J. Field Ornithol., 72(3):412–418

PARENTAL CARE IN RELATION TO BROOD SIZE IN THE HOUSE FINCH

ANDREW M. STOEHR[1], KEVIN J. MCGRAW[2], PAUL M. NOLAN, AND GEOFFREY E. HILL

Department of Zoology and Wildlife Science and Alabama Agricultural Experiment Station Auburn University, Alabama 36849 USA

Abstract.—Studies that quantify parental care in birds are often faced with the confounding effects of variation in brood size. That is, nestlings from broods of varying sizes may receive different quantities of food for reasons not entirely related to the parental quality of the adults. To control for variation in brood size, researchers often divide feeding visitation rates by brood size to yield a per-nestling feeding rate. This presents problems, however, if adults adjust food load size in response to variation in brood size. We examined the relationship between brood size and parental care in the herbivorous House Finch (*Carpodacus mexicanus*) by considering not only visitation rates but also food load sizes. As brood size increased, the overall visitation rate increased but both per-nestling visitation rate and per-nestling food load rate decreased. The relationship between brood size and per-nestling care was similar regardless of whether we considered visitation rate or actual food loads, suggesting that in the House Finch per-nestling visitation rate serves as a reasonable index of total mass of food received by the nestlings. However, we urge caution in assuming that per-nestling visitation rate is an adequate measure of parental care in other species.

CUIDADO PARENTAL EN RELACIÓN AL TAMAÑO DE LA CAMADA EN *CARPODACUS MEXICANUS*

Sinopsis.—Estudios que cuantifican el cuidado parental en aves a menudo se enfrentan a los efectos confusos de la variación en el tamaño de la camada. En otras palabras, crías de camadas de diferentes tamaños pueden recibir diferentes cantidades de alimento por razones no enteramente relativas al cuidado parental de los adultos. Los investigadores dividen las tasas de visitación por el tamaño de camada por obtener una razón de alimentación por cría como método para controlar las variaciones en tamaño de camadas. Sin embargo, este método crea problemas si los adultos ajustan la cantidad del alimento transportado en respuesta a la variación en el tamaño de la camada. Nosotros examinamos la relación entre el tamaño de la camada y el cuidado parental en el herbívoro: *Carpodacus mexicanus* al considerar no solo las tasa de visitación sino la cuantía de alimentos transportado. La tasa básica de visitación incrementa al aumentar el tamaño de la camada, pero tanto la tasa de visitación por cría como la cantidad de alimentos por cría se reduce. La relación entre el tamaño de la camada y el cuidado por cría fueron similares independientemente de que consideremos la tasa de visitación o la cantidad actual de alimentos llevados. Aparentemente, en esta especie la tasa de visitas por cría sirve como un índice razonable de la masa total de alimento recibido por las crías. Sin embargo, instamos cuidado al asumir que la tasa de visitas por cría es una medida adecuada del cuidado parental en otras especies.

Many disciplines within avian behavioral ecology require knowledge of certain attributes of parental care. For example, studies of mating systems and sexual selection often address the relative contributions of each sex to offspring care (Trivers 1972) or the quality of care provided by individual males (Hoelzer 1989). Behavioral endocrinologists often quantify

[1] *Current address: Dept. of Biology, University of California, Riverside, California 92521 USA.*
[2] *Current address: Dept. of Neurobiology and Behavior, Cornell University, Ithaca, New York 14853 USA.*

parental care to examine hormone-influenced trade-offs in reproductive efforts (Beletsky et al. 1995). Studies investigating the evolution of clutch size often quantify parental care to understand how parental effort affects future reproduction (Nur 1984). These studies often consider a variety of aspects of parental care, including feeding rates, food types and load sizes, and sexual dimorphism in parental behaviors. Finally, it is important to consider the number of offspring the parents are provisioning. Except in studies directly addressing the evolution of brood size, variation in brood size is usually considered a problem in studies of parental care because it has the potential to confound the results of experiments and observations. This leads to a need to control for brood size.

The most common method of quantifying parental care is to measure the rate at which parents bring food to a brood and the most common method of dealing with variation in brood size is to divide this rate by brood size to yield a rate per nestling (e.g., feeding visits per nestling per hour). This method makes the assumption that if adult birds respond to variation in brood size, they do so by adjusting the number of visits to the nest that they make. That is, as brood size increases adult birds are expected to increase the number of feeding visits they make to the nest. If they increase their visitation rate enough, nestlings from large broods will receive as much (or possibly more) food as nestlings from smaller broods. If the increase in visitation rate is not proportional to the increase in brood size, the per-nestling visitation rate will be less for nestlings in larger broods.

Controlling for brood size in this way presents problems, however, when adult birds alter other aspects of their provisioning behavior in response to brood size. For example, they may alter either the size or composition of the food loads they bring to nestlings, or possibly some combination of visitation rate, load composition, and load size (Siikamäki et al. 1998; Wright et al. 1998). Thus, by assuming that adult birds respond to variation in brood size only by altering visitation rate, one may mistakenly over- or underestimate the amount of food each nestling receives. This will in turn confound conclusions about male quality, relative contributions towards parental care by each sex, etc.

The purpose of this study was to determine the relationship between brood size and parental care in House Finches (*Carpodacus mexicanus*) by considering not only visitation rates but also the size of food loads provided to nestlings during feeding visits. Our purpose was not to test hypotheses about the evolution of clutch size in House Finches, but rather to examine the relationship between parental behavior and brood size as part of several other studies of House Finch breeding biology that require us to determine parental quality. Thus, we observed the behavior of finches with natural, rather than manipulated, brood sizes.

METHODS

The House Finch is a small (approximately 20 g) biparental passerine. Adult House Finches are exclusively herbivores and feed their offspring

a diet composed solely of plant material (e.g., weed and grass seeds, tree buds and other leafy green matter; Hill 1993). On our study site, brood size varies from one to six nestlings, with a modal brood size of four nestlings (Stoehr et al., unpubl. data).

We conducted this study on the campus of Auburn University, Lee County, Alabama, USA (32°35′34″ N, 85°28′49″ W) during the 1997, 1998, and 1999 breeding seasons. We placed three-sided, open-fronted wooden nest boxes (12 cm × 13 cm × 8 cm) on numerous buildings on the campus, and inside each box we placed a cup made from the bottom 7 cm of a plastic 1.89 (0.5 gallon) milk container. The finches readily nested in these boxes, enabling us to find nests and observe behavior easily.

To avoid problems associated with the possibility that parental behavior might differ among repeated nesting attempts, we included only first nests in this study. Of the nests for which we had reliable data, none of those with one, two, or six nestlings were first nests, so nests with these brood sizes were eliminated. However, this is unlikely to affect our conclusions because these brood sizes are uncommon. In the three years of this study, we monitored 146 nests, and only five, nine, and two had one, two, or six nestlings, respectively, at the time we monitored parental behavior. Thus, our analyses of nests with three, four, or five nestlings reflect the brood sizes of almost 90% of all nests and an even greater percentage of first nests. Our choice to include only first nests resulted in relatively small sample sizes in each year, so we pooled our data from all years prior to analyses. We did not, however, include any adult birds more than once in our data set.

To record parental behavior, we videotaped behavior at the nests by placing video cameras approximately 1 m from the nest boxes when nestlings were 11 days old. We taped nests for 2 h in 1997 and for 8 h in 1998 and 1999, beginning tapings shortly after dawn. Visitation rates were calculated by counting the number of feeding visits made by the adults to the nest and dividing this number by the duration of the taping (to yield feeding visits per brood per hour) and by dividing by both brood size and taping duration (to yield feeding visits per nestling per hour). We quantified food loads using two different methods. First, from the video tapes we counted the total number of provisions made by an adult during a feeding visit. That is, each time an adult placed food in a nestling's mouth was counted as one provision. Thus, each feeding visit consisted of several provisions. This method of quantifying food load size assumed that the mass of the food load brought during a feeding visit was proportional to the number of provisions it took an adult to deliver that food load. Second, we placed a small electronic balance (Acculab Pocket Pro 150-B) under the plastic cup of each nest prior to the start of each taping. These balances measure to 0.1 g, and have a range of 0–150 g. To increase the accuracy and precision of our measurements, we taped the plastic nest cup to the balance which not only centered the nest on the scale but also prevented the nest from touching the sides of the nest box. From the video tapes we could determine the mass of the food

delivered with each feeding trip by subtracting the mass of the nest after the adult left from the mass of the nest just prior to the arrival of the adult.

We measured provisioning behaviors for males and females separately and for each breeding pair combined. In all cases, the relationships were qualitatively similar for the different sexes, so we have presented figures only for the results of the combined analyses. We have, however, provided the results of the analyses by sex in our table. Sample sizes are not equal in all analyses because in some cases data were missing.

RESULTS

Adult House Finches made more feeding visits to larger broods (Fig. 1A; Table 1). The per nestling visitation rate, however, declined with increasing brood size (Fig. 1B; Table 1) as did the per nestling provisioning rate (Fig. 1C; Table 1).

Unfortunately, we were unable to quantify the masses of the food loads provided by adults during many of the feeding visits because in some cases the scales were unreadable due to low light, bad camera angles, restless nestlings, and other similar problems. For this reason, we did not have adequate sample sizes from different brood sizes to compare directly the relationship between brood size and food load sizes. However, for a subset of the nests we were able to determine the masses of all of the food loads and to count all of the provisions. There was a strong correlation between the total number of feedings provided by the adults and the total mass of the food provided in these feedings. This was the case for males ($R^2 = 0.81$, $P < 0.001$, $n = 11$), females ($R^2 = 0.76$, $P = 0.002$, $n = 9$) and for the combined feedings of each pair ($R^2 = 0.86$, $P = 0.001$, $n = 8$), thus validating our assumption that provisioning rate is a reasonable index of the total mass of food received by the nestlings.

DISCUSSION

The relationship between parental care and brood size varies substantially among species. There may be no relationship between brood size and visitation rate (e.g., Schadd and Ritchison 1998) or there may be a relationship only over some part of the range of brood size variation (Smith et al. 1988). A relationship may be present in one sex but not the other (Moreno et al. 1995). Most commonly, however, adult birds make more feeding visits to larger broods (e.g., Nur 1984; Rytkönen et al. 1996; Siikamäki et al. 1998). In most cases, the increased visitation rate does not fully compensate for the increase in brood size, resulting in fewer visits per nestling (Nur 1984; Rytkönen et al. 1996). Our results are consistent with such findings; adult House Finches showed higher visitation rates to larger broods, but lower per nestling visitation rates to nestlings in larger broods. This was true for both sexes, although not always significantly so, and for the data from breeding pairs (i.e., the combined feeding rates of both parents).

Several studies have demonstrated that in some cases, adult birds show

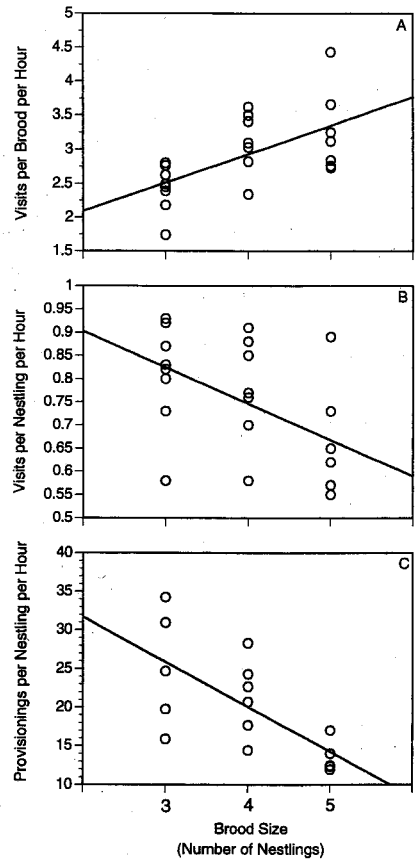

FIGURE 1. The relationship between brood size and absolute visitation rate (A), per nestling visitation rate (B), and per nestling provisioning rate (C). A visit is defined as a trip to the nest in which an adult provides food to nestlings whereas a provisioning is defined as the actual placement of food into the mouth of a nestling. See text and Table 1 for details.

not only higher visitation rates but also differences in load size and/or composition in association with larger brood sizes (Wanless et al. 1993; Siikamäki et al. 1998; Wright et al. 1998). Ideally, we would have determined the mass of all food loads delivered to nestling in order to address whether food load mass varies with brood size. Unfortunately, we were unable to quantify the mass of a sufficient number of food loads to test this hypothesis directly. However, because we observed a strong correlation between the number of provisions and food load mass, it seems that the provisioning rate is a reasonable index of the total mass of food delivered to nestlings. Given this, it appears that in general the relationship between brood size and the amount of food received per nestling (provisions per nestling per hour) is similar to the relationship between brood

TABLE 1. The relationship between brood size and parental care. A visit is a trip to the nest in which a parent feeds the young. A provision is counted as each time a parent places food into the mouth of a nestling.

Relationship to brood size	Sex	R^2	F	P (n)	Slope
Visits/brood/hour	Male	0.26	7.19	0.01 (22)	0.27
	Female	0.10	2.12	0.16 (22)	0.15
	Pair	0.36	11.37	<0.01 (22)	0.42
Visits/nestling/hour	Male	0.07	1.52	0.23 (22)	−0.03
	Female	0.11	2.47	0.13 (22)	−0.05
	Pair	0.25	6.76	0.02 (22)	−0.08
Provisions/nestling/hour	Male	0.21	4.65	0.05 (19)	−2.59
	Female	0.19	3.62	0.08 (17)	−2.50
	Pair	0.49	14.32	<0.01 (17)	−5.80

size and visitation rate (feeding visits per nestling per hour). Thus, for our purposes it appears that quantifying parental behaviors by simply counting feeding visits per unit time and dividing this rate by brood size provides a reasonable approximation of the amount of food each nestling House Finch receives. We did not, however, identify the composition of food brought to nestlings in this study, so we do not know if food load composition varies among different brood sizes in House Finches.

As a final note, we offer some cautionary advice concerning the interpretation of the results of this and similar studies. First, it may be important to consider that House Finches are herbivorous, and as such, their nestling provisioning rules may differ markedly from species which feed their offspring other types of food (e.g., vertebrates or invertebrates). In fact, our review of the literature suggests that insectivorous birds (or at least birds that feed insects to their nestlings) are highly over-represented among studies of parental care and brood size. Clearly, more future research should focus on species that feed their offspring seeds and other plant materials.

Second, care should be taken when interpreting the causal relationship between brood size and visitation rate when brood sizes are not manipulated, and when contemplating how this relationship affects the determination of parental quality. Although studies may report that "feeding rates were unaffected by brood size" (e.g., Schadd and Ritchison 1998), it is possible that the adults' assessment of their potential visitation rate (due to age, experience, general health, etc.) determines brood size. In such a case, no statistical relationship would be expected between brood size and visitation rate even though the adults may differ widely in parental quality.

ACKNOWLEDGMENTS

We thank Shelly Ducharme, Anne Dervan, and Renee Duckworth, as well as numerous undergraduate assistants, for help in the field. For assistance watching video tapes, we are grateful to Hayden Cameron and Katie Mountcastle. This research was supported by a Na-

tional Science Foundation grant to G.E.H (Grant No. IBN9722171) and in part by a research award to A.M.S. from the Association of Field Ornithologists.

LITERATURE CITED

BELETSKY, L. D., D. F. GORI, S. FREEMAN, AND J. C. WINGFIELD. 1995. Testosterone and polygyny in birds. Pp. 1–41, *in* D. M. Power, ed. Current ornithology, Vol. 12. Plenum, New York.

HILL, G. E. 1993. House Finch (*Carpodacus mexicanus*). No. 46, *in* A. Poole and F. Gill, eds. The birds of North America. Academy of Natural Sciences, Philadelphia and American Ornithologists, Union, Washington, D. C.

HOELZER, G. A. 1989. The good parent process of sexual selection. Anim. Behav. 38:1067–1078.

MORENO, J., R. J. COWIE, J. J. SANZ, AND R. S. R. WILLIAMS. 1995. Differential response by males and females to brood manipulations in the Pied Flycatcher: energy expenditure and nestling diet. J. Anim. Ecol. 64:721–732.

NUR, N. 1984. Feeding frequencies of nestling Blue Tits (*Parus caeruleus*): costs, benefits and a model of optimal feeding frequency. Oecologia 65:125–137.

RYTKÖNEN, S., K. KOIVULA, AND M. ORELL. 1996. Patterns of per-brood and per-offspring provisioning efforts in the Willow Tit *Parus montanus*. J. Avian. Biol. 27:21–30.

SCHADD, C. A., AND G. RITCHISON. 1998. Provisioning of nestlings by male and female Yellow-breasted Chats. Wilson Bull. 110:398–402.

SIIKAMÄKI, P., J. HAIMI, M. HOVI, AND O. RÄTTI. 1998. Properties of food loads delivered to nestlings in the Pied Flycatcher: effects of clutch size manipulation, year, and sex. Oecologia 115:579–585.

SMITH, H. G., H. KÄLLANDER, K. FONTELL, AND M. LJUNGSTRÖM. 1988. Feeding frequency and parental division of labour in the double-brooded Great Tit *Parus major*. Behav. Ecol. Sociobiol. 22:447–453.

TRIVERS, R. L. 1972. Parental investment and sexual selection. Pp. 136–179, *in* B. Campbell, ed. Sexual selection and the descent of man, 1871–1971. Heinemann, London.

WANLESS, S., M. P. HARRIS, AND A. F. RUSSELL. 1993. Factors influencing food-load sizes brought in by Shags *Phalacrocorax aristotelis* during chick rearing. Ibis 135:19–24.

WRIGHT, J., C. BOTH, P. A. COTTON, AND D. BRYANT. 1998. Quality vs. quantity: energetic and nutritional trade-offs in parental provisioning strategies. J. Anim. Ecol. 67:620–634.

Received 2 September 1999; accepted 27 November 2000.