FACTORS AFFECTING HOW MALE AND FEMALE BOBOLINKS APPORTION PARENTAL INVESTMENTS

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ABSTRACT.—Male and female Bobolinks (*Dolichonyx oryzivorus*) adjust the amount of time spent brooding and provisioning nestlings at primary nests in light of prevailing weather conditions and food availability. Males brood nestlings less and feed them more (mg/h) when food is scarce, regardless of weather conditions. Primary (i.e., first-mated) females brood nestlings more and maintain feeding rates when food is scarce and weather is stormy. When food is scarce and weather is good, primary females brood nestlings less and feed them more. Increased provisioning results from both faster delivery rates and larger numbers of food items delivered per trip for both sexes.

In this 4-year study conducted in Oregon, male Bobolinks delivered about 60% of the food fed to older primary nestlings when weather was poor and food was scarce, about 50% when weather was good and food was scarce, and about 40% when weather was good and food was abundant. In the year when weather was good and food was scarce, males delivered about 70% of the food during the brooding period and about 50% thereafter.

The results suggest that trade-offs exist among brooding nestlings, feeding nestlings, and self-maintenance. They imply that the relative value of investing in each of these activities differs between parents and changes according to weather conditions and food availability.

Secondary (i.e., second-mated) females did not compensate for reduced male parental assistance by stepping up food delivery rates, except in one year when food was abundant and weather was good. Their cost of losing male parental help was substantial, especially in years when food was scarce and/or weather was poor.

Parental care of nestlings entails feeding, brooding, and sometimes guarding. Performing one of these activities precludes performing the others, and because time is limited, opportunities exist for apportioning as well as possible the amount of time devoted to each activity. Do birds apportion their time as well as possible during the parental care period? If so, how does this balance change as conditions change?

The concept of parental investment provides an opening wedge into these questions. "Parental investment" refers to any contribution invested in current progeny that reduces a parent's ability to invest in other current progeny or in future progeny (Trivers 1972). It includes predation risks taken as well as time and energy spent while caring for young. It measures the limitations imposed on parental abilities to rear current progeny and any reductions in parents' survival that arise from their activities. Parental investment is measured in terms of fitness costs and benefits and, hence, is not easily quantifiable in the field. Nevertheless, the concept provides a theoretical framework for evaluating the trade-offs involved when apportioning effort to various forms of parental care and other activities.

Increased parental investments in individual offspring lower parents' ability to produce other offspring. Parents should continue investing in a particular offspring only as long as the incremental gain in that offspring's prospect for survival outweighs the cost of continued investment to the parent (Patterson et al. 1980). Since both benefits and costs are likely to vary with age, sex, and social status (e.g., number of mates for males; rank order of mating for females) of each parent and with changing environmental conditions, patterns of parental allocation should change with social and environmental conditions if parents are making the best use of their time and energy.

No theory currently exists for predicting how parents should adjust their allocation patterns as conditions change. My purpose here is to establish an empirical basis for formulating such a theory by analyzing the parental allocation patterns exhibited by male and female Bobolinks (*Dolichonyx oryzivorus*) under a variety of social and environmental conditions. The polygynous social system of Bobolinks is well suited for such an analysis because the effects of both social and environmental factors can be investigated. Specifically, I analyze Bobolink parental be-

havior here as a function of sex, female mated status, brood size, and annual variations in food availability and weather. I also evaluate the effects of brood size and time of day on parental feeding rates and nest attendance.

Interpreting the results is made easier by the temporal characteristics of Bobolink breeding biology in Oregon. Males cease defending territories and advertising for mates shortly before the first nestlings hatch, so the analysis is not confounded by the conflicting demands of parental care, territory defense, and mate attraction. Males devote their attention entirely to self-maintenance and parental care during the nestling period, evidently because opportunities for attracting additional mates are absent once nestlings hatch (see Verner 1964, Willson 1966, Emlen and Oring 1977, Wittenberger 1979). New pair bonds are never formed after the earliest nestlings begin to hatch: females are single-brooded, and females do not renest once early nestlings begin to hatch (Wittenberger 1978). Variations in both male and female parental investment patterns can therefore be interpreted without regard to the costs and benefits associated with territory defense, mate attraction, or mate selection.

STUDY AREA AND METHODS

I conducted my field work during 1973–1976 at the south end of Malheur National Wildlife Refuge, about 100 km south of Burns, Oregon. The refuge lies in a river basin surrounded by upland Great Basin desert, at an elevation of about 1,400 m. Grasslands on the refuge stem from drainage of marshes and installation of an irrigation system during the past 100 years (Brimlow 1951). Bobolinks first colonized the area shortly after 1900 (see Wittenberger 1978).

The study area consisted of a 27.3-ha tract of grassy meadows intermixed with sedges (*Carex* spp.) and numerous forbs. Soil moisture conditions and composition of vegetation are described in detail elsewhere (Wittenberger 1976, 1980a, 1981a). The study area paralleled a major irrigation channel, which provided a steady supply of water until late June every year. It was bounded on all sides by undefended flooded meadows, where adult Bobolinks sometimes foraged during the nestling period. Because the study area was essentially curvilinear in shape, these areas were never more than 100 m from any nest.

The study area was situated in what appeared to be the best Bobolink habitat on the refuge. It was the first area occupied by both males and females every spring; it contained on average the smallest territories, the highest frequency of polygynous matings, and the lowest proportion of unmated males anywhere on the refuge (Wittenberger 1978, 1980a).

I identified individual Bobolinks by plastic color bands and by a variety of plumage characteristics (see Wittenberger 1978). Mated status of males and females was determined from season-long pair associations between known individuals, simultaneous sightings of all females nesting on each territory, nest locations, and dates of egg laying. Mating is successive in Bobolinks, with males never acquiring second mates sooner than three days after they acquire their first mates (Martin 1971, Wittenberger 1976, 1978).

Nests were usually found by watching incubating females returning to them, particularly at dusk. Nestlings were weighed collectively to the nearest 0.1 g at midday each day. I inferred nestling starvation from empty stomachs of dead nestlings or disappearance of single nestlings from the nest during mild weather. I assumed that nestlings died of exposure (i.e., hypothermia) when I found rainsoaked bodies in the nest or when single nestlings disappeared during cold weather. I made the latter assumption because all dead nestlings found during such weather had full stomachs (see Wittenberger 1978). I attributed losses of entire broods to predation.

Parental feeding rates were measured by observing nests from a distance of 60 to 100 m, usually from one of two elevated towers or from a stepladder. Up to five nests were watched simultaneously when all were visible along the same line of vision, but usually one to three nests were watched at a time. Eleven nests were monitored in 1973, 18 in 1974, 20 in 1975 (3 during the storm of 15–25 June), and 15 in 1976, for a total of 779 nest-hours at primary nests and 260 nest-hours at secondary nests. Observations were made for most times of day for every nestling age, but sampling intensities varied between years.

During each observation period the times of arrival and departure of parent birds were recorded to the nearest minute. For some observation periods (247 h in total), the number and types of food items taken to nestlings were determined by noting the food items carried in the bill from a blind placed 5 to 10 m from the nest, using 10× binoculars. Parents at these nests consistently perched nearby before entering their nests.

Because data were collected by four observers, who often watched several nests simultaneously, systematic errors could have been introduced into the data. I therefore computed correction factors by analyzing the frequency that each observer failed to record arrivals and departures at nests. The probability of missing

an arrival (P_A) or departure (P_D) was calculated for each observer based on the frequencies that two consecutive departures or arrivals were recorded. An arrival was missed if two departures were recorded in succession, and a departure was missed if two arrivals were recorded in succession. If P_A and P_D were independent, the joint probability $P_J = P_A \cdot P_D$ estimated how frequently entire trips were missed by each observer.

The estimated proportion of male trips missed (P_J) was 0.06%, 0.47%, 0.09%, and 0.24% for the four observers. The estimated proportion of female trips missed was 0.58%, 1.58%, 0.22%, and 0.29%, respectively. Female trips were missed consistently more often than male trips, probably because males are more conspicuous in both plumage and behavior. Although the estimated errors were small, all data on feeding rate for 1973–1975 were converted by the proportionality constant $1 + P_J$. No corrections were necessary in 1976 because all data were collected by watching one nest at a time from a blind 5 m away, and virtually no arrivals or departures were missed.

Missed trips sometimes precluded calculation of nest attendance time. If the interval between successive arrivals or departures was less than 5 min, the time at the nest was assumed to be less than 1 min. Otherwise, the observation period was excluded from analyses of nest attendance times.

Data on feeding rates and nest attendance times were analyzed with respect to nestling age, time of day, and year by a multivariate analysis of variance (MANOVA) for unequal sample sizes, using BMD-VII in the UCLA biomedical statistical package (Dixon 1973). Differences between cells in the MANOVA tables were tested with a Newman-Keuls multiple range test (Zar 1974). Possible interaction effects between time of day and nestling age were tested for both parental feeding rates and nest attendance times, and no significant interaction effects were found (F-test, $P > 0.05$).

The rate at which food delivery rates increased with nestling age was compared across years by computing the mean percentage increase per day for each sex of parent. The computation is equivalent to computing compound interest on a savings account. The formula is $(1 + i)^8 = n_{10}/n_2$, where $100i$ is the mean daily percentage increase in feeding rate, n_{10} is the feeding rate on day 10 computed from the appropriate regression equation, and n_2 is the feeding rate on day 2 computed from the same regression equation. Significant differences between slopes of the regression lines

were analyzed by a Newman-Keuls multiple range test (Zar 1974).

Food items delivered to nestlings were classified into size classes for each prey type (e.g., caterpillars, grasshoppers, odonates) when items of that type varied in size, using bill depth as a reference. These size classes were converted into body lengths by comparing insects caught in sweep samples to bill depth. Relative biomass of food items delivered by each sex could then be computed, using fitted power curves to convert body length into dry weight (see Wittenberger 1976).

Dry weight of the average prey item delivered by females (D_i) to nestlings aged 7 to 10 days in year i was calculated from

$$D_i = \sum_{k=1}^{n} P_{ik} W_{ik},$$

where P_{ik} is the proportion of prey type k (broken down by size classes) delivered by females in year i, W_{ik} is the mean dry weight of prey type k in year i, and n is the number of prey types in year i. Dry weight of the average prey item delivered by males (D_i') was calculated similarly based on the proportion of prey types (P_{ik}') and dry weights of each prey type (W_{ik}') delivered by males.

The mean biomass of food delivered by females to the nest each hour (B_i) on days 7 to 10 (the only ages for which I have data) were then calculated from

$$B_i = D_i N_i \sum_{j=7}^{10} (T_{ij}/4),$$

where N_i is the mean load size and T_{ij} is the mean number of female trips/h on day j in year i. The mean biomass delivered by males (B_i') was calculated similarly, based on dry weight of the average prey item (D_i'), mean load size (N_i'), and mean number of trips/h (T_{ij}') for males.

Maximum temperature, minimum temperature, and daily rainfall were obtained from a standard U.S. meteorological substation located at P Ranch, about 2 km from the study area. Caterpillars and grasshoppers exploited to feed nestlings were sampled with a sweep net in 1975 and 1976. Two samples were taken daily on each of 14 contiguous territories in the area where most nest observations were made (see Wittenberger 1980a, b).

RESULTS

HABITAT AND WEATHER CONDITIONS

Parental efforts varied annually, and interpreting this variability requires an understanding of how environmental conditions differed

TABLE 1.   Mean maximum and minimum temperatures (°C) each year during the period when primary and secondary nests contained nestlings aged one to seven days.[a]

Year	Primary nests			Secondary nests		
	n[b]	Maximum	Minimum	n[b]	Maximum	Minimum
1973	16	26.4 ± 6.4[c]	7.2 ± 4.2	9	30.6 ± 3.8	7.9 ± 4.1
1974	16	29.9 ± 2.8	9.3 ± 3.6	15	29.3 ± 2.5	8.6 ± 3.5
1975	14	19.6 ± 4.2	5.1 ± 2.5	10	22.1 ± 4.4	5.8 ± 4.5
1976	13	25.7 ± 3.4	5.6 ± 4.5	12	26.4 ± 4.3	4.9 ± 4.5

[a] For primary nests temperatures are for the periods 14–29 June 1973, 14–29 June 1974, 16–29 June 1975, and 15–27 June 1976. For secondary nests temperatures are for the periods 26 June–4 July 1973, 18 June–2 July 1974, 24 June–3 July 1975, and 22 June–3 July 1976.
[b] n = number of days.
[c] Standard deviation.

between years. Habitat conditions on the refuge are strongly influenced by water availability, particularly with respect to irrigation flow and spring precipitation. Water management policies on the refuge are such that the study area receives a nearly constant proportion of the total irrigation flow each year, but the total volume of flow changes greatly from year to year. The volume of flow depends on runoff from melting snow on nearby Steens Mountain and on precipitation during spring. Hence, annual precipitation, measured from July through June, indicates water availability as it affects Bobolink habitat each year.

The year ending 30 June 1973 was unusually dry, with total annual precipitation at P Ranch Station measuring 20.3 cm, compared to a 32-year average of 29.2 cm (based on refuge records). As a result, irrigation flow was about 50% lower than normal, and many areas that were occupied by Bobolinks in other years were extremely dry and unsuitable for breeding. Precipitation the following year was 29.5 cm, making occupied habitats substantially wetter than in 1973. Also, many dry habitats not occupied in 1973 were occupied in 1974. The year ending 30 June 1975 was unusually wet, particularly during the breeding season. Annual precipitation was 31.3 cm, half of it falling from April through June. Severe and continuous rainstorms occurred during 15–25 June and coincided with the nestling period of early primary nests that year, causing high nestling mortality in those nests (Wittenberger 1978). Precipitation was again below average (25.8 cm) in 1976, but conditions were not as dry as in 1973 because irrigation flow was near normal.

Temperature is likely to have an important effect on nestling energetics and brooding requirements until nestlings are able to thermoregulate (Kendeigh 1952, Royama 1966, Ricklefs 1974). During the poikilothermic period (first seven days) of primary nestlings, mean maximum and minimum temperatures were highest in 1974 and lowest in 1975 (Table 1). During the poikilothermic period of secondary nestlings, mean maximum temperature was highest in 1973 and 1974 and lowest in 1975. Mean minimum temperature was highest in 1973 and 1974 and lowest in 1975 and 1976. Thus, for primary nestlings 1974 was a hot year, 1973 and 1976 were moderate years, and 1975 was a cold year. For secondary nestlings 1973 and 1974 were hot years, 1976 was a moderate year, and 1975 was a cold year. Mean maximum temperatures were significantly higher for secondary nestlings than for primary nestlings in 1973 but not in other years (t-test, $P < 0.05$).

My data on caterpillar and grasshopper abundance have been published elsewhere (Wittenberger 1980a, b). They show that caterpillars and grasshoppers became much less abundant in 1975 during the rainstorms of 15–25 June and resurged only to a small extent following the end of those storms. These food supplies were less abundant in 1976 than in 1975 despite more moderate weather, probably because overwintering populations were greatly reduced by the adverse weather conditions of 1975. Sweep sample data were not collected in 1973 or 1974, but the favorable weather in those years and in the two preceding years suggests that caterpillars and grasshoppers were probably then more abundant than in either 1975 or 1976.

NUTRITIONAL CONDITION OF NESTLINGS

The mean weight of primary nestlings on day 10 (day 1 = hatching day) was similar in 1973 and 1974 but was significantly lower in 1975 and 1976 (Table 2). Primary nestlings that hatched less than five days before the storms of June 1975 ended were not underweight, but primary nestlings that hatched earlier were. In 1973 and 1974, the mean weight of secondary nestlings was similar to that of primary nestlings. In 1975, secondary nestlings weighed less than primary nestlings even though they hatched after the storm ended. They also weighed less than primary nestlings in 1976.

TABLE 2. Nestling weights in grams just prior to fledging on day 10 post-hatching. Standard deviations indicate variability between broods, not nestlings. Number of broods is given in parentheses.

| Year | Nests[a] | |
	Primary	Secondary
1973	23.5 ± 2.3[a] (5)	24.2 ± 1.9[a] (4)
1974	24.0 ± 1.5[a] (17)	22.8 ± 2.2 (3)
1975 (early)[c]	20.0 ± 1.4[b] (6)	—
1975 (late)[d]	23.3 ± 0.8[a] (7)	19.4 ± 2.2[b] (4)
1976	20.7 ± 2.2[b] (9)	22.2 ± 0.1 (2)

[a] These values are significantly higher than those denoted by [b] superscripts, with comparisons made down columns (multiple range test, $P < 0.05$).
[c] Nests that hatched more than five days before the storm of 15–25 June ended.
[d] Nests that hatched less than five days before the storm of 15–25 June ended.

The nutritional condition of nestlings is also indicated by the strength of gaping responses. In 1975 and 1976 both primary and secondary nestlings extended their necks to the fullest extent possible and gaped vigorously whenever I visited the nest (except in late primary nests in 1975). In 1973 and 1974 nestlings rarely showed much of a gaping response and never extended their necks fully. Nestlings appeared both skinnier and hungrier in 1975 and 1976 than in the previous two years.

Few primary nestlings of polygynous males starved in any year of the study (Table 3). None starved in 1973 or 1974, and fewer than 5% starved in 1975 and 1976. Nearly 40% of nestlings raised by nearby monogamous pairs starved in 1976, compared to less than 5% in the other three years. About 30% of secondary nestlings starved in 1975 and 1976, compared to less than 10% in 1973 and 1974.

All three lines of evidence show that nestlings were generally in poorer nutritional condition in 1975 and 1976 than in 1973 or 1974. Their worst year was 1976, when fledging weights of both primary and secondary nestlings were low throughout the season and when starvation rates were high in broods of both monogamous and secondary females.

NEST ATTENDANCE AT PRIMARY NESTS

Individually and together, parents spent different amounts of time each year attending nests (Fig. 1). This time could not be separated into feeding time and brooding time because nests were in tall grass, but differences between years mainly reflect differences in brooding time.

Differences between years appear related to differing habitat and weather conditions. The time females devoted to attending nests on days 2 to 6 was greatest during the cold, rainy summer of 1975 and least during the hot summer of 1974. Their greater nest attendance in 1975 appeared to be associated with the storm of 15 to 25 June, as most data were collected during the storm and within the first few days following its end. However, mean nest attendance times did not differ significantly during and after the storm.

For nestlings aged five days and older, females spent significantly less time attending nests in 1976, when food was scarce and weather was good, than in other years (MANOVA, multiple range test, $P < 0.05$). Males regularly spent longer than 3 min at the nest on each visit in 1973 and 1974 but rarely did so in 1975 or 1976. Most visits by males in the latter two years lasted about 15 to 45 s. Males almost certainly brooded nestlings during long periods of nest attendance (i.e., greater than 3 min), judging from the broken-wing displays they gave when flushed from the nest, but probably did not brood nestlings during shorter visits. Reduced nest attendance by males was associated with food scarcity and not with particular weather conditions.

The total amount of time that young nestlings (aged 2–4 days) were attended by both parents combined (Fig. 1) was highest in 1975, averaging 82.8% of observation time, compared to 73.0% in 1973, 64.6% in 1974, and 64.0% in 1976. Such nestlings received more brooding during stormy weather than at other

TABLE 3. Rates of nestling starvation in primary nests of polygynous and monogamous males and in secondary nests of polygynous males.

| Year | Polygynous males | | | | Monogamous males | |
| | Primary | | Secondary | | Primary | |
	No. nestlings (and nests)	Percent starved	No. nestlings (and nests)	Percent starved[a]	No. nestlings (and nests)	Percent starved[a]
1973	25 (5)	0.0	26 (5)	7.7	67 (14)	0.0
1974	39 (8)	0.0	23 (5)	8.7	66 (12)	3.0
1975	59 (11)	1.7	61 (13)	29.5	47 (9)	2.1
1976	60 (11)	5.0	49 (12)	32.7	23 (4)	39.2

[a] Monogamous females were in relatively high quality habitats. Unmated females who later chose secondary status could not have done as well as these females, because such habitats were all occupied by the time they paired. Hence, these data do not contradict the polygyny threshold model (see also Wittenberger 1981b).

times, entirely as a result of increased female nest attendance.

Older nestlings (aged 5–6 days) received less brooding in 1976, when total nest attendance averaged 34.5% of observation time, than in other years, when total nest attendance averaged 56.6% in 1973, 55.6% in 1974, and 58.1% in 1975. The same was true for nestlings aged 7 to 10 days. These nestlings were attended by both parents combined for only 11.6% of observation time in 1976, compared to 34.7% in 1973, 32.2% in 1974, and 24.8% in 1975. Older nestlings received less brooding when food was scarce and weather was good than when food was abundant or weather was cold and rainy.

Nest attendance varied to a small extent with time of day (Fig. 2). Data were combined for 1973 and 1974 to increase sample sizes because diurnal patterns were similar both years. In those years, female nest attendance peaked at mid-morning and then declined slightly during the hot part of the day. It was lowest in early morning and just before dusk. Male nest attendance was relatively constant all day, except during the first two hours of the morning, when males mainly foraged for themselves. No territorial displays occurred during that time. In the cold, rainy year of 1975, female nest attendance was high throughout the day, with reductions in early morning and at dusk being less evident. Male nest attendance in 1975 showed morning and afternoon peaks, with low attendance during early morning, early afternoon, and evening hours. Data for 1976 were insufficient for analyzing diurnal patterns.

PARENTAL FEEDING RATES AT PRIMARY NESTS

Females and males both delivered food to nests at progressively faster rates as nestlings grew older (Fig. 3). The rate of increase in feeding rates with nestling age could be obtained from linear regression lines every year, although the relationship was not always precisely linear. For instance, the rate at which males delivered food to nests in 1973 and 1974, when food was abundant, increased until nestlings reached five days of age and then leveled off. In 1975 and 1976, when food was scarce, male delivery rates continued to increase throughout the nestling period. Female delivery rates increased steadily throughout the nestling period in 1974 and 1976 but peaked on day 8 in 1973 and on day 9 in 1975. The slopes of the fitted regression lines were significantly greater than zero for both sexes in every year.

Males increased their food delivery rate each day by an average of 4.5% in 1973, 5.3% in
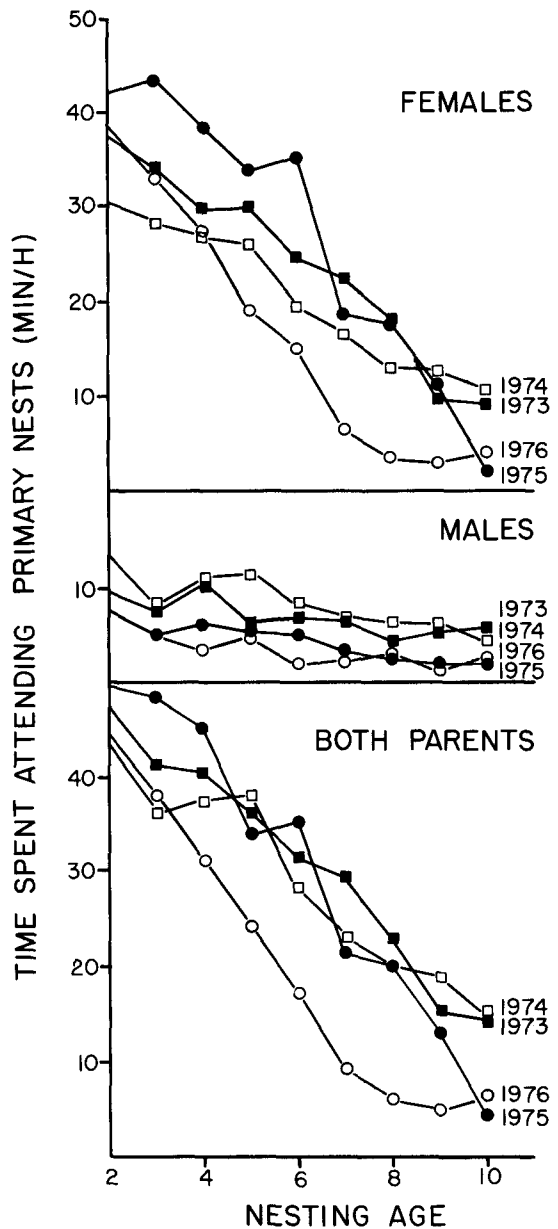

FIGURE 1.   Time spent attending primary nests (min/h) by females, males and both parents combined as a function of nestling age each year. Sample sizes (hours of observation) for each nestling age were: 13, 13, 16, 19, 15, 17, 15, 15, 13 in 1973; 17, 22, 21, 25, 41, 67, 58, 53, 23 in 1974; 21, 24, 24, 20, 4, 3, 8, 32, 12 in 1975; 7, 19, 14, 4, 8, 8, 14, 13, 6 in 1976.

1974, 15.5% in 1975, and 8.3% in 1976. Females increased their food delivery rate each day by an average of 9.4% in 1973, 12.3% in 1974, 12.8% in 1975, and 14.2% in 1976. The slope for males was significantly greater in 1975 than in 1973 or 1974 (multiple range test, $P < 0.05$). The slope in 1976 was intermediate and not significantly different from either extreme. None of the slopes for females differed
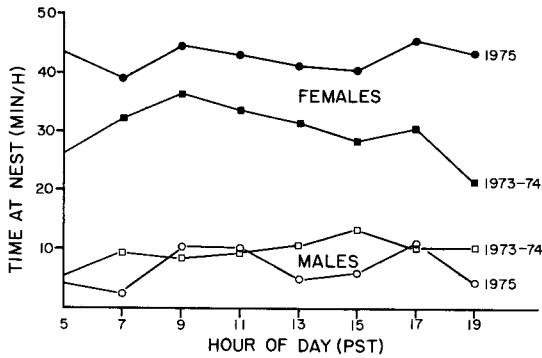
FIGURE 2.   Time spent attending primary nests (min/h) by females and males for nestlings aged two to four days as a function of time of day each year. Sample sizes (hours of observation) for each two-hour time interval were: 10, 16, 14, 12, 11, 13, 22 in 1973–1974; 10, 8, 11, 10, 6, 5, 2, 17 in 1975.

significantly between years. Thus, the rate of increase in male delivery rates was highest when weather was poor and food was scarce, intermediate when weather was good and food was scarce, and lowest when weather was good and food was abundant. The rate of increase in female delivery rates was the same regardless of environmental conditions.

Analysis of the slopes of regression lines gives a reasonable indication of how food delivery rates varied between years. However, the difference in slope does not reflect significantly faster food delivery rates in 1975 and 1976 except for old nestlings. Comparison of food delivery rates for each nestling age across years reveals significantly higher male delivery rates in 1975 for nestlings aged 9 to 10 days and in 1976 for nestlings aged 10 days (MANOVA, multiple range test, $P < 0.05$). Female delivery rates were significantly higher for nestlings aged 10 days in 1976 despite the similar slopes of the fitted regression lines every year. These discrepancies resulted partly from annual variations in the Y-intercepts of the regression lines.

The effect of parental feeding rates on nestlings depends on both food delivery rate and brood size and is therefore best measured by the rate at which food is delivered per nestling. As shown in Figure 4, feeding rates per nestling increased essentially linearly with nestling age in every year except 1975, when a marked increase occurred on day 7 for male parents and on days 7 to 8 for female parents. These sudden increases reflected small sample sizes, the fact that most data were collected on those days just before or after sunset (when delivery rates tend to be higher than usual [see below]), and below-average brood sizes in the sampled
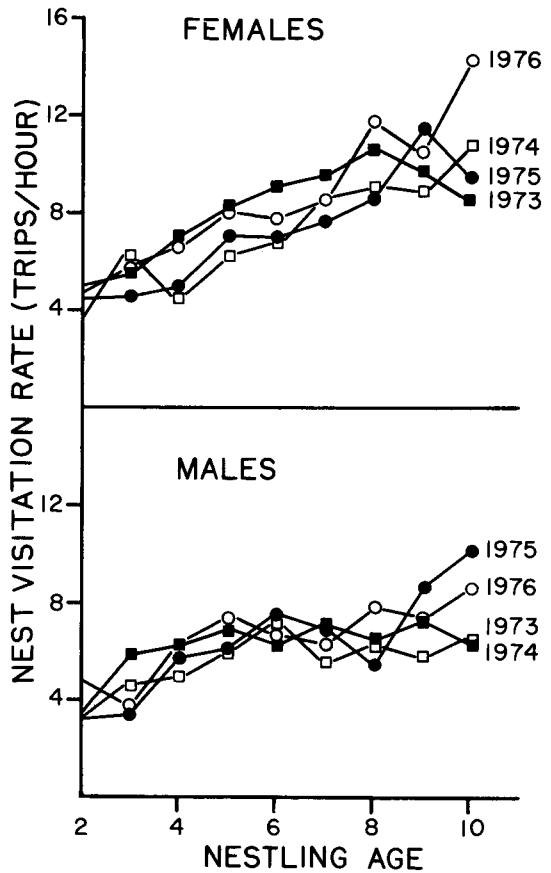

FIGURE 3.   Rate at which parents delivered food to primary nests (trips/h) as a function of nestling age each year. Sample sizes (hours of observation) for each nestling age were: 14, 13, 17, 19, 15, 17, 15, 15, 13 in 1973; 17, 22, 22, 25, 41, 67, 58, 53, 23 in 1974; 21, 24, 24, 20, 4, 3, 8, 32 in 1975; 7, 19, 14, 4, 8, 8, 14, 13, 6 in 1976. Regression lines and regression coefficients for females each year were: $Y = 3.86 + .69X$ ($r^2 = .86$) for 1973; $Y = 2.54 + .78X$ ($r^2 = .89$) for 1974; $Y = 2.37 + .81X$ ($r^2 = .86$) for 1975; and $Y = 2.34 + 1.06X$ ($r^2 = .90$) for 1976. For males they were: $Y = 4.55 + .27X$ ($r^2 = .46$) for 1973; $Y = 3.78 + .30X$ ($r^2 = .53$) for 1974; $Y = 1.52 + .85X$ ($r^2 = .94$) for 1975; and $Y = 3.46 + .50X$ ($r^2 = .73$) for 1976.

nests. The rate at which each nestling received food from females increased significantly with nestling age in every year ($P < 0.05$). The rate at which each nestling received food from males increased significantly with nestling age only in 1975 and 1976.

The amount of food received by each nestling from males increased daily by 5.2% in 1973, 2.3% in 1974, 20.2% in 1975, and 11.0% in 1976. The rate of increase was significantly higher in 1975 than in the other three years, and it was significantly higher in 1976 than in 1974 (multiple range test, $P < 0.05$). The amount of food received by each nestling from females increased daily by 6.6% in 1973,

13.4% in 1974, 11.6% in 1975, and 18.0% in 1976. The rate of increase was significantly higher in 1976 than in 1973 ($P < 0.01$). No other differences were significant.

Male contributions to each nestling increased the most with nestling age when food was scarce and weather was poor, less when food was scarce but weather was good, and hardly at all when food was abundant and weather was good. The faster rates of increase in male contributions resulted from both stepped up delivery rates (see above) and progressive reductions in average brood size (see Fig. 4 caption). Female contributions increased to about the same degree with nestling age under all conditions, although they increased at a somewhat faster rate than usual in 1976 owing to progressive reductions in average brood size.

The above evidence suggests that females did not adjust food delivery rates when conditions were poor in 1975. However, the foregoing analysis was based on average data collected both during and after the rainstorms of 15 to 25 June. Analyzing these data separately discloses that females delivered food to nestlings at significantly faster rates during the storm (6.53 trips/h; n = 35 h) than after the storm (3.08 trips/h; n = 10 h; t-test, $P < 0.05$). The rates at which they fed nestlings aged four to five days were similar during and after the storm. Males did not show a comparable difference for any nestling age.

BROOD SIZE EFFECT

According to Lack's (1954, 1966, 1968) hypothesis that clutch sizes of passerine birds are limited by the ability of parents to feed young, per-nestling feeding rates should be lower for larger broods. To evaluate this hypothesis, I combined the data for 1973 and 1974 to increase sample sizes because weather conditions, food abundance, and mean feeding rates were similar in both years.

The rate at which each nestling received food was not negatively correlated with brood size for nestlings aged 7 to 10 days in 1973 and 1974, when food was abundant (Table 4). This result is consistent with the high fledging weights and low starvation rates found in those years. Per-nestling feeding rates did decrease significantly with increasing brood size for nestlings aged two to five days, primarily due to lower feeding rates by males. The decrease cannot be attributed to an inability to deliver food at faster rates, because males maintained faster feeding rates for older nestlings. Perhaps nestlings in larger broods require less maintenance energy during the brooding period, as surface-to-volume ratio and hence rate of heat
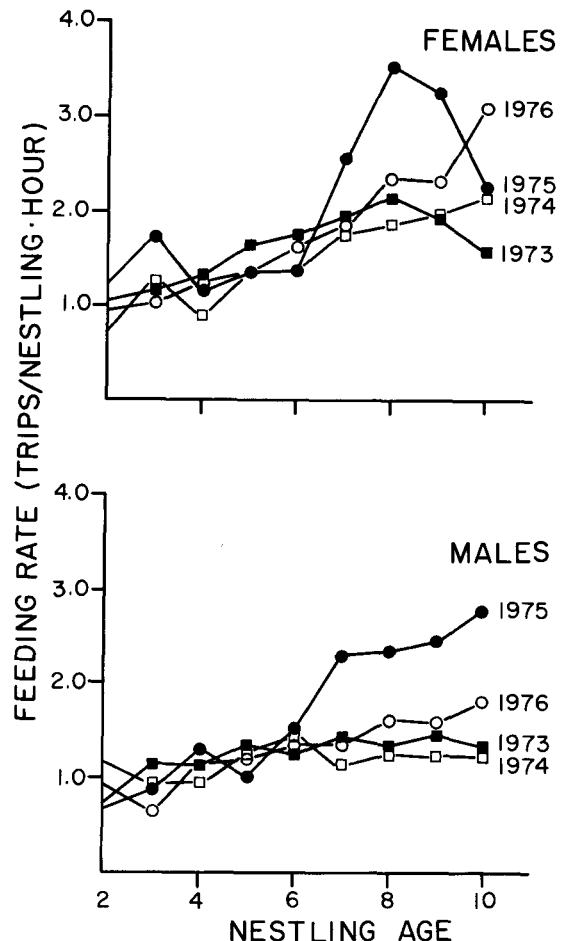

FIGURE 4. Rate at which primary nestlings were provisioned (trips/nestling·h) by females and males as a function of nestling age. Sample sizes were the same as in Figure 3. Mean brood sizes in the nests observed for each nestling age were: 4.9, 4.9, 5.4, 5.3, 5.1, 4.9, 4.8, 5.2, 5.2 in 1973; 5.5, 5.2, 5.3, 4.8, 5.0, 4.8, 4.9, 4.7, 5.0 in 1974; 4.0, 3.2, 4.6, 5.8, 5.0, 3.0, 2.2, 3.7, 4.0 in 1975; 5.0, 5.7, 5.6, 6.0, 4.9, 4.6, 5.0, 4.8, 5.0 in 1976. Regression lines and regression coefficients for females each year were: $Y = 1.00 + .10X$ ($r^2 = .56$) for 1973; $Y = 0.45 + .17X$ ($r^2 = .91$) for 1974; $Y = 0.74 + .20X$ ($r^2 = .56$) for 1975; and $Y = 0.23 + .26X$ ($r^2 = .94$) for 1976. For males they were: $Y = 0.88 + .06X$ ($r^2 = .18$) for 1973; $Y = 1.03 + .03X$ ($r^2 = .21$) for 1974; $Y = 0.07 + .27X$ ($r^2 = .93$) for 1975; and $Y = 0.54 + .13X$ ($r^2 = .89$) for 1976.

loss decreases with increasing brood size (see Royama 1966, Mertens 1969).

The rate at which both young and old nestlings received food decreased with increased brood size in 1975 and 1976, when food was scarce (Table 4). The decreases resulted from lower per-nestling feeding rates by both parents, except for young nestlings in 1975. The negative relationship between feeding rate and brood size in 1975 and 1976 is consistent with the lower fledging weights and higher starvation rates occurring in those years. Thus, my

TABLE 4. Rate at which male and female Bobolinks delivered food to primary nestlings (trips/nestling·h) as a function of brood size.[1]

Feeding rate	Brood size													
	1973–1974				1975					1976				
	3	4	5	6	2	3	4	5	6	3	4	5	6	7
Ages 2–5 days														
Hours of observ.	7	67	79	86	24	3	12	29	37	8	7	14	15	8
Male	0.49[b]	1.03[a]	0.56[b]	0.70[b]	0.80	0.56	1.18	0.88	0.82	0.09[c]	1.56[a]	0.66[b]	0.83[b]	0.89[b]
Female	1.55	1.25	1.21	1.19	2.30[a]	2.07	1.43[b]	0.99[b]	1.19[b]	2.14[a]	1.51[b]	1.00[c]	1.04[c]	1.07[c]
Both parents	2.04	2.29[a]	1.77[b]	1.89[b]	3.10[a]	2.63	2.61[b]	1.87[b]	2.01[b]	2.23[b]	3.06[a]	1.66[b]	1.87[b]	1.96[b]
Ages 7–10 days														
Hours of observ.	—	120	87	83	15	20	23	14	—	4	9	19	7	—
Male	—	1.35[a]	1.11[b]	1.31[a]	1.77[b]	3.02[a]	1.69[b]	1.79[b]	—	2.45[a]	1.92[b]	1.39[c]	1.40[c]	—
Female	—	1.91	2.11[a]	1.73[b]	4.07[a]	2.44[b]	3.68[a]	2.26[b]	—	4.14[a]	2.72[b]	1.85[c]	2.28	—
Both parents	—	3.27	3.23	3.04	5.84[a]	5.46[a]	5.37[a]	4.04[b]	—	6.58[a]	4.65[b]	3.24[c]	3.68[c]	—

[1] Significant differences across rows (within years) are indicated by superscripts, with a > b > c (multiple range test, P < 0.05). Lack of superscripts on intermediate values means that the values are not significantly different from the next higher and next lower values.

data support Lack's hypothesis in years of food scarcity but not in years of food abundance, as one might expect.

TYPE, SIZE, AND NUMBER OF FOOD ITEMS DELIVERED TO NESTLINGS

The composition of nestling diet is shown for 1974–1976 in Table 5. The majority of food items delivered to nestlings by both sexes were Lepidoptera and sawfly larvae. Wiens (1969) reported a similar preponderance of these larvae in the nestling diet of Wisconsin Bobolinks. Males delivered a significantly higher proportion of Lepidoptera and sawfly larvae than did females every year (χ^2_1, $P < 0.05$).

The proportion of Lepidoptera and sawfly larvae in the nestling diet was significantly lower in 1976 than in 1975 and also in 1975 compared to 1974 (χ^2_1, $P < 0.05$). These differences resulted mainly from reduced numbers of arctiid and noctuid larvae in the diet. Arctiid caterpillars were delivered to nestlings much more frequently in 1974 than in 1975 or 1976. Arctiids are black caterpillars with long body hairs, a morphology usually associated with distastefulness (Cott 1940), but neither adults nor nestlings showed any sign of adverse effects after eating them. Adult Lepidoptera, especially a black tenuchid moth (*Cisseps fulvicollis*), were significantly more prevalent in the nestling diet in 1975 than in other years (χ^2_1, $P < 0.05$). Mayflies (Ephemeroptera) were never common in the nestling diet, but they were much more commonly fed to nestlings in 1976 than in other years. They were taken primarily during the hour after sun-

TABLE 5. Percent composition of food items delivered to nestlings aged 7–10 days by male and female Bobolinks each year.

Food type	Males			Females		
	1974	1975	1976	1974	1975	1976
No. birds	4	8	9	5	9	9
No. food items	934	1,083	1,492	1,384	981	1,326
Arctiid larvae	31.9	4.4	3.2	10.6	2.9	0.4
Other caterpillars[a]	32.0	56.5	54.7	44.4	47.0	47.3
Noctuid larvae	5.9	3.3	0.9	8.2	3.4	1.4
Grasshoppers	16.6	6.4	18.1	22.5	13.0	14.0
Adult Lepidoptera	1.8	13.0	2.3	3.5	10.1	3.1
Coleoptera	0.3	4.2	1.3	0.1	3.6	4.4
Diptera	1.9	0.9	2.5	1.6	2.2	3.1
Lepidoptera pupae	1.0	0.0	0.7	0.4	0.0	0.1
Arachnida	1.1	1.1	3.1	0.8	1.4	3.7
Hemiptera	0.9	3.0	4.2	0.6	4.3	6.2
Adult Hymenoptera	0.4	0.2	0.1	0.4	0.4	0.3
Neuroptera	0.3	0.1	0.1	0.1	0.4	0.1
Ephemeroptera	0.0	0.1	5.4	0.0	0.0	5.0
Odonata	2.0	2.6	1.0	2.8	4.0	0.8
Annelida	1.9	0.4	3.2	2.9	7.5	9.9

[a] All Lepidoptera and sawfly larvae except arctiids and noctuids.

set. These differences suggest that annual changes occurred in the relative availability of alternative food resources.

Male Bobolinks are about 9% heavier than females (n = 21 males and 13 females). To determine whether this size dimorphism affects the sizes of prey captured by each sex, I analyzed size classes for the principal prey types delivered by each sex (Table 6). Males captured significantly larger size classes of caterpillars and arctiid larvae than did females in 1974 and 1975 and significantly larger size classes of grasshoppers in 1974, 1975, and 1976 (χ^2_2, $P < 0.05$). No significant differences were found with respect to noctuid larvae.

The number of food items delivered per trip (i.e., load size) was recorded at nests containing nestlings aged 7 to 10 days in 1974, 1975, and 1976. Males delivered significantly larger loads in 1975 and 1976 than they did in 1974 (Table 7). Females delivered significantly larger loads in 1976 than in 1974. Load sizes were similar for both sexes in 1974 and 1976 but not in 1975, when males delivered significantly larger loads than females (t-test, $P < 0.05$). Males delivered larger loads in both years when food was scarce, while females delivered larger loads only in the year when food was scarce and weather was moderate. The observed differences in load sizes could theoretically arise from variability in travel distance to food sources (Orians and Pearson 1978), with larger loads expected for longer foraging distances. I did not measure foraging distances, but no conspicuous differences between years or between sexes were evident.

I measured load sizes delivered to younger nestlings only in 1976. In that year males delivered large loads for all ages of nestlings, with loads on days 3 to 6 being only 10% smaller than on days 7 to 10 (Fig. 6). Females delivered small loads to young nestlings and large loads
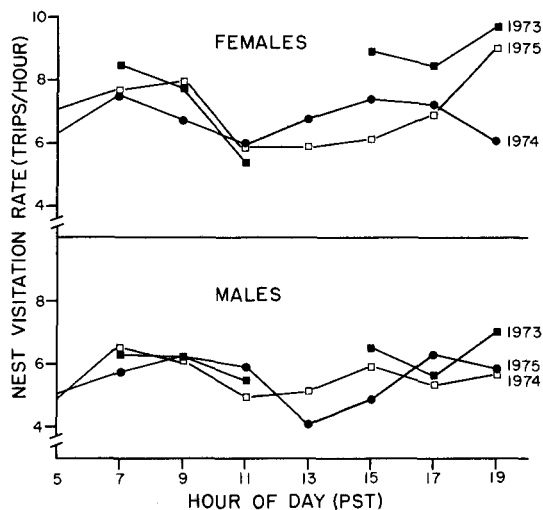

FIGURE 5. Rate at which parents delivered food to primary nests (trips/h) as a function of time of day each year. Sample sizes (hours of observation) for each two-hour interval were: 0, 15, 40, 22, 0, 14, 34, 13 in 1973; 27, 39, 23, 42, 69, 56, 47, 9 in 1974; 16, 24, 28, 19, 9, 11, 8, 33 in 1975.

to older nestlings, with loads being 91% greater on days 7 to 10 than on days 3 to 6. Thus, female loads were reduced substantially during the brooding period and for the first two days following the end of extensive brooding. Load sizes could not be measured for nestlings aged one to two days because most food was carried in the gullet or crop rather than in the bill.

CONTRIBUTION OF EACH SEX TO FEEDING PRIMARY NESTLINGS

The relative contribution of each sex to feeding nestlings can be calculated from food delivery rates, mean load sizes, and caloric content of average food items. An indication of caloric content can be obtained from mean dry weight of each prey type, as caloric content of insect prey is relatively constant per unit of dry

TABLE 6. Size classes of food items delivered to primary nestlings aged 7–10 days by male and female Bobolinks. Data are given as percent frequency for each size class. See Table 5 for sample sizes.

Year/Sex	Arctiid larvae		Other caterpillars[a]			Noctuid larvae			Grasshoppers		
	Small	Large	Small	Medium	Large	Small	Medium	Large	Small	Medium	Large
1974											
Male	12.4	87.6	14.4	64.2	21.4	18.2	76.4	5.4	17.4	46.4	36.1
Female	55.1	44.9	20.0	66.3	13.7	30.1	58.4	11.5	21.8	53.2	25.0
1975											
Male	16.7	83.3	10.6	71.7	17.7	2.8	86.1	11.1	56.5	23.3	20.3
Female	77.8	22.2	16.1	71.5	12.4	3.5	93.1	3.5	79.6	17.7	2.7
1976											
Male	34.3	65.7	9.0	73.3	17.6	—	—	—	25.0	34.5	40.5
Female	—	—	10.3	73.0	16.7	—	—	—	42.0	22.5	35.8

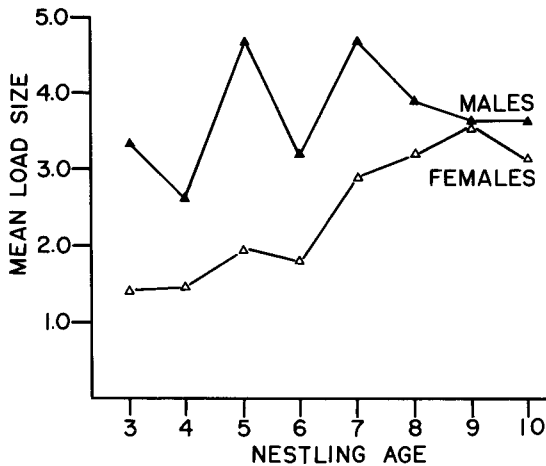[a] All Lepidoptera and sawfly larvae except arctiids and noctuids.

FIGURE 6.   Mean load sizes (number of food items delivered/trip) for males and females at primary nests in 1976. Sample sizes (number of trips) for each nestling age were: 48, 76, 28, 66, 40, 57, 78, 42 for males; 76, 77, 31, 60, 47, 71, 113, 63 for females.

weight for all prey types, averaging about 5,000–5,500 cal/g (Golley 1961, G. H. Orians, unpubl. data). One qualification, however, is that species with heavy exoskeletons such as grasshoppers, dragonflies, and most other adult insects may be less digestible than soft-bodied larvae. Such differences in nutritive quality may be important in determining the relative contribution of each sex, since the two sexes deliver different proportions of prey types to nestlings, but I cannot evaluate their importance with present data.

The mean weight of individual food items delivered to primary nestlings by males (D_i') was 15.2 mg in 1974, 10.0 mg in 1975, and 10.3 mg in 1976. The mean weight of individual prey items delivered by females (D_i) was 11.8 mg in 1974, 8.0 mg in 1975, and 7.7 mg in 1976.

The mean biomass of prey delivered per hour by males (B_i') and by females (B_i) is given in Table 8 for nestlings aged 7 to 10 days. Males delivered substantially more biomass of food per hour in both 1975 and 1976, when food was scarce, than in 1974, when food was abundant. They delivered similar amounts of food in 1975 and 1976 despite the marked

TABLE 8.   Biomass of food delivered to primary nestlings aged 7–10 days (mg/h) by male and female Bobolinks.

Year	Delivered by males	Delivered by females
1974	139.9	188.6
1975	264.6	180.0
1976	295.3	294.5

difference in weather conditions. Females delivered substantially more biomass of food per hour in 1976, when food was scarce and weather was good, than in 1975, when food was also scarce but weather was poor, or in 1974, when food was abundant and weather was good. They delivered similar amounts of food in 1974 and 1975 despite the difference in conditions.

The amount of food received by each nestling from each parent can be computed by substituting trips/nestling·h for trips/h in the calculations (Table 9). The proportion of food provided by males varied significantly between years, being highest in 1975, intermediate in 1976, and lowest in 1974 $(\chi^2_2, P < 0.05)$. Thus, male contributions to feeding nestlings increased in importance when food was scarce, especially when weather was poor.

The total amount of food received by each nestling per day can be estimated by multiplying the hourly rates given in Table 9 by 16, the number of hours that nestlings were fed daily. The results show that each nestling received about 1.1 g/day in 1974, 2.1 g/day in 1975, and 2.0 g/day in 1976. These values compare with estimates of 1.75 g/day consumed by nestling Great Tits (*Parus major*), a hole-nesting species, in broods of 3 young and 0.7 g/day in broods of 13 young (Royama 1966). Since nestling Great Tits weigh only about 60% as much as nestling Bobolinks on day 10, the estimates obtained here appear reasonable.

In 1976 the amount of food delivered by females and males could be calculated for younger nestlings as well. For nestlings aged 3 to 6 days females delivered 14.5 mg/nestling·h, and males delivered about 34.2 mg/

TABLE 7.   Number of food items delivered per trip to primary nestlings aged 7–10 days by male and female Bobolinks.

Year	Male	Female	Ratio (male : female)
1974	1.59	1.77	0.90
1975	3.14	2.17	1.45
1976	3.73	3.45	1.08

TABLE 9.   Biomass of food received by the average primary nestling aged 7–10 days (mg/nestling·h) from male and female Bobolinks and from both parents combined.

Year	Biomass received from			Percent from males
	Males	Females	Both	
1974	29.3	39.5	68.8	42.6
1975	78.5	53.4	131.9	59.5
1976	62.8	62.6	125.4	50.1

nestling·h. Males contributed 70.1% of the food fed to nestlings of those ages. The total amount of food received by nestlings aged 3 to 6 days averaged 0.8 g/day.

PARENTAL FEEDING RATES AT SECONDARY NESTS

The rate at which nestlings of most ages received food from secondary females was significantly higher than it was for primary nestlings in 1973 and 1976, but this was not true in 1974 or 1975 (Fig. 7). The observed differences usually did not make up for the reduction in male assistance at secondary nests. In 1973 secondary nestlings received food at significantly slower rates than primary nestlings until an age of six to seven days, at which time males began feeding secondary nestlings at a substantial rate. In 1974 secondary nestlings received food at significantly slower rates until day 10, although males began making substantial contributions on day 9. In 1975 secondary nestlings received food at significantly slower rates until day 7, even though males began making substantial contributions on day 4. In 1976 secondary nestlings received food as often as primary nestlings during the brooding period even though males rarely helped to feed them.

The faster rates that secondary females fed each nestling in 1973 and 1976, compared to primary females, could have resulted from faster delivery rates, smaller average brood sizes, or both. The effects of these variables are separated in Figure 8. In 1973 mean brood sizes were similar in primary and secondary nests, and secondary females delivered food to nests at significantly faster rates than primary females. In 1974 brood sizes were smaller in the secondary nests observed on days 5 to 9, and secondary females delivered food to nests at significantly slower rates than primary females. In 1975 brood sizes were smaller in secondary nests except on day 4 (when they were larger), and secondary females delivered food to nests at significantly faster rates than primary females only on day 4. The faster rate on day 4 may have been due to differing weather conditions, as most data for primary females were collected during the storm of 15 to 25 June, while all the data for
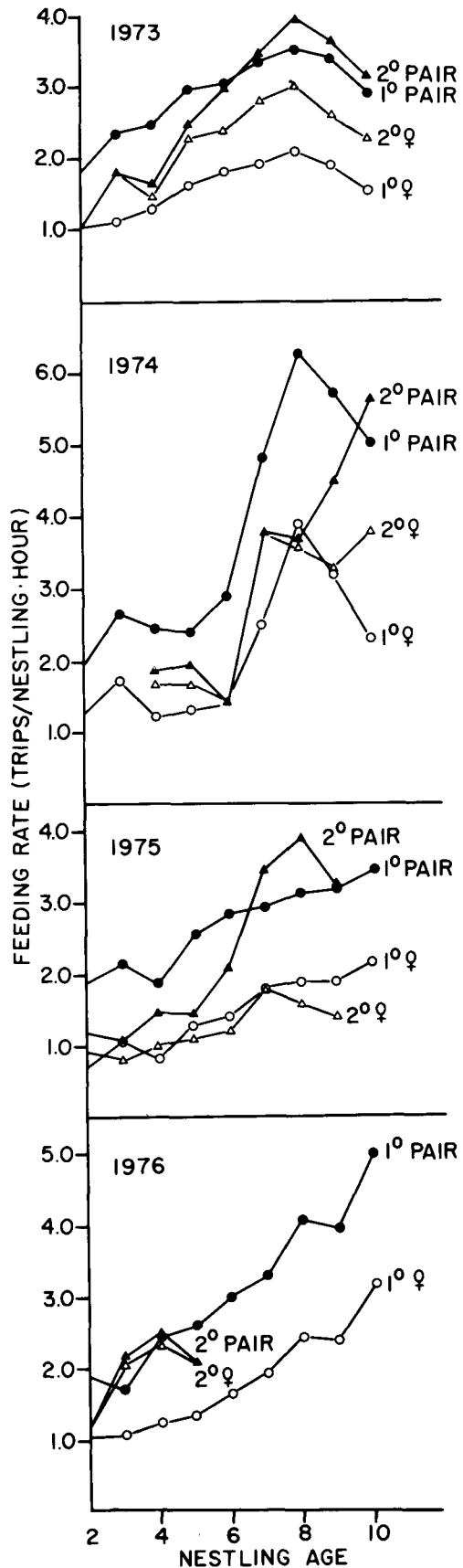

FIGURE 7. Rate at which nestlings were provisioned (trips/nestling·h) by females and by both parents combined at primary (1°) nests and at secondary (2°) nests. Sample sizes for primary nests were the same as in Figure 1. Sample sizes (hours of observation) for secondary nests for each nestling age were: 11, 16, 16, 8, 16, 13, 6, 8, 8 in 1973; 10, 19, 13, 19, 13, 14, 8, 2 in 1974; 0, 0, 5, 7, 5, 5, 2, 6, 7 in 1975; 2, 3, 3, 2, 0, 0, 0, 0, 0 in 1976.
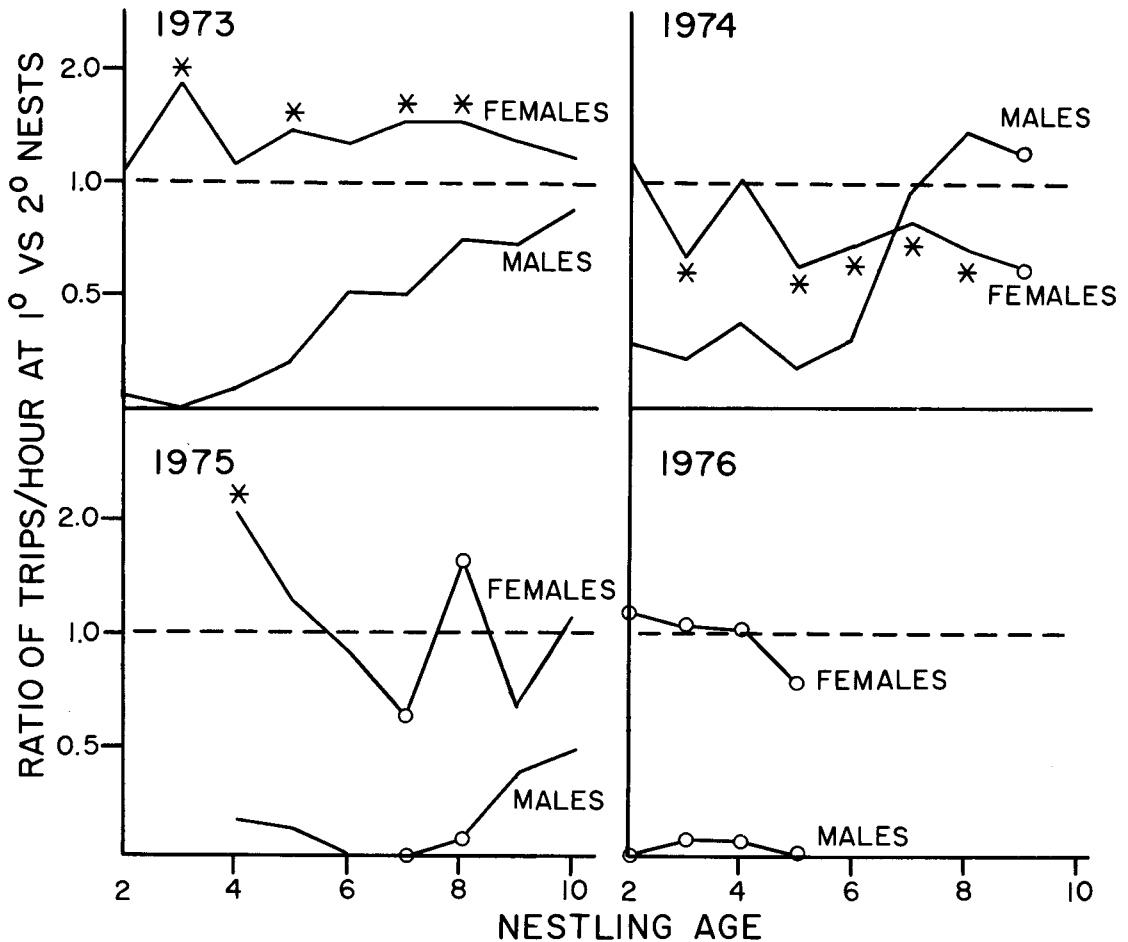
FIGURE 8.   Ratio of food delivery rates (trips/h) by females and by males at secondary (2°) nests versus at primary (1°) nests as a function of nestling age. A ratio higher than 1.0 indicates that food delivery rates were faster at the secondary nest. Significant differences (females only) for each nestling age are indicated by asterisks. Open circles indicate small sample sizes. Sample sizes for primary nests were the same as in Figure 3. Sample sizes for secondary nests were the same as in Figure 7.

secondary females were collected after the storm. In 1976 brood sizes were smaller in the secondary nests observed, and secondary females did not deliver food to nests any faster than primary females. Thus, the faster per-nestling feeding rates observed for secondary females resulted from faster delivery rates in 1973 and smaller brood sizes in 1976.

NEST ATTENDANCE AT SECONDARY NESTS

Secondary females attended nests less than primary females during the brooding period in 1973 and 1975 (day 4), but not in 1974 or 1976 (Fig. 9). Nest attendance may have been more important for secondary broods in 1974 than in the other years because ambient temperatures were higher than those for primary broods in that year. Secondary females attended nests less than primary females just after the brooding period ended (days 7–8) in every year for which I have data.

If a trade-off exists between feeding and attending nestlings, secondary females should have attended nests less than primary females when they were delivering food at faster rates. This prediction holds for most nestling ages in 1973 and for ages four and eight days in 1975. During the brooding period in 1974, secondary females attended nests as much as primary females and fed nestlings at the same or slower rates. When nestlings were older, they attended nests and fed nestlings less than primary females, perhaps in part because male contributions at secondary nests were larger than they had been earlier at primary nests.

NUMBER AND TYPE OF FOOD ITEMS
DELIVERED TO SECONDARY NESTS

I have data on the number and type of food items delivered to only two secondary nests. In 1974 one secondary female delivered 122 items to four nestlings aged eight to nine days
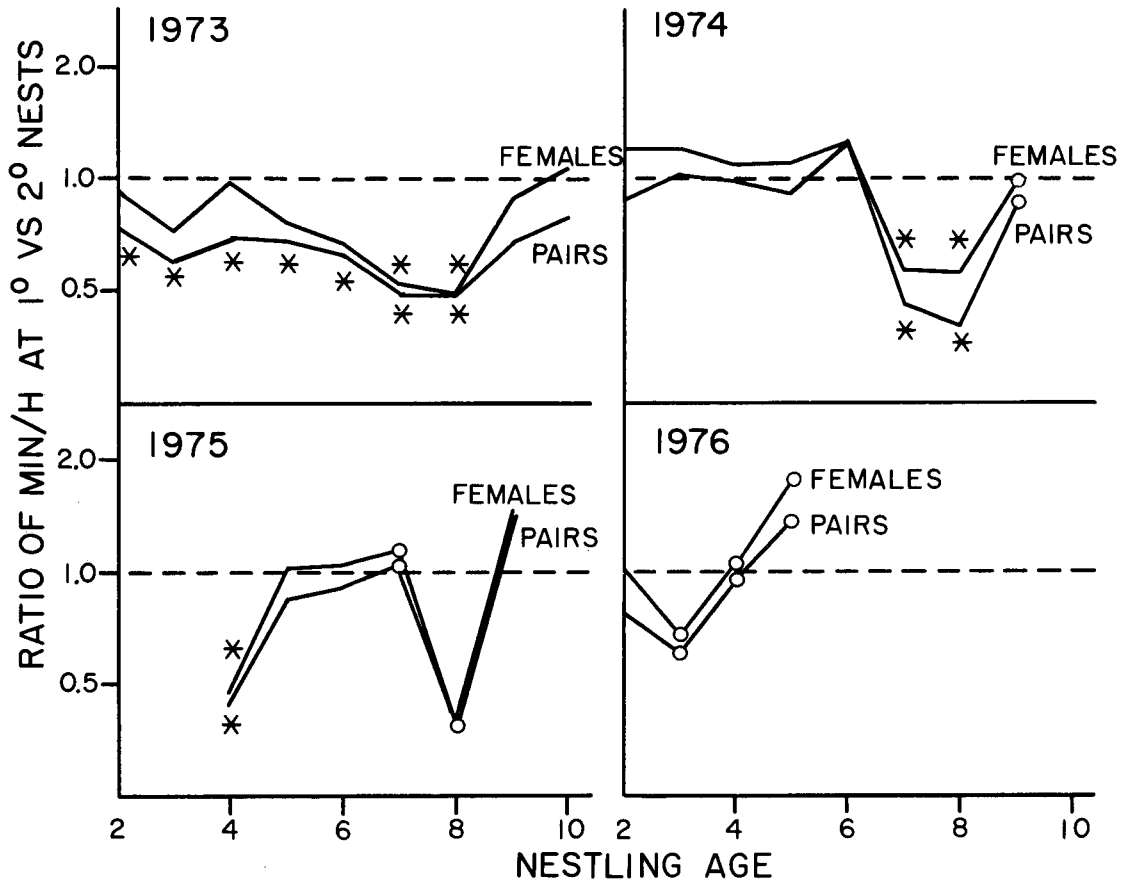
FIGURE 9.   Ratio of nest attendance times (min/h) by females and by pairs at secondary (2°) nests versus at primary (1°) nests as a function of nestling age. A ratio higher than 1.0 indicates that nest attendance was greater at the secondary nest. Data are for nestlings aged two to four days only. Significant differences for each nestling age are indicated by asterisks above the curves for females and asterisks below the curves for pairs. Open circles indicate small sample sizes. Sample sizes (hours of observation) for primary nests were the same as in Figure 1. Sample sizes for secondary nests were the same as in Figure 7.

on 52 trips (mean = 2.35 items/trip). Of these, 11% were arctiid larvae, 57% were caterpillars excluding arctiids and noctuids, and 16% were grasshoppers. This female delivered more food items per trip than did any primary female observed that year. The male delivered 175 food items to the same nest on 70 trips (mean = 2.50 items/trip, as compared to 1.33 items/trip that he delivered earlier to his primary nest). Of these, 4% were arctiid larvae, 65% were caterpillars other than arctiids or noctuids, and 9% were grasshoppers. He delivered significantly fewer arctiid larvae and significantly more caterpillars to his secondary nest (χ^2_1, $P < 0.001$), presumably because of a seasonal change in the relative availability of these resources.

In 1975 an unassisted secondary female delivered 97 food items to six nestlings aged four to five days on 52 trips (mean = 1.87 items/trip). Of these, 1% were arctiid larvae, 48% were caterpillars other than arctiids and noc-

tuids, and 14% were grasshoppers. This female delivered fewer food items/trip than did seven of the eight primary females observed that year. However, primary females were observed only for nestlings aged 7 to 10 days, so the difference may have been due to the younger age of nestlings in the secondary nest rather than to the female's lower mated status.

DISCUSSION

TRADE-OFFS AMONG REPRODUCTIVE ACTIVITIES

During the nestling period parents must make trade-offs between brooding nestlings, feeding nestlings, and self-maintenance. For males, an additional trade-off may exist between these activities and feeding their mates. However, I never saw male Bobolinks feed females at any time of season, unlike observations reported for some other passerines, and males were rarely at the nest at the same time females were there. An increase in the amount of time spent

on any one activity requires concomitant decreases in the amount of time spent on other activities. During the nestling period parents seem to have little excess time for increasing any activity without cost.

The existence of a trade-off between parental care and self-maintenance has been demonstrated for many passerine birds by the weight losses suffered by both sexes during incubation and nestling periods (Ricklefs 1974, Drent 1975, Howe 1979). If a similar trade-off exists between brooding and feeding nestlings, parental feeding rates should be negatively correlated with nest attendance time. For female Bobolinks, the correlation was significantly negative ($P < 0.005$) in every year except 1976, when it was negative and almost significant ($P < 0.10$). The correlation was positive for males in every year (significantly so in 1975 and 1976), probably because much of the time males spent attending nests was used for feeding nestlings.

Male and female Bobolinks devote different amounts of time and energy to brooding and feeding nestlings, suggesting that the relative value of performing each activity differs for the two sexes. Females spend considerably more time than males brooding young nestlings. Since, on average, males and females deliver similar amounts of food to nestlings, females are probably less able to maintain themselves than are males. I have no data for either sex on weight changes that might have occurred during the nestling period, but males began molting about two weeks earlier than females, implying that males invest more in self-maintenance during the parental care period than females.

FACTORS GOVERNING PARENTAL ALLOCATIONS

Both females and males adjust their parental activities to changes in food availability and weather conditions. Three combinations of environmental conditions can be evaluated here on the basis of between-year comparisons: high food availability and good weather (1973, 1974), low food availability and good weather (1976), and low food availability and poor weather (1975).

Under conditions of low food availability and good weather, primary females delivered food to nestlings aged 10 days at faster rates, delivered larger numbers of prey per trip to nestlings aged 7 to 10 days, and delivered a greater biomass of food per hour to nestlings aged 7 to 10 days than they did under either of the other two sets of conditions. When food was scarce and weather was poor, primary females brooded young nestlings aged two to

four days more than they did under other conditions. When food was scarce and weather was good, primary females spent less time attending older nestlings aged 4 to 10 days than they did under other conditions. Similar changes in brooding time as a function of weather conditions have also been reported for other passerine birds (e.g., Kendeigh 1952, Best 1977).

The following conclusions can be drawn: (1) primary females spend more time feeding nestlings and less time brooding them when food is scarce and weather is good; (2) primary females do not increase (or reduce) the time spent feeding nestlings but do increase brooding time when food is scarce and weather is poor. The latter increase is presumably at the expense of self-maintenance.

Under conditions of low food availability, males deliver food to nestlings at faster rates, deliver more prey per trip, and deliver a higher biomass of food per hour, regardless of weather conditions. When food is scarce, males brood nestlings less than when food is abundant. Hence, males allocate more time to feeding nestlings when food is scarce, regardless of weather conditions. This increase is at the expense of brooding time and perhaps to some extent at the expense of self-maintenance (especially when weather is poor).

The relative value of investing in each type of parental activity and in self-maintenance evidently changes with changing food availability and weather conditions. Both parents invested more in feeding nestlings during years of food scarcity. This response is not surprising, as the incremental gain in nestling survival that results from increased parental feeding effort should be larger when food is scarce. Females give higher priority to brooding when weather is poor, even when food is scarce. One might therefore expect that preventing nestling heat loss is energetically more advantageous than feeding nestlings more food. Alternatively, the risk of nestling mortality through exposure (i.e., due to inability of nestlings to convert food into body heat fast enough) is greater than the risk of nestling starvation under such conditions. The high loss of nestlings to exposure during the storm of June 1975 supports the latter interpretation, because many of those nestlings were soaked by rain as well as chilled.

The extent to which males feed nestlings may be adjusted to the nutritional condition of nestlings, and hence it may vary according to the ability of females to feed nestlings. This conclusion is supported by the finding that males contributed the highest proportion of food to nestlings during brooding periods and

when food was scarce and weather was poor. Conversely, males contributed least when food was abundant and weather was good. Results obtained by Power (1980) support the same conclusion: male Mountain Bluebirds (*Sialia currucoides*) provided a lower proportion of the food to nestlings when brood sizes were experimentally reduced.

The relative value of investing in each type of activity also varies with time of day. Nestling food requirements are highest early in the morning and just before dark because nestlings must live on stored fat reserves at night. Consequently, nestlings are fed faster and brooded less at those times of day. This is true for Bobolinks and for various other passerines (e.g., Kendeigh 1952, Dunnet 1955, Best 1977, Johnson and Best 1982). Near midday both brooding and feeding requirements appear lowest, and at that time females probably spend more time foraging for themselves. However, during adverse weather brooding requirements remain high all day, and then females cannot increase the time spent away from nests.

IMPACT OF PARENTAL RESPONSES ON NESTLINGS

Parental adjustments to changing conditions have the following net effects on the amount of care received by each nestling. (1) Young nestlings receive more brooding when weather is stormy and less when food is scarce and weather is good. (2) Older nestlings receive similar amounts of brood care when food is abundant or when weather is poor. They receive less when food is scarce and weather is good. (3) Older nestlings, at least, receive more food when food is scarce, regardless of weather conditions, than when food is abundant.

Despite increased provisioning rates, nestlings do not gain weight as fast and more nestlings starve when food is scarce. This result is not surprising for nestlings reared during stormy weather because under those conditions nestlings probably require more maintenance energy than when weather is good. Why nestlings fared so poorly in 1976 when they received more food than in 1974 is not so clear. One potentially important factor was the lower average temperatures in 1976. Another was the smaller than average brood sizes that arose from starvation of young nestlings. Smaller brood sizes would increase surface-to-volume ratios of broods and hence rates of heat loss (see Royama 1966, Mertens 1969). That could in turn have led to increased maintenance energy requirements of nestlings. Finally, the parental care data may not be representative of the population as a whole. Nest-

lings in the nests where parental data were obtained in that year averaged 23.0 g on day 10, compared to 20.7 g for the population average, suggesting either that habitats around the nests studied were unusually high in quality or that the adults studied were unusually good parents.

RELATIVE CONTRIBUTIONS OF EACH SEX

It is often assumed that male passerines provide less parental care at any given nest than do females (e.g., Trivers 1972). While this appears to be true for Bobolinks, males do play a key role in caring for nestlings. Male feeding of nestlings is especially important during years of food scarcity, periods of adverse weather, and the period when young nestlings still require brooding. At these times females are much less able to feed nestlings adequately without male assistance.

Many studies of avian parental behavior rely solely on parental feeding rates as a relative measure of how much food is fed to nestlings per unit time by each sex. However, the amount of food delivered to nestlings depends on load size and mean weight of individual food items as well as delivery rate. My data show that both load size and mean weight of food items vary with sex of parent, nestling age, and foraging conditions. They may also vary with time of day, although I could not evaluate that possibility with my sample sizes. Therefore, comparisons based solely on delivery rates can easily yield erroneous conclusions. For instance, my estimates of male parental contributions, if based on feeding rates alone, would have been 39% in 1974, 45% in 1975, 41% for nestlings aged 7 to 10 days in 1976, and 46% for nestlings aged 3 to 6 days in 1976. In comparison, estimates based on biomass were 40%, 60%, 50%, and 70%, respectively. Clearly, very different conclusions would have been reached had I based my estimates solely on food delivery rates.

PARENTAL CARE AT SECONDARY NESTS AND THE COST OF POLYGYNY

Secondary females delivered food to nests faster than primary females only in 1973, when food was abundant and weather was good. In the other three years secondary females did not deliver food faster than primary females. Indeed, in 1974 secondary females delivered food at slower rates than did primary females.

Martin (1974) claimed that secondary female Bobolinks in Wisconsin fully compensate for lost male parental assistance, even though secondary nestlings starved more often in his study area than primary nestlings. His conclusion was based on the finding that secondary

females fed nestlings at the same rate, on a per-nestling basis, as primary females and males combined. Pleszczynska (pers. comm.) obtained the same result for Lark Buntings (*Calamospiza melanocorys*), also a polygynous grassland bird, and drew the same conclusion. However, at least part of the compensatory response reported by Martin (1974) resulted from smaller brood sizes and not from increased food delivery rates, since brood sizes in secondary nests averaged only about 70% of brood sizes in primary nests in his study. How much of the response resulted from reduced brood sizes cannot be computed without access to his original data. My results in this regard do not confirm Martin's, as per-nestling feeding rates were generally lower for secondary females in Oregon compared to those for primary pairs. This discrepancy is partly due to the fact that males fed secondary nestlings at a substantial rate in my study while not doing so in Martin's. It is also partly due to the fact that brood sizes were usually not smaller in secondary nests on my study area.

The conclusion that secondary females compensate fully or at all for reduced male parental assistance is not justified unless they deliver food to nests faster than primary females. The fact that secondary females deliver as much food per nestling has no bearing when the similarity results solely from reduced brood sizes in secondary nests, because secondary females are not able to rear as many young as primary females in that case. Compensatory responses must be measured in terms of offspring production, not in terms of food delivery rates per nestling, if they are to have any relevance to evolutionary questions.

Since males delivered substantial amounts of food to secondary nestlings in 1973 and 1974 on my study area, older secondary nestlings were fed as often as primary nestlings and fledged at similar weights. Nevertheless, secondary nestlings starved more often than did primary nestlings. Male feeding of secondary nestlings was lower in 1975 and 1976, and as a result, secondary nestlings were fed less and fledged at lower weights in those years. The starvation rate among secondary nestlings was also considerably higher than it was in 1973 or 1974. Hence, loss of male help represents an important cost for secondary females. The reasons for observed variations in male parental assistance have to do with the nutritional condition of primary nestlings. They are analyzed more fully elsewhere (see Wittenberger 1980b).

Male feeding of nestlings is especially important while nestlings are young because females have less time for foraging then, yet that is the time when males help the least at secondary nests. The importance of this help is likely to be most critical during periods of food scarcity or adverse weather. For this reason, and because males are less likely to help at all under conditions of food scarcity or adverse weather, the cost of accepting secondary mated status is substantially higher for an unmated female under those conditions. It would be interesting to know whether polygyny is less prevalent in such years, as would be expected if females can distinguish between good and bad years prior to mating, but no relevant data are currently available for evaluating that possibility.

ACKNOWLEDGMENTS

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RECENT PUBLICATIONS

Estimating Numbers of Terrestrial Birds.—Edited by C. John Ralph and J. Michael Scott. 1981. Studies in Avian Biology No. 6, Cooper Ornithological Society. 630 p. Paper cover. $20.00. Source: Allen Press, Inc., P.O. Box 368, Lawrence, KS 66044. This hefty volume offers the proceedings of a 1980 conference held to examine the methodology used in gathering and analyzing data on the numbers of birds. The many papers are grouped in sections: Estimating Relative Abundance, Estimating Birds per Unit Area, Comparison of Methods, Species Variability, Environmental Influences, Observer Variability, Sampling Design, Data Analysis, and Overviews. Each section is furnished with introductory and summarizing remarks. The Editors have added a Reader's Guide, a useful aid for finding treatment of specific topics. Eight appendices give a glossary of terms used in avian censusing, reports of working groups, and lists of poster papers and all participants in the symposium. This collection offers avian ecologists and population biologists a wealth of new biological and statistical material. It should become a landmark for the improvement and standardization of census techniques. Illustrations, comprehensive list of references.

Conservation of New World Parrots/Proceedings of the ICBP Parrot Working Group Meeting, St. Lucia, 1980.—Edited by Roger F. Pasquier. Smithsonian Institution Press/International Council for Bird Preservation Technical Publication No. 1, Washington, D.C. 485 p. Paper cover. $14.00. Source: ICBP, Museum of Natural History 336, Smithsonian Institution, Washington, D.C. 20560. The ICBP's Parrot Working Group met in St. Lucia to examine the threats to Caribbean and South American parrots—chiefly loss of habitat and the live-bird trade—and to devise a strategy for the conservation of these birds. Toward that end, 30 papers were given, dealing with the distribution, status, ecology, captive breeding programs, conservation, or importation of various species of parrots, mostly in the neotropics. This volume can serve as a supplement to *The ICBP Bird Red Data Book* (noted in Condor 83:309). Both books are important references for those who have concern and responsibility for the preservation of parrots and their habitats. The papers have individual lists of references; no index.