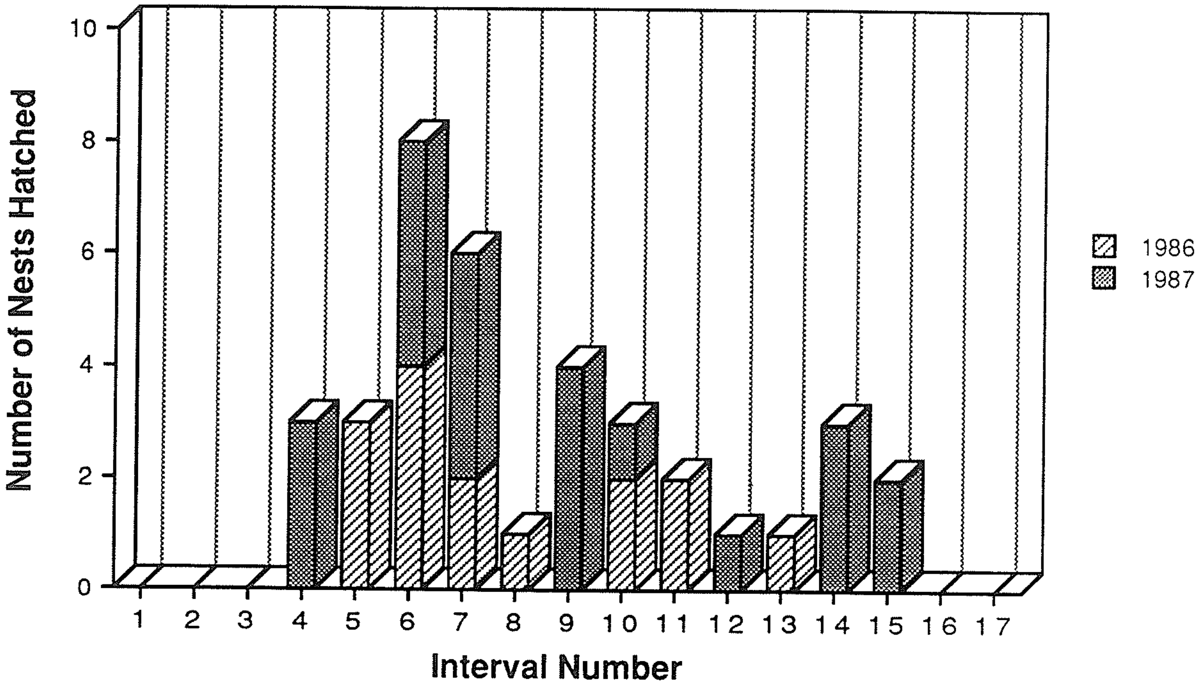

Figure 6. Number of nests that hatched within each 5-day intervals. The first and 17th intervals started on 11 May and 30 July, respectively.

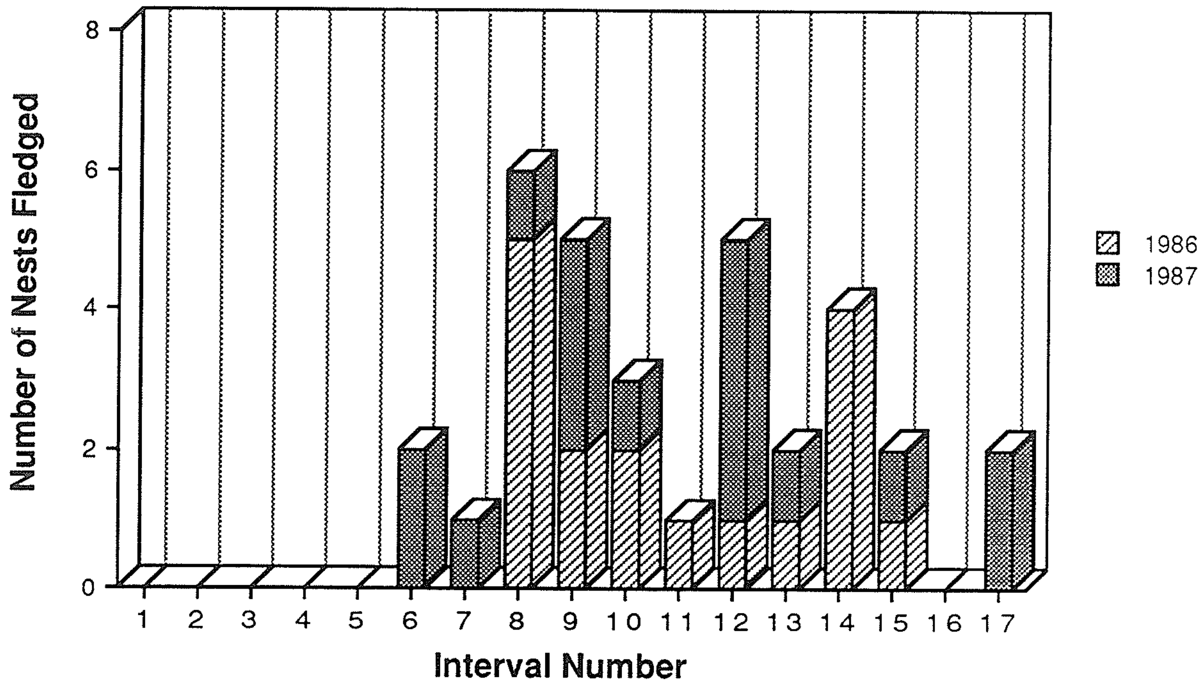

Figure 7. Number of nests that fledged within each 5-day intervals. The first and 17th intervals started on 11 May and 30 July, respectively.

Nest attentiveness, nestling age, and early and late broods

Only females brooded nestlings. As shown in Fig. 8, mean total brooding time decreased significantly with nestling age (Spearman rank correlation test: r_S= -0.943; $P < 0.05$). As the mean brooding time decreased , so did the mean number of brooding bouts (Fig. 9). Nevertheless, the negative relationship with nestling age was not significant (r_S= -0.829; $P > 0.05$).

The time spent perched by the nest was extremely variable; thus, all brood sizes were combined for this analysis to produce the largest sample size. Although differences in perching time between males and females were not significant (Wilcoxon matched-pairs signed-rank test, T(6)= 5, $p > 0.05$, Table 4), male perching values alone showed a significant negative correlation with nestling age (Spearman rank correlation test for the male: r_S= -0.943; $P < 0.05$, for the female: r_S = -0.143; $P > 0.05$) (Fig. 10). For all brood sizes combined, females brooded early broods significantly more than late broods (Wilcoxon matched-pairs signed-rank test, T(6)=0, $p < 0.05$) (Fig. 11).

Feeding rates, nestling age, and brood size

For both summers and all brood sizes combined, a total of 1726 feeding trips was recorded for all the nests observed throughout the nestling period. Males performed significantly more feeding trips than females (Table 5). Mean feeding rate (number of feeding trips $*$ nestling^{-1} $*$ 90 min^{-1}) by the pair, and for each observation day,

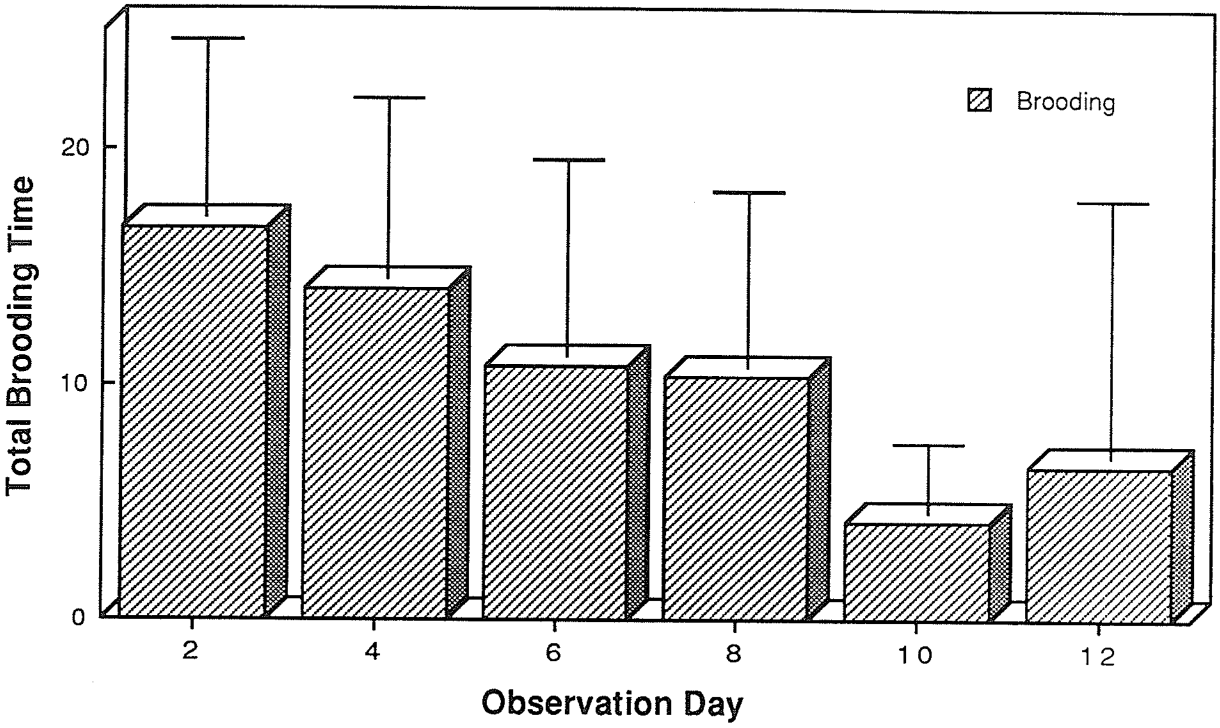

Figure 8. Mean total brooding time by females (total brooding time (min) * nestling^{-1} * 90min^{-1}) per observation day (brood sizes 3 and 4 combined).

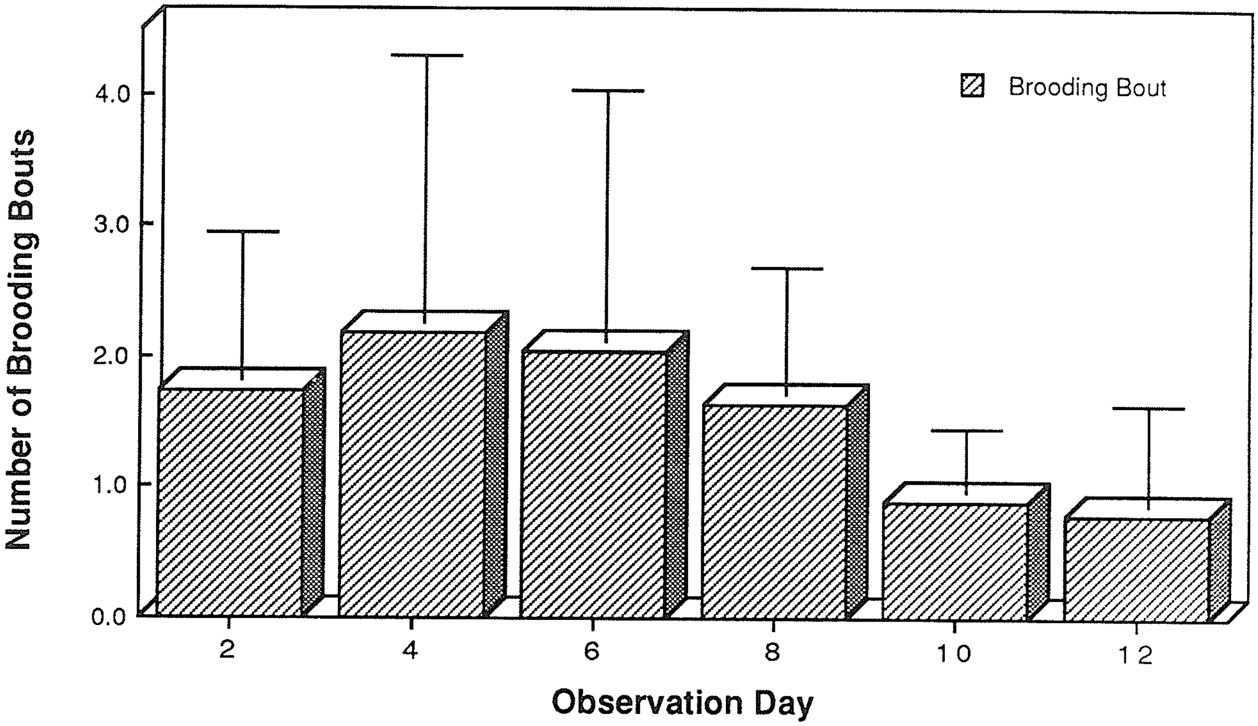

Figure 9. Mean number of brooding bouts (number of brooding bouts * nestling^{-1} * 90min^{-1}) per observation day (brood sizes 3 and 4 combined).

Table 4

Mean daily adult time spent perched by the nest per hour of observation (brood sizes 3 and 4 combined).

	Mean Total Perch Time (min)	
Observation Day	Male	Female
2	1.7	1.1
4	1.3	1.7
6	1.4	1.9
8	1.1	1.8
10	0.6	0.5
12	0.5	1.7

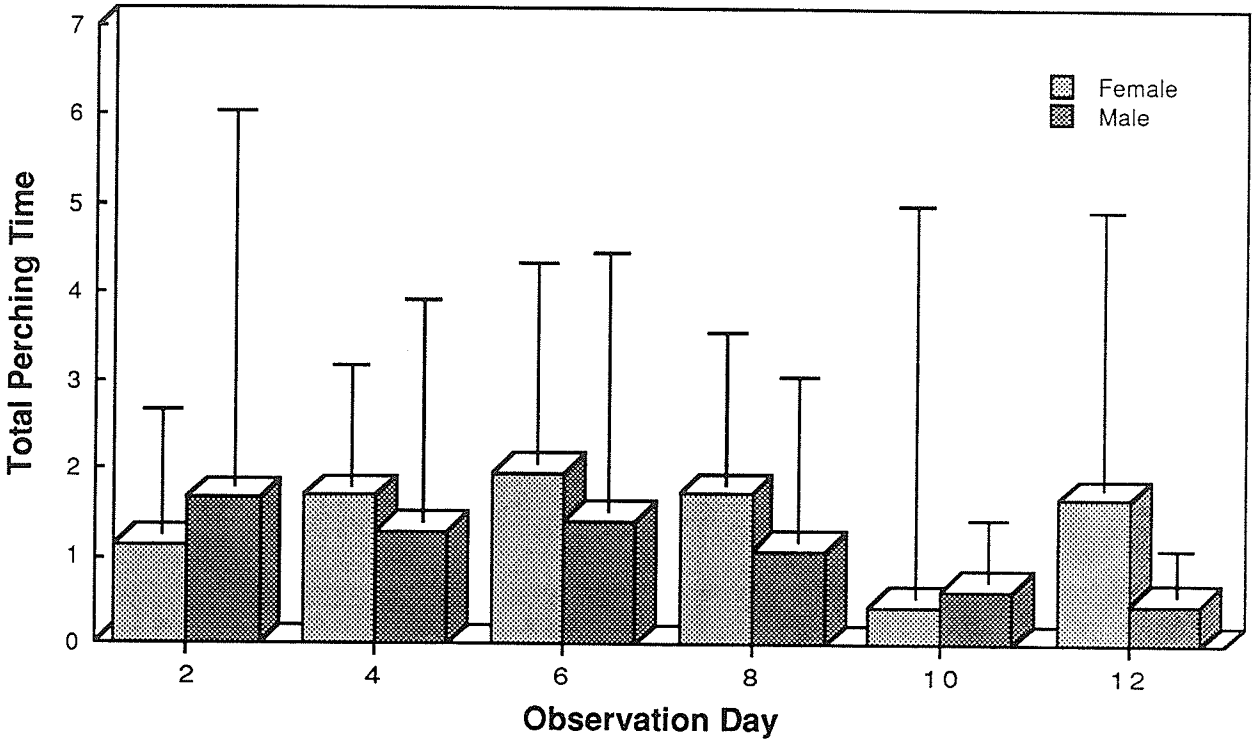

Figure 10. Mean perching time (min $*$ nestling^{-1} $*$ 90min^{-1}) by male and female robins, for each day-period (brood sizes 3 and 4 combined).

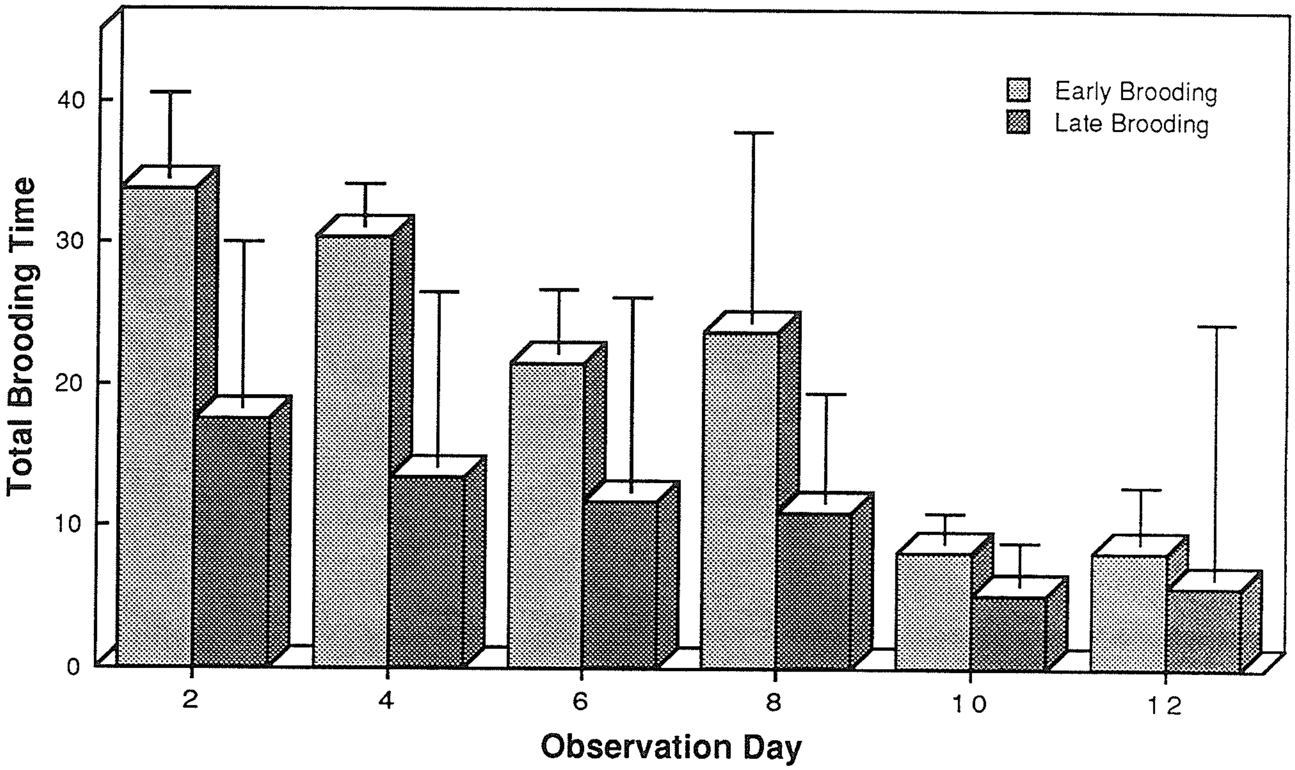

Figure 11. Mean brooding times of female robins (total brooding time (min) $*$ nestling^{-1} $*$ 90min^{-1}) per observation day, compared between early and late broods of 3 and 4 young combined.

Table 5

Total number of feeding trips observed, its relation to sex, and total observation time.

	Male	Female	Both
Total number of feeding trips[1]	1037	689	1726
Sexual percentage of total number	60.1%	39.9%	100%
Overall feeding rates (feeding trips/hour)	3.9	2.6	6.5

[1] Chi- square= 70.6; df= 1; $p < 0.05$

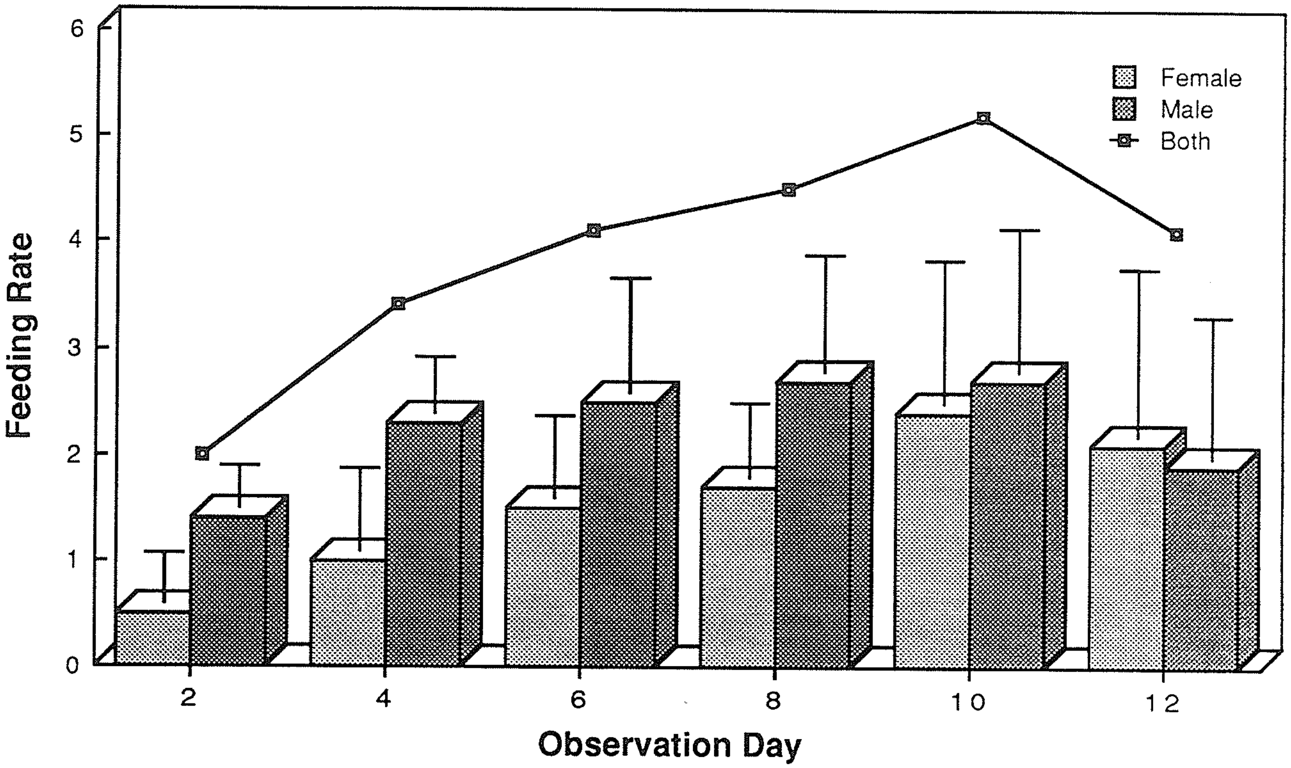

Figure 12. Mean feeding rates by sex and by pair throughout the nestling period (brood sizes 3 and 4 combined).

increased significantly as nestlings grew older, until it peaked on day 10 (Spearman rank correlation test : r_s= 1; $P < 0.05$) (Fig.12). Feeding rates decreased on day 12 . Male feeding rate followed the same pattern of increase as that of the pair's, but by a very small margin it was not significant (Spearman rank correlation test : r_s=

0.975; $P > 0.05$). Female feeding rates, on the other hand, were significantly correlated with nestling age throughout the nestling period (r_s= 0.942; $P < 0.05$). When compared with females, males showed significantly higher feeding rate until day 10, when they were the same as those of their mates. As Fig. 12 shows, female feeding rate increased steadily from approximately a third of those of the male on day 2, to a non-significant difference by observation day 10. On day 12 the average female rate was slightly higher than the male's but this difference was not significant (Table 6). There were no significant differences in the mean feeding rate whether the pair fed 3 or 4 nestlings (Table 7).

Prey types delivered by males and females

Over all prey type categories, 2026 food items were delivered to the nestlings. Males delivered significantly more items than females (Table 8). The 6.0% of the total number of items delivered that could not be identified (Table 8) were discarded from further analysis. Parents fed a wide variety of prey types to their nestlings (Table 9). Males delivered higher percentages for almost every prey type, and for all the ones present in at least 1% of all feeding trips.

Table 6

Mean feeding rates by sex for brood sizes 3 and 4 combined.

	Mean Feeding Rates		
Observation Day	Male	Females	Both
2	1.4 [a] (0.4) [c]	0.5 (0.5)	1.9
4	2.3 [a] (0.5)	1.0 (0.8)	3.3
6	2.5 [a] (1.1)	1.5 (0.8)	4.0
8	2.7 [a] (1.1)	1.7 (0.7)	4.4
10	2.7 [b] (1.3)	2.4 (1.3)	5.1
12	1.9 [b] (1.3)	2.1 (1.6)	4.0

[a] ANOVA to test for difference between male and female; $F > 11.9$; $p < 0.05$.

[b] ANOVA to test for difference between male and female; $F < 2.9$; $p > 0.05$.

[c] SD.

Table 7

Mean feeding rates by sex for broods of 3 and 4 young.

	Mean feeding rates			
	Male		Female	
Observation Day [a]	3 young	4 young	3 young	4 young
2	1.4 (0.2) [b]	1.4 (0.6)	0.6 (0.6)	0.5 (0.4)
4	2.6 (0.2)	1.6 (0.8)	1.0 (0.7)	0.8 (0.8)
6	2.5 (1.0)	2.4 (1.1)	1.5 (0.6)	1.6 (0.9)
8	3.1 (1.5)	2.2 (0.6)	1.6 (0.6)	1.7 (0.8)
10	2.9 (1.2)	2.4 (1.4)	2.3 (1.4)	2.3 (1.3)
12	1.9 (1.3)	2.0 (1.3)	2.2 (1.4)	2.1 (1.7)

[a] ANOVA to test for difference between brood size;
$F < 2.9$; $p > 0.05$.

[b] SD.

Table 8

Total number of food items delivered by parent robins.

	Male	Female	Both
Total number of food items delivered[1]	1250	776	2026
Percentage of total number	61.7%	38.3%	100%
Unknown items out of total	69	53	122
Unknown percentage out of each total	5.5%	6.8%	6.0%

[1] Chi- square= 110.9; df= 1; $p< 0.05$

Table 9

All prey types delivered by male and female robins, for all brood sizes and the two years combined. Prey types are ordered by their affiliation (i.e. all larvae in contiguous lines), and frequency (decreasing order). P.P., percentage of appearance as a food item; T.I., total number of individuals (or units) delivered; P.I.M., percentage of the T.I. delivered by males; P.I.F., percentage of the T.I. delivered by females.

Prey Type	P.P.	T.I.	P.I.M.	P.I.F.
Midge	35.1	4293	60.9	39.1
Earthworm	33.6	1633	63.6	36.4
Thick earthworm	0.64	31	61.3	38.7
Thin earthworm	2.3	90	54.4	45.6 Larvae
6.4	144	73.6	26.4	
Thick larvae	2.8	93	74.2	25.8
Thin larvae	3.3	80	55.0	45.0
Geometrid larvae	1.5	34	67.6	32.4
Tabanid larvae	0.9	28	60.7	39.3
Berry	2.1	87	78.2	21.8
Unknown insect	2.1	42	85.7	14.3
Dragonfly	2.0	39	53.8	46.2 Mayfly
1.2	49	75.5	24.5	
Damselfly	1.1	70	42.9	57.1

continued...

Table 9 continued

Prey Type	P.P.	T.I.	P.I.M.	P.I.F.
Caddis fly	0.9	28	75.0	25.0
Lacewing	0.9	34	35.3	64.7
Crane fly	0.7	13	69.2	30.8
Skimmer	0.7	17	58.8	41.2
Moth	0.6	12	50.0	50.0
Fly	0.4	6	83.3	16.7 Leach
0.3	8	62.5	37.5	Spider
0.3	5	40	60	
Fish	0.2	6	16.7	83.3

When the most common prey categories were considered, males delivered significantly higher percentages for all (Table 10).

The correlation between nestling age and prey type delivered was explored for the most common prey categories: worms, midges, and larvae. For each observation day, worms represented between 60 and 80% of these categories' combined total (Fig. 13). These percentages were positively correlated with nestling age (Spearman rank correlation test : $r_s = 0.900$; $P < 0.05$). Percentages of larvae delivered were also positively correlated with nestling age, but in this case negatively ($r_s = 0.942$; $P < 0.05$). Percentages of midges were not correlated ($r_s = 0.942$; $P > 0.05$), and remained relatively constant throughout.

Dry-weight delivery rates, nestling age, brood size, and early and late broods

A total of 18,305 mg of dry-weight was delivered to all nestlings. Males fed almost twice as much dry-weight as did the females (Table 11). Dry-weight delivery rates by the pair increased significantly with nestling age (Spearman rank correlation test : $r_s = 0.942$; $P < 0.05$) (Fig. 14). This increase followed a pattern that was similar to that of the feeding rate, but here the positive correlation included day 12. In other words, the linear correlation between dry-weight delivery rates and nestling age continued to be significant beyond day 10, although feeding rate did not.

Table 10

Counts of prey categories' presence in all feeding trips, and results of chi-square tests for significant sexual differences.

Prey Category	Males	Females	Chi-square
Midge	381	279	15.8 [a]
Worm	400	232	44.7 [a]
Larvae	89	32	26.9 [a]
Insect	33	7	16.9 [a]
Berry	28	11	7.4 [a]

[a] df=1; $p < 0.05$.

Table 11

Total dry weight delivered to nestlings by males and females, over the total observation time.

	Male	Female	Both
Total dry-weight delivered (mg)	11,687.5	6,618.2	18,305.7
Percentage of total number	63.8%	36.2%	100%

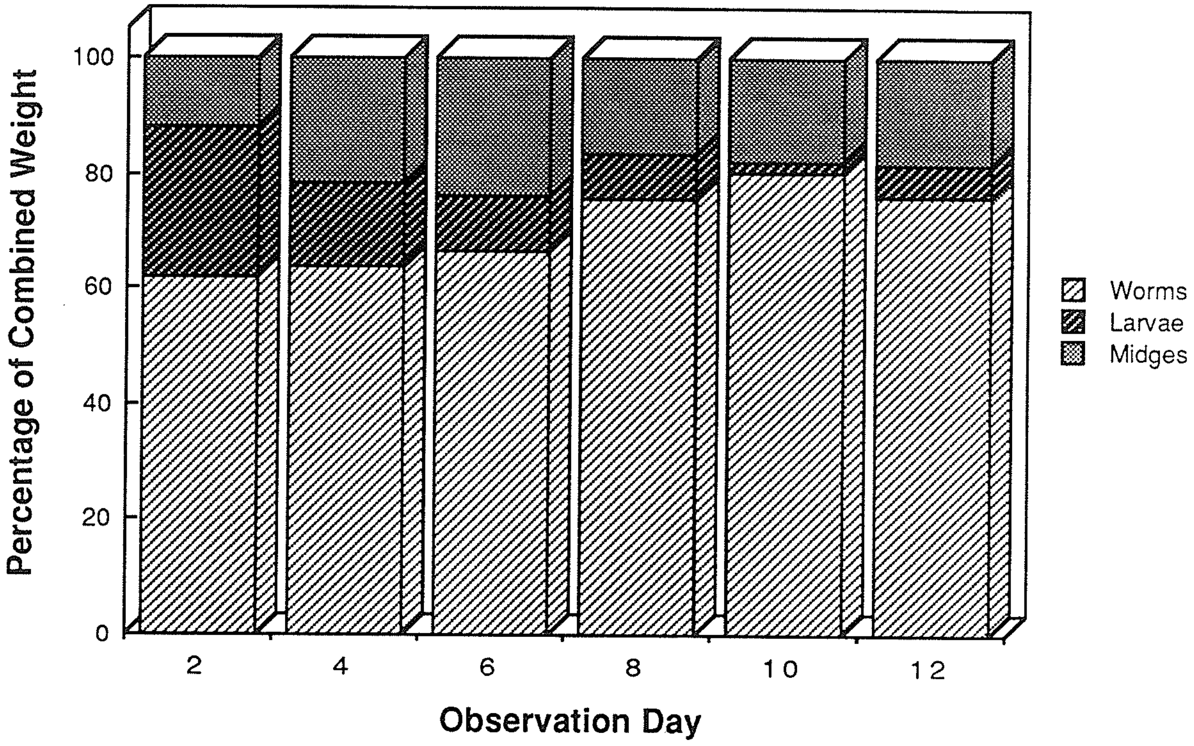

Figure 13. Percentages of individual prey for three major prey types out of their combined total (both years combined).

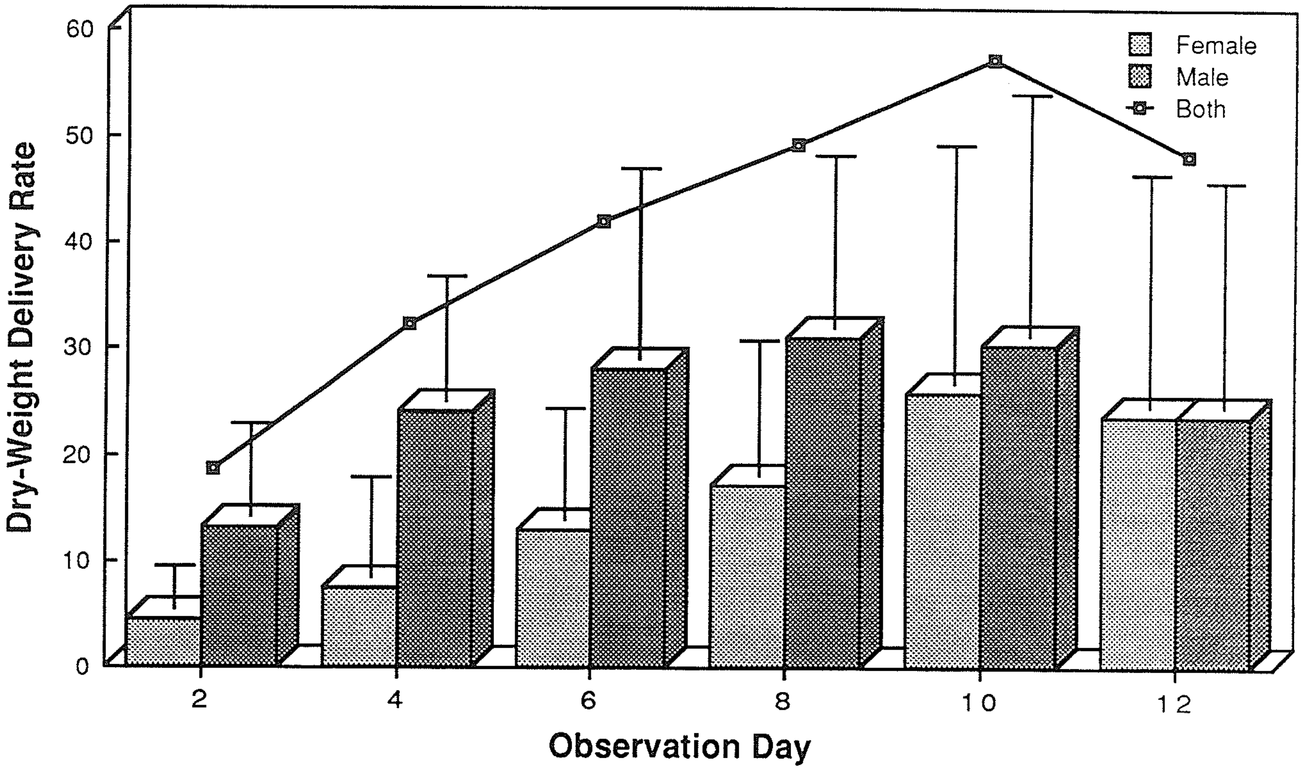

Figure 14. Mean dry-weight delivery rates (trips * nestling^{-1} * 90min^{-1}) by sex and by pair, throughout the nestling period (brood sizes 3 and 4 combined).

Dry-weight delivery rate patterns for males were basically the same as those found for their feeding rate. Again, by a very small margin, they did not represent a significant linear correlation with nestling age (Spearman rank correlation test : $r_s = 0.900$; $P > 0.05$). Female dry-weight delivery rates (as with their feeding rates) were significantly correlated with nestling age throughout the nestling period (Spearman rank correlation test : $r_s = 0.943$; $P < 0.05$). Males delivered significantly more dry-weights than females until day 10, when (although still higher) their deliveries did not differ significantly from those of the females.

On day 12, female and male dry-weight delivery rates were virtually the same (Table 12). Dry-weight delivery rates were not significantly different when the pair was feeding 3 or 4 nestlings (Table13).

The pair's dry-weight delivery rate increased significantly with nestling age in late broods (Spearman rank correlation test: $r_s = 0.9$; $P < 0.05$), but did not vary significantly in early ones (Spearman rank correlation test: $r_s = 0.6$; $P > 0.05$), (Fig. 15). Analyzing each sex individually, male dry-weight delivery rates did not increase significantly with nestling age in early broods (Spearman rank correlation test: $r_s = -0.1$; $P > 0.05$), but did so in late ones (Spearman rank correlation test: $r_s = 0.9$; $P < 0.05$). Female rates increased significantly in both early (Spearman rank correlation test: $r_s = 0.9$; $P < 0.05$), and late ones (Spearman rank correlation test: $r_s = 1.0$; $P < 0.05$).

Dry-weight delivery rate in late broods appeared to be greater than in early ones but this difference was not significant because of a slight reversal of this trend on day 2 (Wilcoxon matched-pairs signed-rank test, T(6)= 1, $p > 0.05$), (Fig. 15). A similar situation occurred with the female rates considered individually, but here the aleged reversal was on day 8 (Wilcoxon matched-pairs signed-rank test, T(6)= 1, $p > 0.05$). Male rates in early and late broods were more similar (Wilcoxon matched-pairs signed-rank test, T(6)= -3, $p > 0.05$).

Instances of defense observed

Table 14 shows that females uttered significantly more alarm calls than males. Females also uttered more distress chirps but this difference was not significant. Males, on the other hand, performed more chases than females but this difference was not significant.

Fledgling care and early and late broods

Females were responsible for 60% of all feedings and 60% of the alarm calls associated with fledglings (Table15). Of all nests observed, 12 were early and 11 were late. At early nests, male and female parents performed equal numbers of feedings and equal numbers of alarm calls. At late nests, on the other hand, females performed significantly more feedings and alarm calls than males (Table 15).

Table 12

Daily mean dry-weight delivery rates (mg * nestling^{-1} * 90min^{-1}) by sex (brood sizes 3 and 4 combined).

	Mean dry-weight delivery rate		
Observation day	Male	Females	Both
2	13.3 [a]	4.4	17.7
4	24.0 [a]	7.4	31.4
6	28.3 [a]	12.9	41.2
8	31.1 [a]	17.2	48.3
10	30.4 [b]	26.0	56.4
12	23.7 [b]	23.5	47.2

[a] ANOVA to test for difference between male and female; $F > 9.5$; $p < 0.05$.

[b] ANOVA to test for difference between male and female; $F < 1.4$; $p > 0.05$.

Table 13

Daily mean dry-weight delivery rates by sex for brood sizes 3 and 4.

	Mean dry-weight deliverey rates			
	Male		Female	
Observation Day [a]	B.Size 3	B.Size 4	B.Size 3	B.Size 4
2	12.3 (9.6) [b]	14.4 (7.7)	5.4 (5.2)	3.3 (2.9)
4	25.1 (10.3)	20.5 (13.2)	6.6 (6.6)	10.0 (12.4)
6	33.3 (20.8)	20.0 (15.1)	13.0 (9.4)	12.8 (11.5)
8	33.3 (20.0)	28.2 (12.7)	16.3 (8.8)	18.3 (16.6)
10	35.6 (23.4)	25.1 (21.8)	29.8 (24.4)	22.2 (20.2)
12	23.9 (13.0)	23.3 (29.3)	24.8 (15.7)	21.5 (28.5)

[a] ANOVA to test for difference between brood size; $F < 2.2$; $p > 0.05$.

[b] SD

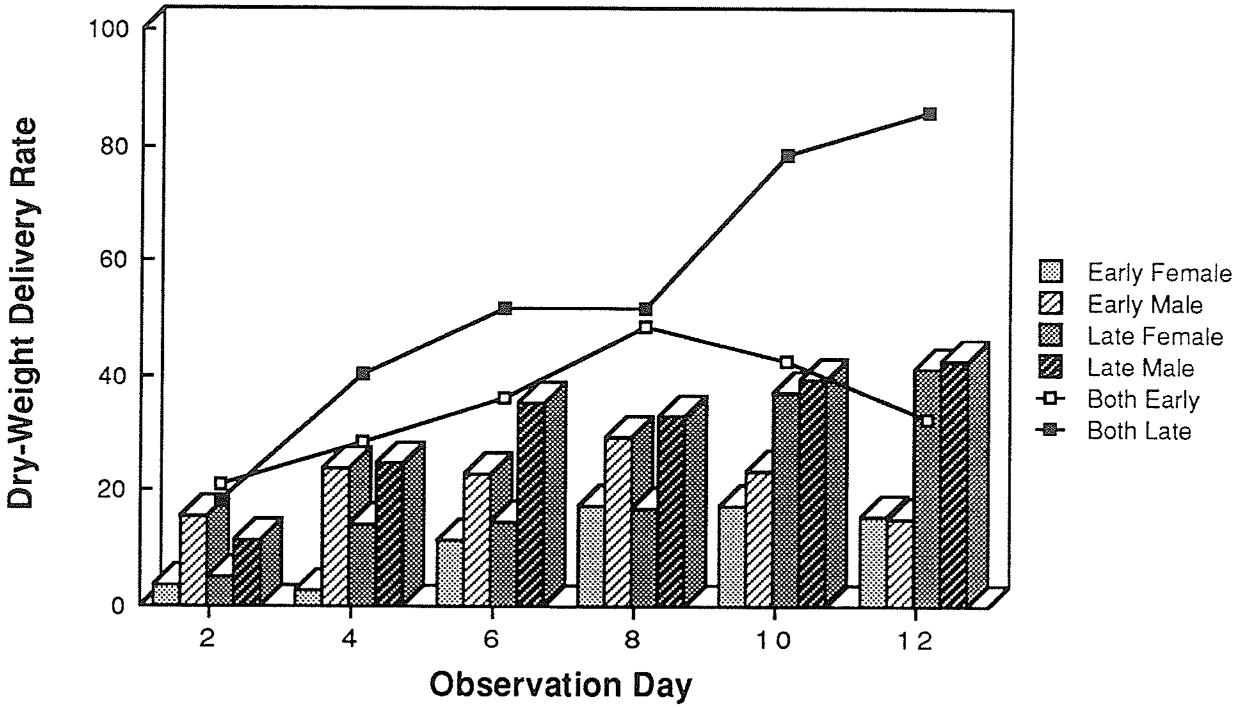

Figure 15. Mean dry-weight delivery rates (trips * nestling^{-1} * 90min^{-1}) by sex and pair, in early and late broods (see text).

Table 14

Total count of defensive actions performed by parent robins.

	Male	Female	Total	Chi-square
Alarm Call	4	19	23	9.8 [a]
Distress Chirp	3	6	9	1 [b]
Chase	29	19	48	2.1 [b]

[a] df=1; $p < 0.05$.

[b] df=1; $p > 0.05$.

Table 15

All feedings and alarm calls recorded for adults associated with fledglings, in early and late broods.

	Feedings			Alarm Calls		
Brood	Males		Females	Males		Females
Early & Late	16	[a]	24	18	[a]	27
Early	12	[b]	12	14	[b]	13
Late	4	[a]	12	5	[a]	13

[a] Chi- square test; df=1; $p < 0.05$.

[b] Chi- square test; df=1; $p > 0.05$.

DISCUSSION

The information available on patterns of PI apportionment in passerines is limited. Nevertheless, the patterns reported are diverse. This diversity, though, must be taken with caution. This problem is relatively new, and there is no consensus amongst different authors about which are the key variables that might affect these patterns. This in turn has resulted in PI being measured in different ways, by different methodologies, and for differing brood sizes (see Grundel 1987 for a comparison of the different estimators of feeding effort used). A note of caution then has to be kept in mind as (at least in theory) this lack of consensus could yield different results that are, in fact, artifacts of different methodologies.

American Robin feeding effort and the diversity of patterns reported for other monogamous passerines

To my knowledge, the following is an updated, brief review of the patterns of nestling feeding effort among monogamous passerines. Different groupings of species based, first, on their temporal nestling feeding patterns, and secondly on that shown in the relative effort of each parent. Kendeigh (1952) attempted a more comprehensive review in order to find phylogenetic or ecological trends. Unfortunately, his review did not yield a synthesis. What follows is intended to give an idea of how relatively common each pattern is amongst monogamous passerines studied so far.

In the present study, the feeding rates for both sexes increased as nestlings grew older, peaked on day 10, but then decreased. This pattern is similar to that in several other species (Royama 1966, Seel 1969, Leffelaar and Robertson 1986, and Grundel 1987). Biermann and Sealy (1985) and Breitwisch et al. (1986), on the other hand, found a continuous increase in feeding rate with nestling age; and still Carlson and Moreno (1986) found an increase until approximately the third quarter of the nestling period, and then leveled until the young fledged.

Male American Robins delivered more prey than the females. A similar asymmetrical pattern has also been reported for several other monogamous passerine species: Brown Thrashers (*Toxostoma rufum*, Heagy and Best 1983), Common Grackles (*Quiscalus quiscula*, Howe 1979), Gray Catbirds (*Dumetella carolinensis*, Johnson and Best 1983), Great Tits (*Parus major*, Royama 1966), Fieldfares (*Turdus pilaris*, Carlson and Moreno 1986), Mountain Chickadees (*Parus gambeli*, Grundel 1987), Rooks (*Corvus frugileus*, Røskaft 1983), and Yellow Warblers (*Dendroica petechia*, Biermann and Sealy 1982).

Equal contributions by both sexes have been documented for House Martins (*Delichon urbica*, Bryant and Westerterp 1980), Dot-winged Antwrens (*Microrhopias quixensis*, Greenberg and Gradwhol 1983), Eastern Kingbirds (*Tyrannus tyrannus*, Morehouse and Brewer 1968), Field Sparrows (*Spizella pusilla*, Best 1977), Nashville Warblers (*Vermivora ruficapilla*, Knapton 1984), Northern Mockingbirds (*Mimus polyglottos*, Breitwisch et al. 1986), Savannah Sparrows (*Passerculus sandwichensis*, Bédard and Meunier 1983), and Tree Swallows (*Tachycineta bicolor*, Leffelaar and Robertson 1986).

To my knowledge, only two species have been found in which females feed nestlings proportionately more than males (Eastern Bluebirds, *Sialia sialis*, Pinkowski 1978, and House Sparrows, *Passer domesticus*, Seel 1966).

Nestling food

Nestling robins were fed more worms and fewer larvae as they grew older, while midges were fed at constant rates. Worms were the largest of the major prey types fed to nestlings. Thus robins appear to feed larger prey items as the nestlings grow larger. Best (1977) showed that girth (more than length) of the prey determined the ingestability of a nestling food item, and Fägerstrom et al. (1983) argued that this should be the case if parents delivered prey loads optimally. Nevertheless, different nutritional contents and/or prey availability rather than prey size may be important here.

The same prey pattern of prey size against time has been observed in other studies (Best 1977, Pinkowski 1978, Carlson and Moreno 1986). The findings of the later two studies might have special relevance to the robin's case, since only thrushes are involved. Pinkowski concluded that prey availability, ingestability, and nutritional value influenced the choice of prey delivered to Eastern Bluebirds. The three major prey categories for the robin contained virtually the same protein percentages (based on literature values): midges 60%, larvae 63% (Biermann 1980), and worms 60% (Krapu and Swanson 1975). Midges apparently were readily available (Busby and Sealy 1979, Guinan and Sealy 1987), and probably are easily digested because of their soft abdomens. In fact, they were fed at fairly constant rates throughout the nestling season by both parents. Larvae, on the other hand, were fed predominantly to younger nestlings, as were smaller worms. This prey, when compared to the larger worms, was easily ingested by the nestlings (personal observation). Earthworms were the only food item delivered by fieldfares (Carlson and Moreno 1986) and thus the nutritional argument is excluded. In their study, the size of this prey increased with nestling age. They concluded that fieldfares fed smaller worms (infra-optimal in terms of energy maximization per feeding trip) because they were more easily ingested by younger nestlings. As nestlings grew this constraint disappeared; the adults then preferentially loaded the largest worms as food items. Although robins certainly were not single-prey feeders, the preponderance of worms as food permits a reasonable extrapolation of Carlson and Moreno's conclusions to this study. Moreover, the fact that the frequency of larvae and worms as meals vary inversely over time (assuming they have the same nutritional value) seems to point to the same conclusion. Larvae were probably preferred over worms as more manageable food units for younger nestlings, but were later abandoned for larger units of food when the nestlings were old enough to handle them.

Brood size and food delivery

No differences were found in the feeding rates or dry-weight delivery rates to nestlings between broods of 3 or 4 young. A similar situation was found by Best (1977), Pinkowski (1978), Bédard and Meunier (1983), and Breitwisch et al. (1986). In other cases, food deliveries have been noted to be fewer in larger broods (Royama 1966, Morehouse and Brewer 1968, Leffelaar and Robertson 1986, Grundel 1987). As Royama (1966) argued, the number of nestlings in the nest should inversely affect the rate of heat loss of the brood as a whole. More young generate more metabolic heat and hence require less brooding time, and less food from the tending adults (the latter, at least, being more relevant in the early stages before thermoregulation is achieved). Nevertheless, Royama found differences when he compared broods of 3 with broods of 8, 10, and 13 (the last three broods fed at the same rate). It would not be meaningful (based on a comparison between brood sizes 3 and 4), to conclude that unlike the Great Tits, food delivery in the robin is not affected by brood size.

The pitfalls of the methodological artefact mentioned above seem to be particularly relevant here. It is difficult to decide which brood sizes are different enough (as perceived by the caring adults), and consequently there are no hard grounds to refute or support the effect of this variable based on a comparison between a set of arbitrarily chosen brood sizes.

Brooding, feeding and defense behavior

Female feeding rates and dry-weight delivery rates in the robin increased more dramatically than those of the male but nevertheless were below the males' until day 10 when the two were no longer significantly different. This sharp increase in female feeding rate has also been reported by other authors (Morehouse and Brewer 1968, Pinkowski 1978, Biermann and Sealy 1982, Johnson and Best 1983, Carlson and Moreno 1986, Grundel 1987). These studies associated this increase with the decrease in the female's brooding activity, and greater food demand by the young. As argued by Carlson and Moreno (1986) and Grundel (1987), the early-brooding female (due to her high nest attentiveness schedule) performed few foraging trips and, whenever such trips were made often ate the prey herself. Furthermore, Swihart and Johnson (1986) reported that on average during the nestling period, female robins ate more of the prey captured per foraging trip than did males.

Female robins decreased both their brooding time and number of brooding bouts as the nestlings grew. This observation, tied in with the parallel increase in feeding, supports the hypothetical existence of a compromise between the time allocated to brooding and to self feeding. Thus, when a female leaves on a brooding recess, she is primarily moved by the nutritional needs of herself rather than of her young (early in the nestling period).

In addition, brooding females more actively defended their broods than did males (Carlson and Moreno 1986). I measured two descriptors of nest defense, vocalizations and chases. Vocalizations uttered mainly by the females were usually performed either from or near the nest. It is interesting to note that this type of defense did not require the female to leave the nest, particularly important if her main role is brooding. On the other hand, males appeared to be the main actors in most chases, which involved leaving the nest; usually; the male reappeared on the next feeding trip.

In short, it seems that female robins are specifically tied up with PI components involving a close spatial association with the nest , namely brooding and (probably as a corollary of this) nest defense. Males, on the other hand, seem to be in charge of most of the feeding duties and PI components like defense chases that do not involve a necessarily close association with the nest.

Female PI apportionment patterns

Female robins brooded early broods more than late broods.ß On the first two thirds of the nestling period, males fed late broods and early broods at similar rates, but females (although not significantly) fed late broods at higher rates. Both parents increased their feeding effort from day 10 on in late broods but did not in early ones. The implication of this is discussed below.

Only two studies, to my knowledge, compared parental feeding of early with late broods, Royama (1966) on Great Tits, and Seel (1966) on House Sparrows. Female Great Tits fed late broods less than early ones. Royama argued, first, that the smaller late broods possibly can be fed efficiently by a single parent, the male, and secondly that, since the female has the greatest immediate past investment of the pair (the laying of the clutch), she is the first to slack off. Basically, Royama argued on the basis of parental fatigue. Seel (1966), Finke et al. (1987), and Smith et. al. (1987) tested the fatigue hypothesis by exploring the effect of large brood sizes in first broods on brood size and brood success of the second, but none of the studies found any relationship and concluded there was no such thing as parental fatigue.

Seel's study did not consider the feeding effort of the sexes separately. Pairs of breeding House Sparrows showed slightly lower feeding rates in late broods for 3 out of the 4 brood sizes considered. Seel speculated that higher temperatures might be the reason, as nestlings' temperature could be easily maintained when the air temperature was close to theirs. Warmer weather could probably explain lower brooding times in the robin, but were this the case, the now contradictory higher female feeding rates would remain even more puzzling. Unfortunately, Seel's study does not refer to each individual parent's component in the combined feeding rates nor in any other form of PI. In addition, feeding rates were argued later to be poor estimators of total feeding effort.

The present application of the conclusions of these two studies is limited. Even if the fatigue hypothesis were correct, Royama's (1966) results do not apply in the case of the robin because the females behave oppositely. Seel's temperature hypothesis can not be ignored, but I feel that the explanation of these differences lies in the asymmetry that exists between the reproductive futures of early and late broods. A pair that cares for an early brood has time to attempt a future brood. Then, and for all practical concerns, the pair must (if Trivers' PI definition is correct) behave as if **in fact** it will invest in another reproductive attempt. At least theoretically, there should be a conflict on how much of the limited resources to allocate to this present investment and how much to allocate to the next. Thus, the lower rate of feeding received by the first brood may represent a diversion of PI resources to the "planned" second brood.

Other things being equal, time has been shown to be the main constraint on whether or not to start a new brood (Keller 1979, Finke et al. 1987, Smith et al. 1987). Similarly, older and presumably more experienced females started their first broods earlier and showed smaller inter-brood intervals in all of the double-brooding species studied (Snow 1958, Keller 1979, Smith and Roff 1979, Harper 1985, Smith et al. 1987). The point I am trying to make here is that the possibility of renesting seems to be limited basically by the time in the season. If the pair is brooding an early brood, then the potential for a late brood exists and (assuming robins were selected to maximize their reproductive output each season in the manner described by PI theory), the early-breeding pair should allocate their resources in order to attempt it.

In fact, Finke et al. (1987) working on House Wrens (*Troglodytes aedon*) explored the effects of several variables on the frequency and success of second broods. Neither adult weight nor clutch (or brood) size was correlated with the frequency, size, or success of second broods. The only variable that was significantly correlated (supporting the PI reasoning above) was the time of the season when the first brood fledged.

Similarly, Smith et al. (1987) found the same pattern in Great Tits, although here a second factor correlated significantly. The number of nestlings in the first brood was inversely correlated with the frequency of second broods attempted. Smith and collaborators argued interestingly that this number did not express the magnitude of PI cost, or energy depletion in the female, because the mass of females tending second broods was constant regardless of the size of the previously fledged brood. Hence Smith et al. suggested instead that the size of the first brood was not a depleting cost, or source of parental fatigue, but was an immediate target for the allocation of a certain amount of PI. If the first brood is large enough, more resources are needed, and allocated to fledge it, and fewer are left to "gamble" with the production of the next clutch.

At least two relevant factors seem to have emerged from these studies: the availability of time and facultative allocation of PI resources. Both are maximized in order to rear two broods per season. Finke et al. (1987) found that House Wrens apparently were not limited by clutch/brood size, but Great Tits, and other species reviewed were constrained by time. To my knowledge, only Royama (1966) quantified sexual daily patterns of PI allocation in early and late broods, and, as expected from the previous argument, he reported different patterns of PI allocation in the two. Hence PI resources in early broods seem to be allocated in the form of a compromise between the present brood and the next one; no such compromise should exist with the allocation of PI in late broods since they are not followed immediately by another brood. In early broods females allocate PI resources simultaneously to the nestlings of that brood and the eggs of the next one. Hence, females tending late broods could (at least in theory) allocate PI exclusively to nestlings of that brood. This might explain the greater feeding effort reported by female robins rearing late broods.

Male PI apportionment patterns

Male robins apparently had a restricted set of alternative strategies open to increase their reproductive success, the main one was double-brooding. In fact, every double brooded pair in this population doubled or nearly doubled the number of fledglings they produced in a single year when compared to the single-brooded pairs.

Male robins invested heavily and similarly in first and second broods. Following Maynard Smith (1977, 1982) this would require some combination of the following factors to be maintained: greater efficiency of biparental care over uni-parental care, negative effects of parental care on female egg production, and low probability of remating with a new female after deserting the first.

No remating, i. e. changing mates after pair formation, or (for practical means in this study) clutch initiation was recorded at Delta Marsh. Though further research is needed, there seems to be little (if any) advantage in this population for a male to desert in order to remate, since this will only lower his RS. For this study, the other two factors that should influence the male's choice between caring or deserting: uni- versus biparental care effectiveness, and effect of female care on egg production, might be more relevant as determinants of the male's pattern of PI allocation. Because remating is improbable, the remaining alternatives for males to increase their fitness seem to be somehow dependent on those chosen by the female.

The most obvious channel of male investment seems to be that of producing an optimal supply of sperm in order to maximize the chances of the mate's ova. This investment is known to be energetically inexpensive (Ricklefs 1974, King 1978). Nest defense is another alternative. In this study the male specialized on that defense, i. e. chases that took the mobbing parent away from the nest. This makes sense, since the female spent most of her time at the nest brooding.

A third, high investment alternative is an increase in feeding effort. Increased feeding effort would have a three-fold advantage if the brood is an early one. First, the male should thereby enhance nestling or fledgling survival. Second, he shortens the nestling period, and thus relaxes (to some extent) some of the time constraint involved in starting a second brood. The third aspect may be the most important. Because feeding effort is the greatest energetic expense in this and the previous period (Bryant and Westerterp 1980, Biedenweg 1983, Jones 1987), a male that increases his share over his female's probably permits her to allocate the necessary amount of energy to produce a larger second brood.

This is a two-fold strategy of direct investment in the present brood, and simultaneous indirect investment in the next one. A male that behaves so as to maximize his reproductive success should, in early broods, invest in high feeding effort to maximize fledgling survival and chances of a second brood, and in late broods, solely (but sufficiently) to enhance fledgling survival.

PI apportionment patterns in the fledgling period

Only for one double brooded-species, the Chipping Sparrow (*Spizella passerina*, Keller 1979), did the male exclusively feed fledglings from the early brood, while the female starts the late brood.

Usually both sexes care for early brood young at varying degrees. Nevertheless, the male has generally been reported to have a greater share of parental care duties than the female (Snow 1958, Smith and Roff 1979, Harper 1985). In late broods, both adults taking care equally have been reported for all of the above species.

In the present study, American Robins differed radically from the species mentioned above. With early brood young, equal number of feedings and alarm calls were recorded for each sex. In contrast, youngs from late broods were fed and defended almost entirely by females. Further investigation is required to clarify PI in this stage, as my results could be missleading if brood division occurs in this species.

As a closing remark, it is interesting to point out that Trivers' (1972) influential paper on PI initiated also an approach to the study of male PI patterns that hinges heavily on the problem of mate desertion (with the exception of Maynard Smith 1977, 1982). This approach could be characterized as follows. First, one should ask whether or not the deserted mate would care for the deserted offspring, and, if so, how effectively would it do so (see Grafen & Sibly 1978, Breitwisch et al. 1986). If both answers were positive, mate desertion was supposed to be favored by selection. In other words, the optimal strategy was that of no PI by the deserter. Though this attitude is not strictly wrong, it is biased towards one side when the problem is in actuality a two-sided one. Although deserting might in fact be the cheapest strategy, more expensive strategies (within sensible limits) would still be favored if they result in higher fitness values. Throughout this discussion I have focused my hypotheses (following Maynard Smith's work) not exclusively on the desertion approach, but also on whether or not deserting _per se_ would increase the fitness of the would-be-deserter (and thus be favored by selection) **more** than the strategy of staying and continuing to invest. I believe that this line of reasoning, incorporating both aspects, reflects more closely the mechanics of the selective process at work and should be preferred over the former.

LITERATURE CITED

Baerends, G. P. , R. H. Drent, P. Glas, and H. Groenewold. 1970. An ethological analysis of incubation behavior in the Herring Gull. Behaviour Suppl. 17:135-235.

Bateman, A. J. 1948. Intrasexual selection in *Drosophila*. Heredity 2:349-368.

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

Bent, A. C. 1964. Life histories of North American thrushes, kinglets, and their allies. New York, Dover Publications, Inc.

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

Biebach, H. 1981. Energetic costs of incubation on different clutch sizes in Starlings. Ardea 69: 141-142

Biebach, H. 1984. Effect of clutch size and time of the day on the energy expenditure of incubating Starlings (*Sturnus vulgaris*). Physiol. Zool. 57:26-31

Biedenweg, D. W. 1983. Time and energy budget of the Mockingbird (*Mimus polyglottos*) during the breeding season. The Auk 100:149-160.

Biermann, G. C. 1980. Parental care, growth rates and pre-fledging condition of Yellow Warbler nestlings in different brood sizes. Unpublished M. Sc. thesis, University of Manitoba, Winnipeg.

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

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

Breitwisch, R., P. G. Merrit, G. H. Whitsides. 1986. Parental investment by the Northern Mockingbird: male and female roles in feeding nestlings. The Auk 103:152-159.

Bryant, D. and K. R. Westerterp. 1980. The energy budget of the House Martin (*Delichon urbica*). Ardea, 68:91-102

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

Carlson, A. and J. Moreno 1986. Foraging behavior and parental care in the Fieldfare. Ardea 74:79-90

Cartar, R. V. and R. D. Montgomerie. 1987. Day-to-day variation in nest attentiveness of White-rumped Sandpipers. The Condor 89:252-260

Curio, E. K., K. Regelmann, and U. Zimmermann. 1985. Brood defence in the Great Tit (*Parus major*): the influence of life-history and habitat. Behav. Ecol. Sociobiol. 16:273-283.

Darwin, C. R. 1904. The descent of man and selection in relation to sex, 2d. ed. vol. 1. New York, J. A. Hill and Company.

Dawkins, R. and T. R. Carlisle. 1976. Parental investment, mate desertion and a fallacy. Nature 262:131-133.

Drent , R. H. and S. Daan. 1980. The prudent parent: energetic adjustment in avian breeding. Ardea: 68:225-252.

Drent, R. 1973. The natural history of incubation. Pp. 263-311 in Breeding biology of birds (D. S. Farner, Ed.) Washintong D.C., National Academy of Sciences.

Emlen, S. T. and L. W. Oring. 1977. Ecology, sexual selection, and the evolution of mating systems. Science 197:215-223.

Fägerstrom, T., J. Moreno, and A. Carlson. 1983. Load size and energy delivery in birds feeding nestlings: constraints on and alternative strategies to energy-maximization. Oecologia 56:93-98.

Finke, M. A., D. J. Milinkovich, and C. F. Thompson. 1987. Evolution of clutch size: an experimenta l test in the House Wren (*Troglodytes aedon*). J. Anim. Ecol. 56:99-114.

Grafen, A. and R. Sibly. 1978. A model of mate desertion. Anim. Behav. 26:645-652.

Grafen, A. 1982. How not to measure inclusive fitness. Nature 298:425-426.

Greenberg, R. and J. Gradwohl. 1983. Sexual roles in the Dot-winged Antwren (*Microrhopias quixensis*), a tropical forest passerine. The Auk 100:920-925.

Greenlaw, J. S. and W. Post. 1985. Evolution of monogamy in Seaside Sparrows, *Ammodramus maritimus*: test of hypothesis. Anim. Behav. 33:373-383.

Grundel, R. 1987. Determinants of nestling feeding rates and parental investment in the Mountain Chickadee. Condor 89:319-328.

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

Guinan, D. M. and S. G. Sealy. 1987. Diet of the House Wren (*Troglodytes aedon*) and the abundance of the invertebrate prey in the dune-ridge forest, Delta Marsh, Manitoba. Can. J. Zool. 65:1587-1596.

Harper, D. G. C. 1985. Brood division in Robins. Anim. Behav. 33:466-480.

Heagy, P. and L. B. Best. 1983. Factors affecting feeding and brooding of Brown Thrasher nestlings. Willson Bull. 95:279-303.

Hohman, W. L. 1986. Incubation rhythms of Ring-Necked Ducks. The Condor 88:290-296.

Howe, H. F. 1979. Evolutionary aspects of parental care in the Common Grackle, *Quiscalus quiscula*. Evolution 33:41-51.

Howe, R. H. Jr. 1898. Breeding habits of the American Robin (*Merula migratoria*) in eastern Massachusetts. The Auk 15:162-167.

Howell, J. C. 1942. Notes on the nesting habits of the American Robin (*Turdus migratorius L.*). Amer. Midl. Nat. 28:529-603.

Inglis, I. R. 1977. The breeding behavior of the Pink-footed Goose: behavioral correlates of nestling success. Anim. Behav. 27:747-764.

Johnson, E. J. and L. B. Best. 1982. Factors affecting feeding and brooding of the Gray Catbird nestlings. The Auk 99:148-156.

Jones, G. 1987. Time and energy constraints during incubation in free-living Swallows (*Hirundo rustica*): an experimental study using precision electronic balances. J. Anim. Ecol. 56:229-245

Keller, M. E. 1979. Breeding behavior and reproductive success of Chipping Sparrows in northwestern Minnesota. Unpublished M.S. thesis, University of North Dakota, Grand Forks.

Kendeigh, S. C. 1952. Parental care and its evolution in birds. Illinois Biol. Monogr. No. 22.

King, J. R. 1973. Energetics of reproduction in birds. Pp. 78-107. in Breeding biology of birds (D. S. Farner, Ed.). Washinton, D. C., Natl. Acad. Sci.

Knapton, R. W. 1984. Parental feeding of nestling Nashville Warblers: the effect of food type, brood size, nestling age, and time of the day. Willson Bull. 96:594-602.

Krapu, G. L. and G. A. Swanson. 1975. Some nutritional aspects of reproduction in prairie nesting Pintails. J. Wildl. Manage. 39:156-162.

Krebs, J. R. 1970. The efficiency of courtship feeding in the Blue Tit *Parus caeruleus*. Ibis 112:108-110.

Lack, D. 1968. Ecological adaptations for breeding in birds. London, Methuen Press.

Leffelaar, D. and R. J. Robrtson. 1986. Equality of feeding roles and the maintenance of monogamy in Tree Swallows. Behav. Ecol. Sociobiol. 18:199-206.

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

Martin, K. 1973. Breeding density and reproductive success of Robins in relation to habitat structure on logged areas of Vancouver Island, British Columbia. Unpublished M.Sc. thesis. Edmonton, Univ. of Alberta.

Maynard Smith, J. 1977. Parental Investment: a prospective analysis. Anim. Behav. 25:1-9.

Maynard Smith, J. 1982. Evolution and the Theory of Games. Cambridge, Cambridge University Press.

Mock, D. W. 1983. On the study of avian mating systems. Pp. 55-84. in Perspectives in ornithology (A. H. Brush and G. A. Clarck, Jr., Eds.). Cambridge, England, Cambridge Univ. Press.

Morehouse, E. L. and R. Brewer. 1968. Feeding of nestling and fledgling Eastern Kingbirds. The Auk 85:44-54.

Oniki, Y. 1985. Why Robin eggs are blue and birds build nests: statistical tests for Amazonian birds. Ornithol. Monogr., No. 36.

Orians, G. H. 1969. On the evolution of mating systems in birds and mammals. Amer. Nat. 103:589-604.

Oring, L. W. 1982. Avian mating systems. Pp. 1-92 in Avian biology, vol. 6 (D. S. Farner, J. R. King, and K. C. Parkes, Eds.). New York, Academic Press.

Pinkowski, B. C. 1978. Feeding of nestling and fledgling Eastern Bluebirds. Wilson Bull. 90:84-98.

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

Røskaft, E. 1983. Sex-role partitioning and parental care by the Rook *Corvus frugileus*. Ornis Scand. 15:180-187.

Royama, T. 1966. Factors governing food requirement and brood size of nestling Great Tits *Parus major*. Ibis 108:315-347.

Seel, D. C. 1969. Food, feeding rates and body temperature in nestling House Sparrow *Passer domesticus* at Oxford. Ibis 111:36-47.

Shedd, D. H. 1982. Seasonal variation and function of mobbing and related antipredator behaviors of the American Robin (Turdus migratorius). The Auk 99: 342-346.

Skutch, A. F. 1962. The constancy of incubation. Wilson Bull. 74:115-152

Skutch, A. F. 1976. Parent birds and their young. Austin, Univ. Texas Press.

Slack, D. 1976. Nest guarding behavior by male Gray Catbirds. The Auk 93:292-300.

Smith, J. N. M. and D. A. Roff. 1979. Temporal spacing of broods, brood size, and parental care in the Song Sparrow (*Melospiza melodia*). Can. J. Zool. 58:1007-1015.

Smith. H. G., H. Kallander, and J. Nilsson. 1987. Effect of experimentally altered brood size on frequency and timing of second clutches in the Great Tit. The Auk 104:700-706.

Snow, D. W. 1958. The breeding biology of the Backbird (*Turdus merula*) at Oxford. Ibis 100:1-30.

Swihart, R. K. and S. G. Johnson. 1986. Foraging decisions of American Robins: somatic and reproductive tradeoffs. Behav. Ecol. Sociobiol. 19:275-282.

Thompson, S. C. and D. G. Raveling 1987. Incubation Behavior of the Emperor Geese compared with other geese: interaction of predation, body size, and energetics. The Auk 104:707-716

Trivers, R. L. 1972. Parental investment and sexual selection. P.p. 136-179 in Sexual selection and the descent of man 1871-1971. (B. Campbell, Ed.). Chicago, Aldine Publishing Company.

Verbeek, N. A. M. 1970. Breeding ecology of the Water Pipit. The Auk 87:425-451.

White, F. N. and J. L. Kinney. 1974. Avian incubation. Science, 186:107-115.

Williams, G. C. 1966. Adaptation and natural selection. Princeton, Princeton Univ. Press.

Wittenberger, J. F. and R. L. Tilson. 1980. The evolution of monogamy: hypothesis and evidence. Ann. Rev. Ecol. Syst. 11:197-232.