DETERMINANTS OF NESTLING FEEDING RATES AND PARENTAL INVESTMENT IN THE MOUNTAIN CHICKADEE[1]

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Abstract. The influence of parental sex, brood size, and nestling age in determining the rate of feeding of nestling Mountain Chickadees (*Parus gambeli*) is examined. Male Mountain Chickadees provide a majority of the food delivered to nestlings. For most of the nestling cycle, the male feeds each nestling a greater volume of food than does the female. His relative share of feeding visits increases with increasing brood size. Although the male's feeding contribution is large, the female predominates in other aspects of parental investment. Throughout the nestling cycle, female nest attendance times are at least twice as long, on average, as the male's. Her attendance time increases as brood size declines. Each nestling in a smaller brood receives a greater volume of food and more feeding visits than counterparts in larger nests. Prey volume per nestling, visits per nestling, size of individual prey, and prey volume per trip all exhibit a rising phase over the initial 5 to 10 days of the nestling cycle followed by a level phase till near fledging time. Load size, however, increases almost continuously throughout the cycle. Three solo measures (number of feeding visits, prey size, and number of prey) were evaluated as estimators of daily prey volume. Effectiveness of any one of these estimators varied between sexes and each of these variables generally explained less than 50% of the variation in daily prey volume returned by an adult. Therefore, care should be taken in equating such estimators to more complex measures of feeding effort like prey volume.

Key words: Mountain Chickadee; Parus gambeli; *parental investment; brood size; nestling feeding.*

INTRODUCTION

Important tradeoffs can occur between the effort expended by a parent bird in gathering food for nestlings and the number of that parent's offspring which ultimately survive to reproduce. Low fledgling survival rates can result, for example, from low nestling weights which, in turn, often reflect parental success in delivering sufficient food to each nestling (Lack 1954, Perrins 1965, Klomp 1970). Of course, parents face constraints in their ability to adequately provision nestlings. Theoretical and field evidence suggest that avian parents often work near prudent energetic limits during the most intensive food gathering phase of the nestling cycle (Royama 1966, Hails and Bryant 1979, Drent and Daan 1980, Ricklefs and Williams 1984). Implied in these findings is that as adult metabolic boundaries are approached during the nestling cycle, limits are reached on the amount of food delivered to each nestling. Such tradeoffs should most likely be seen as nestlings' age and brood size increases.

Other tradeoffs are anticipated during the nestling phase. Because of the large energetic expenditure in eggs made by female birds, some theories of parental investment (e.g., Trivers 1972) predict that the larger share of subsequent nestling care should be made by her. Whether this is true, and how male and female investment in nestlings vary under different conditions of nestling food need, is the subject of this study. Specifically examined will be determinants of nestling care in *Parus gambeli,* the Mountain Chickadee, to see how feeding rates are influenced by nestling age, brood size, and intersexual differences in parental contributions to nestling rearing.

STUDY AREA

The feeding and foraging activity of parent Mountain Chickadees was studied for 1,700 hr during three summers—16 June to 11 July 1979; 27 May to 6 August 1980; and 4 June to 5 July 1981—in the Modoc National Forest, 12 km northeast of Adin, California. Three study sites were used: (1) Roney Flat, elevation 1,600 m, (2) Tom's Creek, 1,900 m, and (3) Yellowjacket

Springs, 2,100 m (Dahlsten and Copper 1979). Dominant natural vegetation of these areas is ponderosa pine (*Pinus ponderosa*) and sugar pine (*Pinus lambertiana*). Selective removal of these two species, however, has left 5- to 25-m tall white fir (*Abies concolor*) as the most abundant tree. Additional information on site characteristics can be found in Dahlsten and Copper (1979) and Grundel (1984).

METHODS

Cement nesting boxes have been set out at the three study sites as part of a separate study (Dahlsten and Copper 1979). Mountain Chickadees occupying these boxes became the subjects of this investigation. For each nest observed, the frequency of nestling feeding, and the size of prey delivered, was recorded with the aid of automated photography. Three automated camera systems were constructed around cement nesting boxes identical to those normally occupied by the chickadees. A Super 8 mm movie camera and an electronic flash were mounted behind the nesting box and photographed adult birds as they entered or left the nest hole. A photocell activated by a bird crossing the nest entrance was responsible for triggering the camera shutter and flash. In this way, a frontal view of the parents, the prey they were delivering, and a watch located next to the nest entrance were filmed on entry. The exiting bird produced a similar, though posterior view, which allowed determination of nest attendance time, or how long the adult remained inside the nesting box. Male and female parents were differentiated by painting green or red, 5-mm dots of model airplane paint on the bird's forehead during routine banding of the Mountain Chickadee adults (Dahlsten and Copper 1979). At least one day always elapsed between banding and marking of these adults and gathering of data for this study.

Nests and eggs, or nestlings, from the regular nesting boxes were transferred to the camera nesting boxes anywhere from two days prehatching to 12 days posthatching, depending on the availability of nests and camera systems. The regular nesting boxes were then removed and the camera boxes were attached to the same location on a tree as the original box. After this transfer, and the activation of camera and flash, data were not collected for at least one day.

Each frame of the resultant movie film was examined under 25× magnification using a binocular microscope. The length and width of prey items were measured with an ocular micrometer which was calibrated against a scale present in each picture. Measurements obtained in this way were compared to measurements of live specimens to ensure reliability. From these lengths and widths an estimate of total prey volume was calculated, using the formula for volume of a cylinder. This calculation was used for larval, and cylindrical adult, insect bodies which constituted 84% of the 54,000 arthropods identified. For the remaining tapered prey, minimum and maximum prey widths were averaged to improve the accuracy of the volume estimate.

Direct measurements of nestling growth were obtained in 1981 from eight nests at Yellowjacket Springs; six with seven nestlings, one with six nestlings, and one with nine nestlings. These nests were not used in the photographic study but were from the same plot of nesting boxes. At each nest the total weight of a brood was recorded every second day, in late afternoon, to the nearest 0.1 g, using an Ohaus Centogram balance. The young chickadees were weighed for the first 12 days of the normal 21-day nestling period. Weighings were then discontinued to prevent premature fledging.

RESULTS

NESTLING GROWTH

The nestling phase for Mountain Chickadees lasted 21 days in 17 of 18 nests observed. One nest fledged on day 22 (with day 1 equaling the day of hatching of the first egg in a brood). During the first 12 days, Mountain Chickadee nestling weight increased 1.03 g/day on average ($r^2 = 0.951$, $n = 41$). These data are best described (Ricklefs 1967) by the logistic growth equation:

$$\text{Weight (g)} = 13.4/(1 + e^{-0.384(t-6.8)})$$

where t is nestling age and 6.8 days is the point of inflection for the growth curve ($r^2 = 0.954$). t_{10-90}, the estimated number of days required for growth from 10% to 90% of maximum weight, is 11.4 days, indicating that by day 12 nestling weight is within 10% of its peak value.

THE EFFECT OF NESTLING AGE ON FEEDING RATES AND NEST ATTENDANCE

The effect of nestling age on several indicators of parental feeding effort, and nest attendance, were examined in detail (Figs. 1–6). To test for
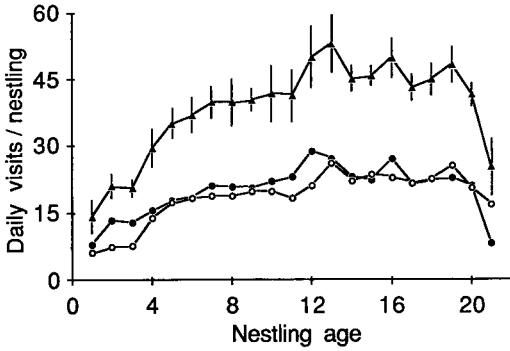
FIGURE 1.   Daily number of feeding visits per nestling as a function of nestling age. Darkened circles represent Mountain Chickadee males; open circles represent females. Darkened triangles are for combined male and female rates. Entries represent averages over all nests observed. Bars represent 1 SE but have been omitted from the bottom two lines in this graph for purposes of clarity.

FIGURE 3.   Volume of prey delivered per trip, in mm³, as a function of nestling age. For explanation of symbols, refer to Figure 1.

statistically significant differences among these variables due to age, feeding rates, and nest attendance times were grouped over four-day age categories (Table 1) and differences between categories evaluated by the Tukey-Kramer multiple comparisons' test (Sokal and Rohlf 1981; Fig. 7).

Total nest attendance time declines over the first 7 to 10 days and then is level till the final day or two before fledging (Figs. 6 and 7h). Number of prey per trip (load size) generally increases with nestling age (Figs. 5 and 7g). The remaining feeding rate variables (Figs. 1–4 and 7a–f) show a common pattern—feeding rate is distinctly lower only in the youngest nestlings (<1 week old). For the middle third of the nestling cycle these variables do not exhibit statistically sig-
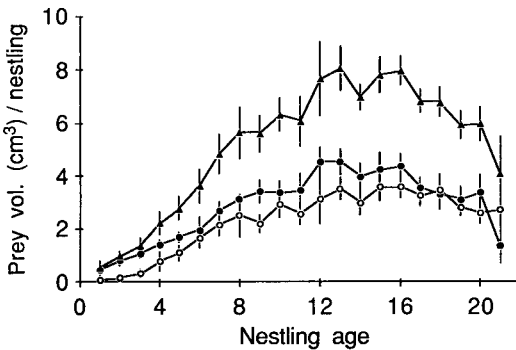
nificant differences. They do usually decline a few days before fledging.

All references to visit rates are to visits where food is delivered. This is important to note because, during the first third of the nestling phase, female Mountain Chickadees frequently visit without bringing food to the young (Fig. 8).

EFFECT OF BROOD SIZE ON FEEDING RATES AND NEST ATTENDANCE

To test the effect of brood size on feeding rates and nest attendance, two brood sizes were examined—those with fewer than seven nestlings, which represents all nests containing fewer than the mean number of young per nest previously reported for this population of Mountain Chickadees (Dahlsten and Copper 1979), and those broods with seven or more nestlings (Table 2).

Figures 9a–e illustrate the effect of brood size on feeding and nest attendance variables. In those

FIGURE 2.   Daily volume of prey, in cm³, delivered per nestling as a function of nestling age. For explanation of symbols, refer to Figure 1.
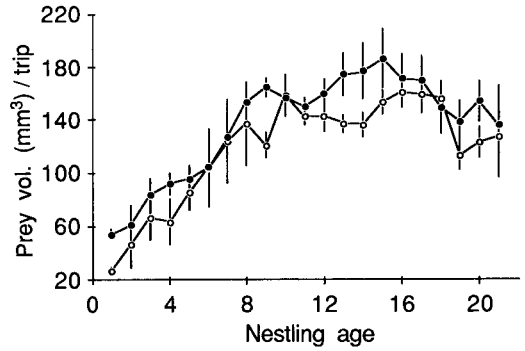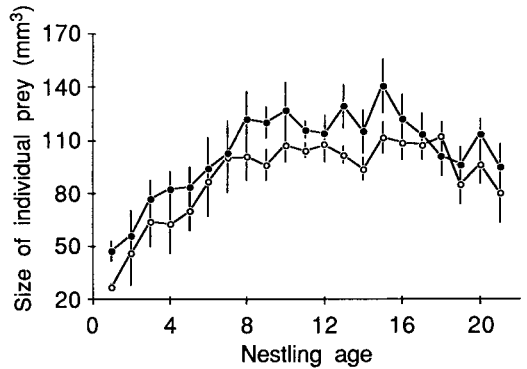

FIGURE 4.   Size of individual prey, in mm³, delivered to nestlings as a function of nestling age. For explanation of symbols, refer to Figure 1.
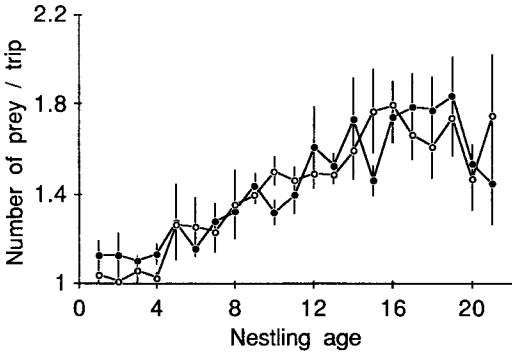
FIGURE 5. Number of prey delivered per feeding trip as a function of nestling age. For explanation of symbols, refer to Figure 1.

VARIABLE	AGE CLASS RANKING HIGHEST ----> LOWEST				
A) Daily visits / brood	(13 - 16)	(9 - 12)	(17 - 21)	(5 - 8)	(1 - 4)
B) Visits / nestling	(13 - 16)	(17 - 21)	(9 - 12)	(5 - 8)	(1 - 4)
C) Prey volume / brood	(13 - 16)	(9 - 12)	(17 - 21)	(5 - 8)	(1 - 4)
D) Prey volume / nestling	(13 - 16)	(9 - 12)	(17 - 21)	(5 - 8)	(1 - 4)
E) Prey volume / trip	(13 - 16)	(9 - 12)	(17 - 21)	(5 - 8)	(1 - 4)
F) Size of individual prey	(13 - 16)	(9 - 12)	(17 - 21)	(5 - 8)	(1 - 4)
G) Number of prey / trip	(17 - 21)	(13 - 16)	(9 - 12)	(5 - 8)	(1 - 4)
H) Nest attendance time	(1 - 4)	(5 - 8)	(9 - 12)	(13 - 16)	(17 - 21)

FIGURE 7. Evaluation of statistical differences due to nestling age, for feeding and nest attendance variables. Averages for five age categories (see Table 1 for categories) are ranked from highest to lowest values (left to right) for each variable. Age categories connected by underscores did not differ significantly ($P > 0.05$) from each other as determined by the Tukey-Kramer multiple range test (Sokal and Rohlf 1981).

figures only per brood feeding rates and variables with overall significant brood size effects are graphed. Table 3, column A, however, summarizes analyses of variance (ANOVA) on all variables, and shows whether brood size is a significant factor ($P < 0.05$), over all ages, in a two-way ANOVA with age as the second factor. In those ANOVAs, age is significant at $P < 0.001$ in all analyses and the age by brood size interaction is not significant except as indicated. Per nestling visit rates, per nestling prey volume, and nest attendance time tend to decrease with increased brood size according to the ANOVA results in column A and Figures 9B, D, and E. In the case of prey volume per nestling, however, this overall trend is not apparent till the level phase of feeding is reached (Fig. 9D).

PARENTAL DIVISION OF LABOR

Table 4 summarizes sexual differences in prey delivery and nest attendance (see also Figs. 1–6), showing whether the male parent (M) or female parent (F) has the highest value for each variable and whether this sexual difference is significant (as determined by paired t-tests).

Although the results of Table 4 strongly suggest that males make a greater contribution to nestling feeding, especially in the first half of the nestling phase, and females provide the majority of nest attendance, it is important to examine whether any diurnal complementarity, or switching of relative feeding effort during the day, exists between the sexes. To test complementarity in feeding visit patterns, a Spearman's rank corre-
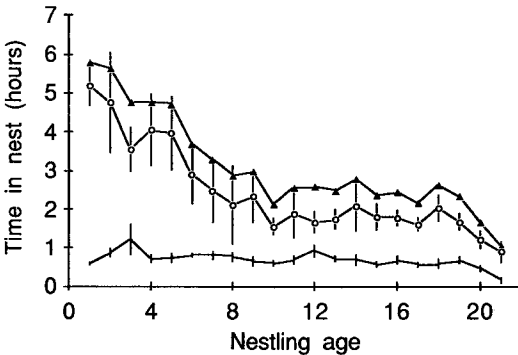

FIGURE 6. Total amount of time (hr) per day spent within the nesting cavity as a function of nestling age. For explanation of symbols, refer to Figure 1. Standard error bars have been omitted from top line (male plus female total) and darkened circles (male) have been omitted from bottom line for purposes of clarity.
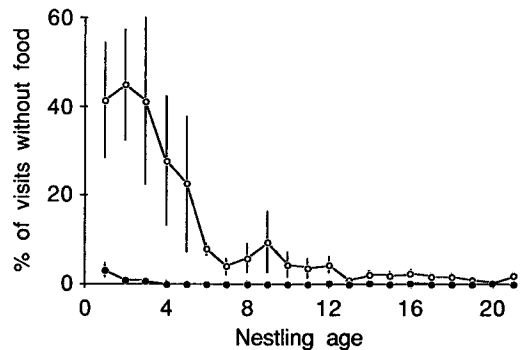

FIGURE 8. Percentage of visits to the nest on which no food was seen to be returned. For explanation of symbols, refer to Figure 1.

TABLE 1. Number of observations and mean brood size in different age categories.

Age category	n (days)	Mean age ± SE	Mean brood size[a] ± SE	No. feedings observed
1–4	12	2.5 ± 0.34	6.0 ± 0.43	1,286
5–8	13	6.4 ± 0.33	5.8 ± 0.42	2,644
9–12	21	10.8 ± 0.26	6.1 ± 0.30	5,277
13–16	33	14.5 ± 0.20	5.9 ± 0.19	9,136
17–21	37	18.6 ± 0.22	6.2 ± 0.18	9,459
Total	116[b]	13.0 ± 0.51	6.0 ± 0.11	27,802

[a] Mean brood size is not significantly different (ANOVA, $F(4, 111) = 0.234$, $P = 0.919$) among age categories.
[b] A total of 116 days are used in most analyses. For some analyses hatching and fledging days are eliminated leaving 109 days.

lation (r_s) was calculated, for each day, on male visits in an hour versus female visits in that hour, over all hours of a given day. A significant, positive r_s indicates that male and female patterns of feeding are very similar; a significant, negative r_s indicates that peak activity of one sex coincides with activity troughs for its mate; a nonsignificant r_s implies no relationship between feeding patterns of the two parents. Overall, 25 positive, significant, 62 positive, nonsignificant, 25 negative, nonsignificant, and 4 negative, significant Spearman's correlations were calculated. Therefore, male and female feeding visit patterns are similar, or at least not opposite, on most days.

Prey volume returned per trip also follows a constant pattern throughout the day. This was tested by comparing the male : female ratio for prey volume delivered per trip, over the entire day, to the male : female ratio during five daily time intervals. Table 5 shows that the ratio at any time of the day is rarely different from the overall daily ratio. This too is evidence for a lack

of diurnal complementarity between sexes in prey delivery.

In response to brood size, male and female Mountain Chickadees differ from each other in some respects (Table 3, columns B and C). Male Mountain Chickadees visit large broods more often than small broods. This response is not significant in the female. Females bring more prey per trip to larger broods. Males do not show a significant tendency to do the same. Females average more time in the nest with smaller broods during all five age intervals. This difference is significant ($P < 0.05$, t-test) during the final four age intervals (5 to 21 days). Male nest attendance shows no significant change with brood size.

One way of assessing the overall impact of brood size on intersexual differences in parental investment is to test whether male percentage of total daily visits or prey volume changes with brood size. Data from the level phase of parental feeding activity (>10 days of age) were investigated to test for such trends. This interval was chosen to help eliminate intersexual effects at-

TABLE 2. Number of observations and average nestling ages between brood sizes.

Age category	No. visits	n (days)	Mean brood size ± SE	Mean age[a] ± SE
Small broods (<7 nestlings)				
1–4	365	4	4.0 ± 0.00	2.5 ± 0.65
5–8	793	5	4.0 ± 0.00	6.2 ± 0.58
9–12	1,705	7	4.3 ± 0.29	11.1 ± 0.46
13–16	5,699	21	5.3 ± 0.21	14.6 ± 0.25
17–21	5,784	23	5.5 ± 0.18	18.8 ± 0.29
Large broods (>6 nestlings)				
1–4	921	8	7.0 ± 0.00	2.5 ± 0.42
5–8	1,851	8	7.0 ± 0.00	6.5 ± 0.42
9–12	3,572	14	7.0 ± 0.00	10.6 ± 0.31
13–16	3,437	12	7.0 ± 0.00	14.5 ± 0.34
17–21	3,675	14	7.2 ± 0.11	18.4 ± 0.36

[a] Mean ages do not differ significantly ($P > 0.05$, t-test) between brood size groups, within any age category.

TABLE 3. Results of two-way analysis of variance indicating whether feeding and nest attendance variables change with brood size within age categories.

Variable	(A) Both parents	(B) Male		(C) Female	
Prey volume/brood	ns[a]	ns		ns	
Prey volume/nestling	*** −	***	(I) −	***	−
Visits/brood	ns	**	+	ns	
Visits/nestling	*** −	**	(I) −	***	−
Prey volume/trip	ns	ns		ns	
Prey size	ns	ns		ns	
No. prey/trip	ns	ns		**	+
Nest attendance time	*** −	ns		***	−

[a] Significance of brood size as a factor is indicated as follows: ns not significant; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$. (I) Indicates that the age category × brood size category interaction is significant. (+) Variable *increases* significantly with increased brood size; (−) variable *decreases* significantly with increased brood size.

TABLE 4.   Intersexual differences in feeding and nest attendance variables as a function of nestling age.

Variable overall	1–4	5–8	9–12	13–16	17–21	
Volume/brood	M**[a]	M**	M**	M	M	M***
Volume/nestling	M***	M*	M***	M*	M	M***
Visits/brood	M**	M*	M**	M	F	M**
Visits/nestling	M*	M	M**	M	F	M
Volume/trip	M***	M	M**	M**	M	M***
Prey size	M***	M	M**	M**	M	M***
No. of prey/trip	M*	F	=	F	M	M
Nest attendance	F***	F***	F***	F***	F***	F***

[a] (M) Indicates that male adult's average value for the variable in question exceeds the female's. (F) Indicates that the female exceeds the male. (=) Indicates equal means. Significance of differences, based on paired t-tests between mates, are as follows: $*P < 0.05$; $**P < 0.01$; $***P < 0.001$.

tributable to brooding and nestling growth. For nestlings older than 10 days, males account for 49.3% ± 1.86 (SE) of all feeding visits for small broods (<7 nestlings) and 54.4% ± 1.45 for average sized broods (>6 nestlings). This difference is significant ($P < 0.05$ based on t-test, $n = 49$ for small broods, $n = 34$ for large broods). His percentage of total volume also increases, on average, going from 53.6% ± 2.55 to 56.1% ± 1.37. This difference, however, is not statistically significant.

As a final examination of sexual differences in feeding patterns, the relative effect on total prey volume of male and female feeding frequency, prey size, and number of prey per trip was estimated by multiple regression analysis. The coefficient for female prey size is not significant in this regression ($t = -1.57$, $P = 0.120$, $n = 109$) and is not included in the final regression equation. The remaining five variables are significant ($P < 0.001$) and their standardized regression coefficients indicate that increases in prey size delivered by males most influences increases in total prey volume. Specifically:

TABLE 5.   Intersexual differences in prey volume delivered per trip as a function of time of day.

	Time of day				
Age range	05:30–07:59	08:00–10:59	11:00–13:59	14:00–16:59	17:00–20:30
1–4	ns[a]	ns	F*	ns	ns
5–8	ns	ns	ns	ns	ns
9–12	F*	ns	ns	M*	ns
13–16	ns	ns	ns	ns	ns
17–21	ns	ns	ns	ns	ns

[a] Entries indicate whether the ratio of male prey volume per feeding trip to female prey volume per feeding trip, for a given time interval on a given day, is significantly different from the overall ratio for the day. Significance is based on paired t-tests and is indicated as follows: (ns) no significant difference; (F*) or (M*) the female or male, respectively, has returned a significantly larger average volume of prey per trip ($P < 0.05$), relative to its mate, during that time interval.

Total prey volume (cm³) = 0.239·Male feeding visits + 0.395·Female feeding visits + 0.695· Male prey size + 0.265·Male prey per trip − 0.153·Female prey per trip

($R^2 = 0.928$, $n = 109$, all coefficients are standardized regression coefficients).

ESTIMATORS OF PREY VOLUME

Different methods are in use in ornithology for estimating the quantity of food provided to nestlings. Number of feeding visits, average prey size, and total number of prey have all been used as estimators of total food quantity. To evaluate how well each of these three variables explains variation in total daily prey volume, coefficients of determination (r^2) were calculated. Results show that the relative values of r^2 differ for the sexes. For example, number of daily male visits ($r^2 = 0.486$) and average prey size of the male ($r^2 = 0.490$) are more effective in explaining variation in male prey volume than is total daily number of prey donated by the male ($r^2 = 0.314$). The figures for the female are almost reversed (visits $r^2 = 0.303$, prey size $r^2 = 0.469$, prey number $r^2 = 0.446$). Combining the male and female contributions shows that the total number of daily visits from both parents ($r^2 = 0.613$) best explains total combined daily prey volume, followed by average prey size ($r^2 = 0.537$), and total number of prey ($r^2 = 0.352$).

Finally, the ability of feeding visits and prey volume to estimate parental investment differs. The average percentage of feeding visits made by the male, over the five age categories, was (1 to 4) 68%, (5 to 8) 55%, (9 to 12) 57%, (13 to 16) 52%, (17 to 21) 49%. The percentage of total volume he delivered was 76, 58, 60, 56, and 52. In each category the prey volume percentage is
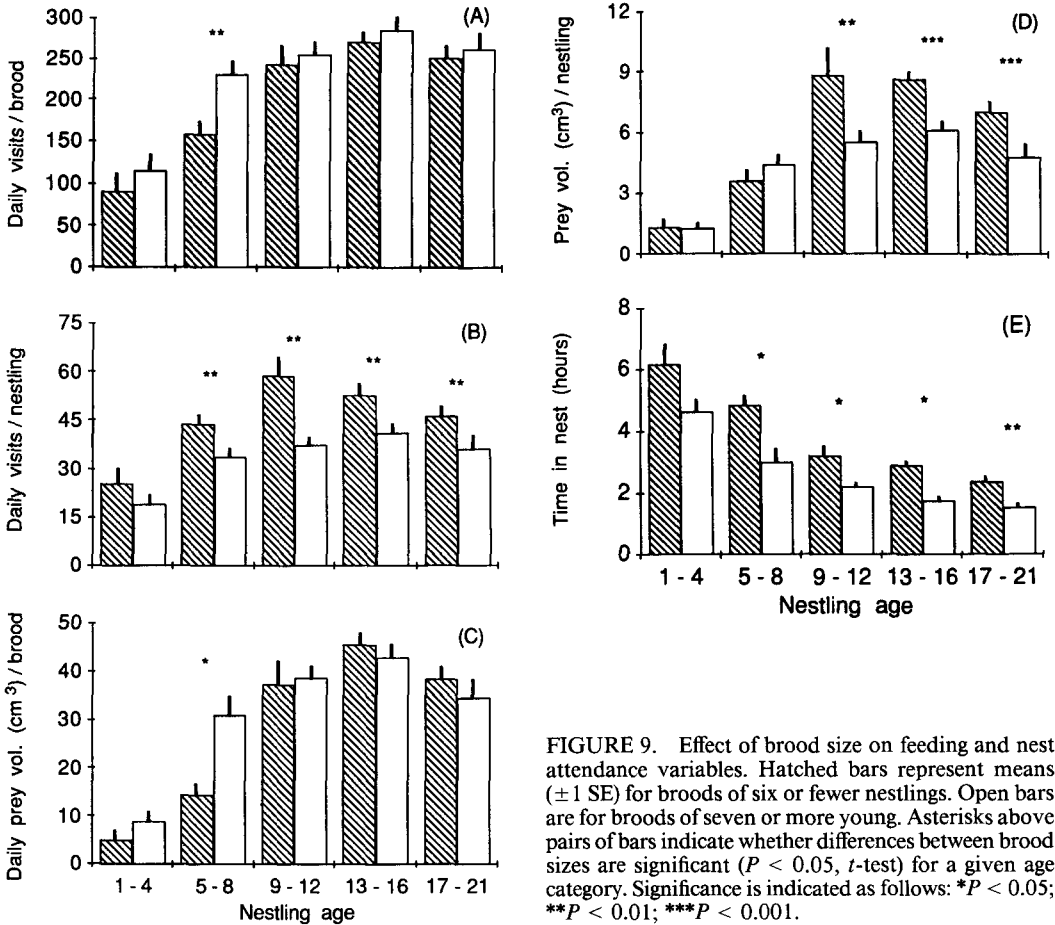
FIGURE 9. Effect of brood size on feeding and nest attendance variables. Hatched bars represent means (± 1 SE) for broods of six or fewer nestlings. Open bars are for broods of seven or more young. Asterisks above pairs of bars indicate whether differences between brood sizes are significant ($P < 0.05$, t-test) for a given age category. Significance is indicated as follows: $*P < 0.05$; $**P < 0.01$; $***P < 0.001$.

greater. This difference is significant (t-test, $P < 0.05$) for all categories except ages 5 to 8.

DISCUSSION

DEFINING FEEDING EFFORT

In the absence of direct measurement of energy expenditure, parental investment in nestling feeding is estimated in this study, and in many others, by surrogate measures such as feeding visits, prey number, or prey biomass or volume. However, previous work (Royama 1966, Biermann and Sealy 1982, Wittenberger 1982, Bédard and Meunier 1983) has suggested that these different measures of parental contribution to nestling diet do not change in synchrony. Wittenberger (1982), for example, demonstrated for Bobolinks (*Dolichonyx oryzivorous*) that male contribution to nestling food supply is consis-

tently lower when estimated by visits than when estimated by biomass. The same is true for dietary volume in the Mountain Chickadee.

Prey volume presumably incorporates much information on parental feeding effort by virtue of being the product of prey number, prey size, and feeding frequency. Therefore, the potential for inconsistency in estimating parental investment from dietary information can be illustrated from the part of this study that examined how well simpler estimators predict prey volume. The relative ability of only feeding visits, average prey size, or total number of prey to explain variation in total prey volume is not only nearly reversed in male and female Mountain Chickadees, but less than half of the variation in prey volume is generally explained by any one of these variables taken alone and applied to one sex. These results emphasize the importance of simultaneously in-

vestigating several aspects of food quantity when assessment of parental feeding effort during the nestling phase is based on dietary information.

FACTORS AFFECTING PARENTAL EFFORT

Feeding effort in the Mountain Chickadee can be divided into two major temporal phases—a period of increasing prey size and visit rates for most of the first week of the nestling phase, followed by a period of a week or more during which feeding effort does not vary significantly. Nestling feeding then declines till near fledging time. This pattern corresponds to the rising and plateau phases of parental feeding effort noted for Great Tits, *Parus major* (Gibb 1950, Royama 1966, van Balen 1973), House Sparrows, *Passer domesticus* (Seel 1969), European Starlings, *Sturnus vulgaris* (Westerterp 1973, Tinbergen 1981), Purple Martins, *Progne subis* (Walsh 1978), and Tree Swallows, *Tachycineta bicolor* (Leffelaar and Robertson 1986). With the exception of load size (number of prey per trip), which increases for most of the phase, all feeding variables examined (Fig. 7) follow the same general pattern of rising phase and plateau.

A decrease in feeding effort per nestling with increases in brood size has been noted in several previous studies of passerine species (Lack and Silva 1949; Gibb 1950, 1955; Gibb and Betts 1963; Royama 1966; Morehouse and Brewer 1968; Walsh 1978; Zammuto et al. 1981; Johnson and Best 1982; Leffelaar and Robertson 1986) although exceptions are common (Pinkowski 1978, Bédard and Meunier 1983). In the Mountain Chickadee neither total volume of prey delivered per brood nor number of feeding visits per brood change with increased brood size. Because per brood rates remain essentially constant, volume and visit rates per nestling decrease in larger nests. This decline in total volume per nestling is not mainly due to changes in prey size or load size which do not exhibit significant differences between brood sizes (Table 3). Therefore, nestlings in larger broods receive less food because they are fed less frequently and not because they are fed smaller prey. Carlson and Moreno (1986) recorded the same pattern in the Fieldfare. Most of the observed changes with brood size hold for both Mountain Chickadee sexes, with an important exception. Males visit the larger broods, which in this case are broods slightly larger than the population average, more frequently than smaller broods. Females do not.

This is evidence that males play a critical role in maintaining broods of normal size.

Nest attendance is also significantly affected by brood size, but only in the females. Her time spent in the nesting cavity decreases in larger broods, not only while brooding, but also throughout the rest of the nestling phase. Similar observations of an inverse relationship between brood size and nest attendance have been published by Royama (1966), Walsh (1978), Johnson and Best (1982), and Bédard and Meunier (1983). Because no observations of activity in the nesting cavity were made for the Mountain Chickadee it is only possible to speculate as to the reasons why nest attendance time declines as brood size increases. However, the data does justify the idea that young nestlings in larger broods enjoy a thermoregulatory advantage over their counterparts in smaller nests (Royama 1966) and hence require less brooding. Less easy to explain is the brood size effect for older nestlings. The decrease for older nestlings, however, probably does not represent the female rushing off to feed her larger brood more frequently because, as previously seen (Table 3, column C), brood size does not affect per brood feeding visits by the female.

PATTERNS OF PARENTAL INVESTMENT IN NESTLING CARE

Given a female passerine's high initial investment in egg laying, Trivers (1972) hypothesized that she will protect her investment by continuing to provide the larger share of total care for the young after hatching. In attempting to assess Trivers' hypothesis for Mountain Chickadees it is best to say that differential division of labor occurs between the sexes during the nesting period, with the male assuming the majority percentage of nestling feeding. The female Mountain Chickadee, however, spends substantially more time attending the nest than does her mate. This extra female effort holds even when the nestlings should be homeothermic—during the final week she still spends an extra hour a day, beyond her mate's time, in the nesting cavity. When it comes to what is probably the more energetically demanding tasks of food gathering, however, the male generally provides the majority of the total investment. Based on several methods of looking at feeding effort (Figs. 1 to 5), male and female patterns of feeding nestlings are similar but, over the initial 80% of the nestling cycle, the male Mountain Chickadee generally provides a statis-

tically significant majority of each nestling's food (Table 4). This result is reached both because he usually feeds the nestlings more frequently and because his prey are usually larger. The remaining input into daily prey volume, load size, yields few noticeable intersexual differences although, just as reported for the Bobolink (Wittenberger 1982) and the Fieldfare, *Turdus pilaris* (Carlson and Moreno 1986), the female Mountain Chickadee initially delivers significantly smaller loads than the male. A possible explanation for this trend is that for the first few days the female might return fewer of the prey she captures perhaps to compensate for her lack of personal feeding time while brooding.

The intersexual feeding trends just noted are consistent over the course of the day. There is no evidence that switching of nestling-feeding responsibility between the sexes occurs; the relative share of the feeding burden taken by the male or female remains fairly constant throughout a day. This was verified for both frequency of feeding visits and volume of prey delivered per feeding trip.

When all of the inputs into total prey volume—feeding frequency, load size, and prey size—are considered, it is change in male prey size which has the greatest effect in changing total amount of prey delivered to each nestling. The male, therefore, not only feeds the young more than the female throughout much of the cycle, but the most important factor contributing toward increase of total daily prey volume is the size of prey he delivers. In addition to this, the male's relative proportion of feeding visits increases significantly as brood size increases during the final half of the nestling cycle. His proportion of prey volume also increases, on average, even though this difference is not statistically significant. Thus just as Power (1980), Wittenberger (1982), and Bédard and Meunier (1983) have all concluded, the relative Mountain Chickadee male contribution to nestling feeding seems to increase when a difficult feeding situation arises, e.g., during rapid nestling growth or scarce food periods or, in this case, for larger, fully grown broods. The relatively large male Mountain Chickadee contribution may be critical in maintaining the nestling phase for as short a duration as possible. Shortening this duration is important because nestlings of this species seem to grow slowly. The Mountain Chickadee nestling logistic growth constant, $K = 0.384$, indicates less rapid growth

than that for *Parus caeruleus* ($K = 0.416$) and *P. atricapillus* ($K = 0.480$), two congeners similar in adult size to *P. gambeli,* ca. 12 g (Ricklefs 1968). The Mountain Chickadee's nestling phase of 21 days is also longer than that of *P. atricapillus* (mode = 18 days, Kluyver 1961) or *P. caeruleus* (mean = 19.7 days, Gibb 1950). Even among passerines with a 21-day phase, *P. gambeli*'s time to reach 90% of estimated maximum weight is longer than those passerines described by Ricklefs (fig. 7 in Ricklefs 1968).

All of this evidence—the majority of prey volume per nestling coming from the male during the first 16 days, the importance of male prey size in determining total volume, and his increasing proportion of feeding visits in large, mature broods—suggests that male Mountain Chickadees provide the majority of parental investment in terms of providing food to the young during the nestling phase. While these results imply that, in at least one important respect, female Mountain Chickadees do not conform to Trivers' (1972) generalization, Wittenberger's hypothesis (1979) that monogamy should evolve under conditions where male parental care is critical for offspring survival is well supported in this monogamous species.

ACKNOWLEDGMENTS

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