PARENTAL INVESTMENT BY THE NORTHERN MOCKINGBIRD: MALE AND FEMALE ROLES IN FEEDING NESTLINGS

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ABSTRACT.—Analysis of 3,293 feeding trips to nestling Northern Mockingbirds (*Mimus polyglottos*) in the first 11 days of nestling life showed that males and females fed young at similar rates. Young were fed a mixed diet of animal prey and fruits, and males and females fed similar volumes of animal prey and of fruits. Females displayed a monotonic increase in feeding rate during nestling life but did not significantly increase load size. Males significantly increased both feeding rate and load size with age of nestlings, and their feeding rate peaked in the mid-nestling period, when young grow most rapidly. Males and females fed broods of two and three young at similar rates. There was a biased breeding-adult sex ratio in this population, with males outnumbering females. The unbalanced sex ratio may allow females to demand a high level of male parental care in feeding nestlings and in other behaviors included in parental investment. *Received 19 April 1985, accepted 10 September 1985.*

PARENTAL investment (PI) is defined as "any investment by the parent in an individual offspring that increases the offspring's chances of surviving (and hence reproductive success) at the cost of the parent's ability to invest in other offspring" (Trivers 1972). When offspring are typically aggregated in clutches, some components of PI (e.g. nest defense) may be viewed as a compromise among clutches separated in time and space rather than among individual offspring (Wittenberger 1981: 362-363). Parental care (PC) is the nongametic subset of PI comprising those behaviors involved in raising young to independence.

In many monogamous bird species, both males and females invest substantial amounts of time and energy in offspring, particularly in feeding nestlings and fledglings. In many monogamous passerines, males and females make roughly equal numbers of food deliveries to nestlings (Kendeigh 1952, Lack 1968, Emlen and Oring 1977, Oring 1982, Greenberg and Gradwohl 1983). However, the schedule of feeding nestlings and the amounts fed by the sexes seldom have been quantified rigorously.

We studied parental feeding of altricial nestlings by Northern Mockingbirds (*Mimus polyglottos*). Parental feeding of nestlings is a major time and energy investment in offspring (Ricklefs 1974, Skutch 1976, Breitwisch et al. 1984). Therefore, selection should favor male and female distribution of investment in feeding nestlings in proportions that maximize genetic contributions to succeeding generations (Fisher 1958). We attempted to assess the relative contributions by males and females to feeding nestlings; to establish if the patterns of feeding by males and females were similar, both daily and throughout the nestling period; to find if the quality of food brought to nestlings by males and females was similar; and to see if there was a relationship between brood size and relative investment by males and females in feeding nestlings. In light of the limited theory related to these questions, we submit our empirical findings and interpretation as a partial basis for future development of theory regarding apportionment of parental investments by males and females.

STUDY AREA AND METHODS

This study was conducted on individually color-banded Northern Mockingbirds inhabiting the main campus of the University of Miami, Dade Co., Florida (Merritt 1985). We observed parental provisioning of nestlings during 25 12-h periods (0600-1800) for a total of 300 h of observations. Data were gathered on 12 broods of 9 pairs of birds from 5 April to 9 July 1981 (23 of 25 periods between 1 May and 9 July). Four broods were observed for one day each, 4 broods for two days, 3 broods for three days, and 1 brood for four days. Broods sampled on two or more days were observed on nonconsecutive days, with one exception (see Breitwisch et al. 1984). We observed 1 brood when the young were six days old (= day 6), 3 broods at days 10 and 11, and 2 broods for each of the nine remaining days (days 1-5, 7-9, 12). Mockingbirds in southern Florida fledge at about 12 days of age. Brood sizes ranged from 1 to 4 ($\bar{x} = 2.4$, SD = 0.79, $n = 12$).

Feeding trips to the nest were recorded to the nearest second with digital watches. Using binoculars, we identified food items to major type (e.g. fruit, insect, spider, lizard), with finer levels of resolution whenever possible (e.g. species of fruit or order of insect). We estimated lengths of animal prey (<½, ½-1, 1-2, 2-3, 3-4, 4-5, 5-6, 6-7, 7-8, ≥8 cm; size classes with lower limit closed and upper limit open). We estimated relative volumes of foods on an arithmetic scale of 1-5; volume per centimeter was estimated for animal prey. Volumes of all individual fruits were between 1 and 5, inclusive, although parents frequently brought more than one fruit in a single delivery. Volumes of all animal prey ≤1 cm in length were between 1 and 5, inclusive. Volumes of animal prey >1 cm in length were calculated as (volume per centimeter) × (length in centimeters). Daily mean load sizes (= volume/trip) ranged from 2.51 to 6.85 for animal prey and 3.11 to 6.50 for fruit trips. We calculated total volume of animals and fruits fed per nest each day and divided these values by (12 × brood size) to yield mean food volume$\cdot$nestling$^{-1}\cdot$h^{-1}. Unknown foods were distributed between fruit and animal categories based on the proportions of known items fed by each parent. We assigned to unknown foods the mean relative volumes of animals and fruits fed by each parental sex to nestlings at that age.

RESULTS

All feedings by males and females.—Female mockingbirds made 1,874 feeding trips to nestlings (52.7% of total), and males made 1,680 trips (47.3%) during the 12-day nestling period. Behavior on day 12 departed from that on the previous 11 days as one pair member (the male in one pair, and the female in a second pair) spent a large proportion of time nest building instead of feeding nestlings. We therefore excluded data from day 12 from analyses. In the first 11 days of nestling life, females made 1,724 (52.4%) trips, and males made 1,569 (47.6%) trips. Feeding rates by the sexes were similar (Wilcoxon matched-pairs signed-ranks test, $T = 122.5$, $P \gg 0.05$, $n = 23$). Estimates of the relative volumes of food brought to nestlings may provide a greater level of resolution than numbers of trips (Royama 1966, Wittenberger 1982, references in Klomp 1970), but here yielded a similar conclusion. We calculated the mean total volume of animal food and fruit delivered per nestling by each sex for each day of nestling life. Summing over the first 11 days of nestling life gave an estimate of the total volume of animal food and fruit brought to a nestling by each parent. Males and females delivered similar amounts of all foods combined during nestling life [males: 1,518 (48.1%) volume units, females: 1,640 (51.9%) volume units; Wilcoxon matched-pairs signed-ranks test, $T = 120$, $P \gg 0.05$, $n = 23$].

Trips with unknown foods.—In 511 feeding trips (15.5%), unknown foods were delivered. Females made more trips delivering unknown food items than males (323 vs. 188 trips; Wilcoxon matched-pairs signed-ranks test, $T = 52$, $P < 0.05$, $n = 23$).

Day-to-day feeding patterns.—Both males and females increased feeding rates as nestlings aged from day 1 to 11 (Spearman rank correlation for males: $r_s = 0.518$, for females: $r_s = 0.693$; both P's < 0.05, n's $= 23$) (Fig. 1). We divided the nestling period into three parts (days 1-4, 5-8, 9-11) in relation to the sigmoidal growth pattern (Oniki and Merritt unpubl. data) and compared feeding rates (by trip) by males and females in each of these periods. No difference was significant, although in the mid-period, male predominance in feeding rate approached significance [Wilcoxon matched-pairs signed-ranks tests, T (days 1-4) = 12, $P \gg 0.05$, $n = 8$; T (days 5-8) = 3, $0.10 > P > 0.05$, $n = 7$; T (days 9-11) = 9, $P \gg 0.05$, $n = 8$].

Total volumes of food delivered per nestling by males and by females both were correlated with nestling age (Table 1). We compared feeding rates (by volume) by males and females for days 1-4, 5-8, and 9-11 (Wilcoxon matched-pairs signed-ranks tests). Females fed more during days 1-4 ($T = 4$, $P < 0.05$, $n = 8$). Males fed more during days 5-8, but the difference was not significant ($T = 3$, $0.10 > P > 0.05$, $n = 7$). There was no difference in volumes fed during days 9-11 ($T = 10$, $P \gg 0.05$, $n = 8$).

In the latter part of the nestling period, females continued to increase feeding rate; total volume of food$\cdot$nestling$^{-1}\cdot$h^{-1} delivered was significantly correlated with nestling age for days 5-11 ($r_s = 0.567$, $P < 0.05$, $n = 15$). During the same period, male feeding rate (total food volume$\cdot$nestling$^{-1}\cdot$h^{-1}) decreased significantly ($r_s = -0.509$, $P = 0.05$, $n = 15$).

Males increased the load size of animal trips as nestlings aged, but females did not (Table 1). Neither sex changed load size for fruit trips as nestlings aged (Table 1).

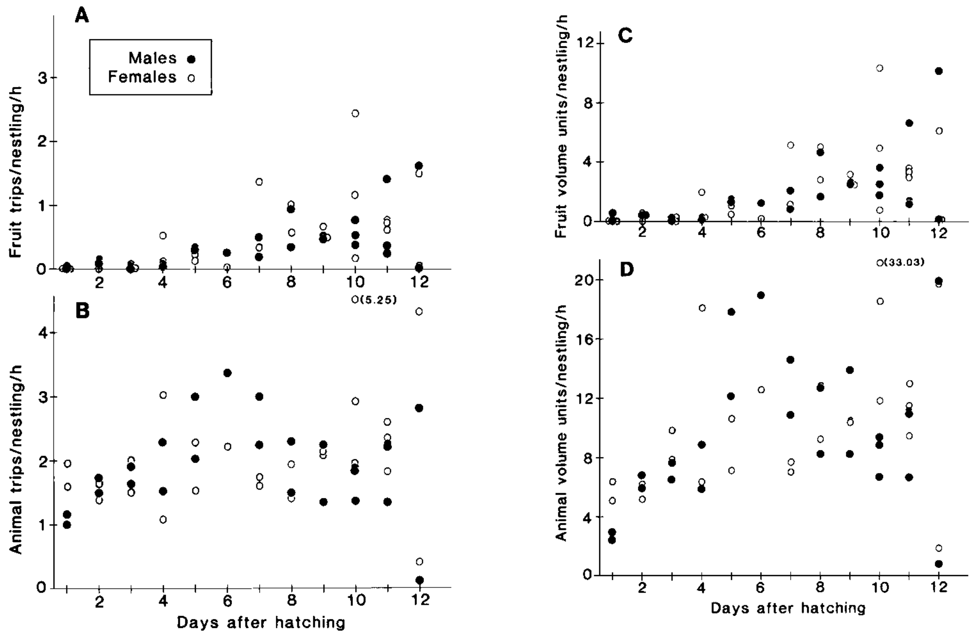

Fig. 1. Food delivery·nestling^{-1}·h^{-1} by male and female Northern Mockingbirds: (A) fruit trips, (B) animal trips, (C) fruit volume, (D) animal volume.

Females were responsible for 301 of 310 brooding bouts (97.1%), and frequency of brooding decreased sharply from day 1 to 7, remaining low through day 12 (Breitwisch et al. 1984). Although there was a strong inverse relationship between frequency of brooding bouts by females and their feeding rate ($r_s = -0.872$, $P < 0.05$, $n = 23$), the correlation was confounded by generally increasing energetic demands of the nestlings during this period. In addition, at the highest brooding frequencies (days 1-4), females fed more than males.

Feeding patterns within days.—There was a negative correlation between hour of day (0600-1800 = hours 1-12) and number of animal trips·nestling^{-1}·h^{-1} by females ($r_s = -0.636$, $P < 0.05$, $n = 12$) but not by males ($r_s = -0.193$, $P \gg 0.05$, $n = 12$). Both sexes displayed a positive correlation between hour of day and number of fruit trips·nestling^{-1}·h^{-1} ($r_s = 0.723$ for females, $r_s = 0.699$ for males, both P's < 0.05, n's $= 12$).

Quality of food brought to nestlings.—Most animal prey contain much higher percentages of protein than are contained by most fruits. Using this protein difference as a rough measure of quality of food items, we compared the relative quality of foods delivered to nestlings by males and females.

Both sexes brought fruit in addition to animal prey to nestlings, and both fed more of each type of food as nestlings aged (Fig. 1, Table 1). A nonsignificant correlation between male animal trips and nestling age was offset by males bringing larger loads of animal foods as nestlings aged. Males and females delivered similar volumes of animals and fruits to nestlings during nestling life (males: 1,320 animal volume units and 198 fruit volume units; females: 1,383 animal volume units and 257 fruit volume units) [Wilcoxon matched-pairs signed-ranks tests, $T = 113$ (animal volume), $T = 89.5$ (fruit volume), $T = 120$ (total volume), all P's $\gg 0.05$, all n's $= 23$].

Parental feeding and brood size.—We compared feeding rates by males and females for broods of two ($n = 10$) and three young ($n = 7$). First, we tested the assumption that sampling of broods of two and three young was random with respect to nestling age (randomization test, $P > 0.05$). The daily feeding rates by males, females, and the sexes together were compared for broods of two and three young. All tests were nonsignificant [Kolmogorov-Smirnov two-sample tests (Siegel 1956), all P's > 0.05; Table 2]. There was a tendency, however, toward smaller total volume of food·nestling^{-1}·h^{-1} delivered to larger broods.

TABLE 1. Correlations between parental feeding rates or load sizes and nestling age in the Northern Mockingbird.[a]

	Parent		
	Male	Female	Both
Trips·nestling^{-1}·day^{-1}			
Animal	0.127 NS[b]	0.411	0.429
Fruit	0.770	0.787	0.836
Combined	0.518	0.693	0.675
Volume·nestling^{-1}·day^{-1}			
Animal	0.440	0.669	0.580
Fruit	0.791	0.805	0.836
Combined	0.549	0.754	0.696
Load size (mean relative volume/trip)			
Animal	0.661	0.314 NS	0.534
Fruit	0.197 NS	0.427 NS	0.330 NS
Combined	0.658	0.322 NS	0.482

[a] Nestling age 1-11 days after hatching.

[b] Spearman rank correlation coefficients; $P < 0.05$, except where indicated by NS. All n's = 23, except fruit load sizes ($n = 20$ for males, 19 for females, 21 for both sexes).

TABLE 2. Feeding rates by Northern Mockingbird parents with brood sizes of two and three young.

	Feeding rate[a]			
Parent	Brood size = 2	Brood size = 3	D[b]	D[c]
Male	12.91 (5.603)	10.85 (4.066)	0.305	0.257
Female	12.61 (5.747)	12.00 (4.692)	0.266	0.229
Both	25.52 (8.392)	22.85 (7.721)	0.285	0.229

[a] Mean food volume·nestling^{-1}·h^{-1} (SD in parentheses). $n = 10$ for broods of two young; $n = 7$ for broods of three young.

[b] Maximum deviation calculated in the Kolmogorov-Smirnov two-sample test. All comparisons nonsignificant ($P > 0.05$). Cumulative distribution across days 1-11 after hatching.

[c] Maximum deviation calculated in the Kolmogorov-Smirnov two-sample test. All comparisons nonsignificant ($P > 0.05$). Cumulative distribution across days 1-11 after hatching, disregarding temporal sequence.

DISCUSSION

Comparison of feeding patterns by males and females.—Male and female mockingbirds made similar contributions to feeding nestlings, in both quantity and types of food [although our data are from only a single year; see Wittenberger (1982) for differences among years in male and female Bobolink (*Dolichonyx oryzivorus*) nestling feeding rates]. Some aspects of temporal patterns of feeding were different between the sexes, however. Equal overall feeding rates by the sexes have been documented for a variety of monogamous passerines (Kendeigh 1952, Lack 1968, Best 1977, Knapton 1984). In other passerines, females (e.g. Nolan 1978, Pinkowski 1978, Howe 1979) or males (e.g. Biermann and Sealy 1982, Johnson and Best 1982) provide more food. The reasons for these differences among monogamous species are unknown, but we suspect the possible influence of the population breeding-adult sex ratio.

Females displayed an increase in feeding rate (both animals and fruit) from day 1 to 11. The feeding rate of animal prey by males paralleled nestling growth rate and peaked in the mid-nestling period, when young grow most rapidly and food (especially protein) requirements are greatest. Similar patterns were found for Savannah Sparrows (*Passerculus sandwichensis*; Bédard and Meunier 1983). Most pairs of mockingbirds nested at least once more in 1981, and we had expected females to feed at lower rates in the latter days of the nestling period as they prepared for the next nesting attempt. However, male predominance in the mid-nestling period may indicate that females conserve energy in this demanding period by feeding below their maximal rate. When females increase feeding rate later in the nestling period, they (as well as males) typically bring a higher ratio of fruits to arthropods than do parents feeding younger nestlings. Females may then benefit from providing a mixture of foods less costly to obtain than a nestling diet of arthropods only, and the young may benefit directly from receiving more fruit (Breitwisch et al. 1984).

The greater percentage of unknown food items brought to nestlings by females resulted from greater female crypticity in delivering food, or because females delivered smaller, less easily identified items, or both. Our impression was that females were more cryptic in nest visitation behavior than males. This, in turn, may suggest that males are at slightly greater risk when feeding nestlings because of their greater visibility.

Total parental investment.—The resources available to parent mockingbirds to convert to PI are time and energy; the same is true for all animals. On spending these resources on particular behaviors, parents also incur the risk of injury or death. PI theory predicts that parents will spend time and energy efficiently, weighing risk, so as to maximize their lifetime fitness

(Fisher 1958, Trivers 1972). How males and females achieve this may be different.

Factors that affect the level of PI by a parent include: (1) the value of a given level of PI to the young, (2) the ability of each parent to provide additional PI, (3) the magnitude of decline in a parent's residual reproductive value for a given level of PI, and (4) the probability that a parent that deserts its mate and offspring will find and mate with another individual (Maynard Smith 1977). If factor 1 or 2 is large or 3 or 4 is small for one sex, a high level of PI by that sex will be favored by selection. Where PC is the major portion of PI, these arguments should also pertain to PC. Indeed, the advantages of PC (especially "nonshareable" forms of PC; *sensu* Wittenberger 1979) to both sexes have favored the evolution of monogamy in many altricial birds (Wittenberger and Tilson 1980). Trivers (1972) predicted comparable levels of PI by males and females in monogamous birds.

We studied only one aspect of PI by mockingbirds, although feeding of nestlings is probably the largest single time and energy expenditure by parents. Other aspects of PI by mockingbirds include nest building (males and females), egg production, sperm production, incubation of eggs and brooding of young (females), feeding of fledglings (males and females), and defense of young (males and females). Several of these investments (sperm production, incubation, and brooding; King 1973) are small relative to energy expenditure in feeding young, although incubation can be time-consuming. Nest building is shared by mates and requires less time and energy than feeding. Defense of young is shared, with males defending young more strongly than do females (Merritt 1984, Breitwisch MS).

Although the level of risk involved in feeding young is not known, it seems likely to be less than that incurred in defending eggs and nestlings (Breitwisch MS). Incubation and brooding also may involve risk; females perform these duties and may be subjected to greater probability of nocturnal predation than roosting males (Lack 1954: Ch. 10). Whether risks incurred in the predominantly male defense of offspring more than offsets any risks incurred by females in incubation and brooding remains unknown.

Both male and female mockingbirds feed fledglings, and this is a considerable expenditure of time and energy (Zaias and Breitwisch unpubl. data). In southern Florida, mockingbirds are multibrooded, and frequently pairs build succeeding nests and females lay eggs and begin incubation while fledglings are still on their natal territories. In these instances, males provide fledglings with most of their food (Zaias and Breitwisch unpubl. data), as described for Song Sparrows (*Melospiza melodia;* Smith 1978) and Chipping Sparrows (*Spizella passerina;* Keller 1979).

Comparison of relative levels of PI by mockingbirds may be simplified by examining a subset of major components of PI: nest building by both sexes, egg production, incubation, and brooding by females, defense of young by both sexes (but more strongly by males), and fledgling feeding (more by males). For a nesting attempt, males initially invest in laying the nest foundation of twigs. Females reduce this disparity as they line the nest with grasses, form, lay and incubate eggs, and brood nestlings. Males defend eggs and nestlings more strongly than females, the sexes feed nestlings at equal levels, and males feed fledglings more. PI expenditures in a nesting attempt may therefore present a cumulative pattern of investment by the sexes different from that suggested by Trivers (1972) for monogamous birds but like that suggested by Burger (1981) for monogamous Black Skimmers (*Rynchops niger*) (see also Gladstone 1979). Biedenweg (1983) directly measured energy expenditures by male and female mockingbirds in the breeding season and concluded that males expended at least as much energy in PI as did females.

The influence of the breeding-adult sex ratio.— What alternatives do the sexes have for time and energy expenditures? An obvious alternative for male mockingbirds is whether they could effectively court other females with time made available by a reduction in PC.

The usual explanation for a high level of PC by male birds is that it is more profitable for males than engaging in a mixed strategy of decreasing PI and increasing mating effort (Emlen and Oring 1977, Mock 1983). That is, nestlings that receive less male PC fledge at lighter weights or remain in the nest an extra day or two, and this results in fewer young ultimately reaching independence. In the extreme, no young fledge when males decrease or withhold PC (Wittenberger and Tilson 1980). There may also be direct benefits to males from maintaining a short nestling period in this population because of high nestling predation (Breitwisch unpubl. data). This argument assumes that growth rate is responsive to feeding rates and that well-fed nestlings can fledge sooner than poorly fed nestlings (see Ricklefs 1983).

However, the population sex ratio may dramatically influence levels of PC. There is a male-biased breeding-adult sex ratio in this population of mockingbirds, as documented for other passerines (Mayr 1939, Lack 1954, Trivers 1972). In each of six breeding seasons (1980-1985), there have been unmated, territorial males (Merritt 1985, Breitwisch unpubl. data). In the 1981 breeding season, between 6 May and 17 June, the sex ratio was 24 males : 18 females (Merritt 1985). Furthermore, Merritt (1985) removed females from 11 pairs in this population in April 1983, and during the ensuing several weeks, no females replaced those removed. A female mockingbird can change her mate if the male provides less than the desired level of PC, and females in this population have changed mates following nesting failure (Merritt and Breitwisch unpubl. data). Males probably have little opportunity to change mates or acquire additional females. As a result, females may demand a level of male PC greater than males would give if they could obtain additional mates.

If the breeding-adult sex ratio were unity or biased toward females, males might be able to decrease their level of PC at no cost to their fitness (or increase their fitness if they could acquire additional mates with time made available by reduced PC). This could occur because (1) females might compensate for a reduced level of male PC, so the young would not suffer from this reduction because total PC remains the same, or (2) the rate of gaining weight by nestlings might decrease very little, and young would fledge at only slightly lighter weights. In both cases, males may not experience a reduction in fitness.

A male would thus make time available for courting other females. The skewed sex ratio, however, makes it very unlikely that he will find an unmated female (see Pierotti 1981). Even if he does, his current mate can punish him by deserting after raising the present brood; she has options for remating that the male does not have. The most profitable male behavior is to invest more time and energy in caring for young—and perhaps take on greater risks— if the quality of the young increases as a result of the male's increased efforts.

In this context, it is critical to know how the skewed sex ratio arises. There is no reason to suspect a skewing of the sex ratio before the end of PC; females are slightly smaller than males and, if anything, we might predict biasing in the opposite direction (Lack 1954, Fisher 1958, Fiala 1981, Charnov 1982). Two remaining alternatives are greater female mortality associated with either greater distances of female natal dispersal, or the physiological rigors of nesting, or both. If the former is of greater importance (see Greenwood 1980), then females may indeed expend less PI than males. If the latter is more important (see Cody 1971), then females expend greater PI. In contrast to Trivers's (1972) prediction, in the former alternative, males would continue to compete for females—the limiting sex—even though males would be the sex expending greater PI. Our argument claims that mortality patterns of the sexes influence PI patterns to the extent that male birds may contribute more PI than females in other than polyandrous mating systems, in contrast to the arguments of Trivers (1972) and Burley (1977). Last, in either alternative, males may provide PC of greater importance to the young (e.g. nest defense) than that provided by females (Maynard Smith 1977).

In our view, the population breeding-adult sex ratio is a critical piece of information necessary to explain fully the particular patterns of PI by the sexes. We suggest that females, as the limiting sex in this mockingbird population, may thus exert strong influence on male PC patterns. The large male contribution to feeding nestlings may be a consequence of this influence. Similarly, male predominance in defending eggs and nestlings and in feeding fledglings may be viewed as conditions favored by the skewed sex ratio. We predict similarly high levels of male PC in populations of other birds characterized by male-biased breeding-adult sex ratios.

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100 Years Ago in The Auk

From "Third Meeting of the American Ornithologists' Union" (1886, Auk 3: 117-118):

"It became apparent more than a year ago that the work of this Committee [on the Migration and Geographical Distribution of North American Birds—Ed.] was fast assuming such formidable proportions that the Union would soon be unable to sustain the financial burden thus entailed, and at the meeting of the Union last year the Council was instructed to prepare a memorial to Congress asking for Government aid. In considering this matter the Council decided to advise the establishment of a Division of Economic Ornithology under the Department of Agriculture, which should not only carry on the investigations necessary to a thorough understanding of the movements and distribution of our birds, but should also enter upon a systematic inquiry into their food-habits and practical relations to Agriculture. The Chairman of the Committee was accordingly requested to prepare and present a draft of a memorial, embodying this plan, to the Council, which was in due time received and approved by the Council. The Chairman, on presenting this memorial to Congress, was accorded a hearing before the House Committee on Agriculture, through the assistance of Prof. C. V. Riley, Chief of the Division of Entomology of the Department of Agriculture. Prof. Spencer F. Baird had the kindness to appear before the Agricultural Committee and personally urge the practical importance of the investigations thus proposed, while Senator Warner Miller, Chairman of the Committee on Agriculture, not only brought the memorial favorably to the notice of the Committee on Agriculture, but afterward made an influential speech in its behalf on the floor of the Senate, and secured for the work contemplated an appropriation of $5000, after the item had been dropped in the House. It is thus to Senator Miller that ornithologists are indebted more than to any other person for the appropriation, as without his efficient aid the appeal to Congress would have been in vain. The House Committee on Agriculture, however, placed the work under the Division of Entomology, instead of creating for it an independent division, as contemplated in the memorial.

"The appropriation became available July 1, 1885, at which time the investigations in Economic Ornithology now in progress under the Department of Agriculture were begun. The Council of the Union was invited by the Commissioner of Agriculture and Professor Riley—in recognition of the interest in the work manifested by the Union, and of its efforts in securing the appropriation from Congress for these investigations—to nominate a person to take charge of, and conduct, the work. This the Council did at a meeting held in Washington on the 21st of last April, unanimously and very fittingly selecting for this position the Chairman of the A. O. U. Committee on the Migration and Geographical Distribution of North American Birds, Dr. C. Hart Merriam, to whom also had fallen the labor of presenting the memorial and

(*continued on p. 203*)