The Condor 103:851–855

THE NUMBER OF PROVISIONING VISITS BY HOUSE FINCHES PREDICTS THE MASS OF FOOD DELIVERED

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Abstract. One classic means of assessing variation in avian foraging success and provisioning effort, counting the number of trips to the nest, assumes that parents bring equal amounts of food during each trip. We tested this assumption in male House Finches (*Carpodacus mexicanus*) by using video cameras to record both the number of nest visits and the mass of food delivered as measured by an electronic balance. We compared the number of feeding visits and mass of food delivered at each of three stages in the nest cycle: incubation, young nestlings, and older nestlings. The number of provisioning trips was significantly correlated with the mass of food provided by a male to his mate or to their offspring during each stage of the nesting cycle. Furthermore, this correlation became stronger as the breeding cycle progressed. These observations support the assumption that, for this species and perhaps others that carry food in their crop, the number of provisioning visits to the nest is a reasonable predictor of the mass of food provided.

Key words: Carpodacus mexicanus, *electronic balance, offspring provisioning, parental care, provisioning trips.*

Manuscript received 1 December 2000; accepted 21 May 2001.

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El Número de las Visitas del Aprovisionamiento de *Carpodacus mexicanus* Predice la Masa del Alimento Entregada

Resumen. Un método clásico para establecer la variación en el éxito de forrajeo y esfuerzo de aprovisionamiento en aves, que consiste en contar el número de viajes hacia el nido, asume que los padres llevan igual cantidad de alimento durante cada viaje. Probamos este supuesto en machos de *Carpodacus mexicanus* mediante cámaras de video que registraron tanto el número de visitas al nido como el peso del alimento entregado, este último medido mediante una balanza electrónica. Comparamos el número de visitas al nido y el peso del alimento entregado en cada uno de los tres estados del ciclo de nidificación: incubación, pichones jóvenes y pichones tardíos. El número de viajes de aprovisionamiento se correlacionó positivamente con el peso del alimento provisto por un macho a su pareja o a su progenie en cada estado del ciclo de nidificación. Además, esta correlación se hizo más fuerte a medida que el ciclo de nidificación progresó. Estas observaciones apoyan el supuesto que, al menos para esta especie y otras que transportan alimento en el buche, el número de visitas de aprovisionamiento al nido predice razonablemente bien la masa de alimento provista.

Observations of food provisioning have played a central role in a variety of avian studies. Research into mating systems often focuses on the relative contributions of males and females to parental effort, while questions regarding the evolution of clutch size or

brood size require knowledge of a male's ability to provision his mate and their young (Leffelaar and Robertson 1986, Smith et al. 1988, Schadd and Ritchison 1998, Siikamäki et al. 1998, Wright et al. 1998). Similarly, optimal foraging theories can only be examined empirically if the returns on an investment of time can be measured, particularly with regard to breeding birds (Nur 1984, Wright et al. 1998).

Provisioning rates have been measured directly by capturing adult birds at the nest and examining the food items they carried (Siikamäki et al. 1998) or by using choke collars to prevent nestlings from swallowing the food they are provided (Wright et al. 1998). Both of these techniques are invasive and potentially stressful manipulations of the animals being studied, and repeated capture or handling may alter an individual's behavior in unpredictable ways. Consequently, many researchers have estimated provisioning rates by observing the birds from a distance and counting the number of trips made to the nest (Ketterson and Nolan 1994), by measuring the time interval between visits (Hill 1991), or by comparing the size of prey to the bird carrying it (Carss and Godfrey 1996).

Unfortunately, estimation techniques have their own suite of problems. It may be difficult to estimate the size of food items being carried, particularly when the estimate is being made through binoculars or a telescope. Small food items carried by the bird can easily be missed by an observer, causing an under-representation of both the amount and diversity of food types provided to the young or to a mate. Additionally, variation in food size goes undetected by methods that rely on simple counts of the items provisioned.

In the absence of a simple means of measuring the amount of food provided by breeding birds to their chicks and mates, researchers approximate the amount of food delivered to nestlings by simply counting the number of times parents bring food. This approach rests on the assumption that all provisionings are equal. Our purpose in this study was to test the idea that counting provisioning trips to a nest is an accurate means of assessing the amount of food delivered by House Finches (*Carpodacus mexicanus*). We compared the number of feeding trips made by breeding males with the mass of food brought in those trips.

METHODS

The House Finch is a small cardueline finch with biparental care, and males provide a large proportion of the mate's food during incubation (Hill 1993). The female and male provision chicks with a nearly equal number of visits (Hill 1993). In the present study we present only data from male House Finches. Our study site was the campus of Auburn University in east-central Alabama (32°36′N, 85°30′W). Throughout the study site we placed wooden nest boxes (12 × 13 × 8 cm) under walkways and in the eaves of buildings. These nest boxes had a wooden exterior that was open on the top and on one side. Into these wooden frames we placed the bottom portion of a 1.9-L plastic milk or juice container, which was held in place by a removable metal clip. House Finches accepted this design readily, building over 60 nests per year in them in each of the two years for which we present data.

For each nest on our study site, we made one videotaped recording of male provisionings to the female during incubation. We also recorded male provisionings during one observation period in the young nestling stage (from hatch until six days old) and one observation period in the older nestling stage (days 7 to 12 after hatch). House Finch chicks fledge at roughly 17–20 days of age, and any manipulation of the nest more than 12 days after hatch risks premature fledging. We made all observations in the morning, when we expected substantial amounts of provisioning to occur. In 1997 all observation periods were 2 hr long and started before 10:00 CST, typically within 2 hr after dawn. In 1998 all observation periods were started within 2 hr after dawn; the incubation and young nestling observations were 4 hr long and observations of older nestlings were 8 hr long.

To measure the amount of food provided per trip, we placed a small electronic balance (Acculab Pocket Pro 150-B; Newtown, PA) underneath the plastic container holding the nest. These balances have a range from 0 to 150 g, with a readability of 0.1 g. The total weight of a nest with four chicks and a provisioning parent is <120 g, well within the accuracy range of these balances. By taping the plastic container to the surface of the balance, we prevented the container from touching the side of the wooden box, which greatly improved the accuracy of weights recorded. The tape also centered the nest on the balance, further improving accuracy of the masses recorded.

We recorded the number and timing of visits that involved provisionings, and also determined the mass of food delivered in each trip, by placing a video camera approximately 1 m from the nest. We are confident that the cameras did not affect behavior at the nest, because most birds approached the nest within 10 min after we left, and because House Finches typically build their nests in high-traffic areas such as public walkways and parking garages and are accustomed to disturbances.

When watching the videotape of a provisioning visit we were usually able to read the electronic balance from the video before and after the visit, and to determine by subtraction the mass of the food provided. Unfortunately, we were unable to determine accurately the mass of food transferred in some of the provisionings. In some instances, low light levels prevented us from reading the balance with certainty. In other cases the chicks were too active or the adults removed fecal sacs after providing food, in either case making it impossible to determine the exact mass of the provision. The data we present here describe only the feeding visits and associated masses we could record with full confidence.

We adopted a standardized definition of a provisioning visit. In a similar population of House Finches on the campus of the University of Michigan, Hill (1991) observed 32 nests and found that the shortest interval between actual provisioning trips made by males was 20 min. So that we would not underestimate the number of provisioning visits, we considered any trips to the nest occurring within 15 min of each other to be part of a single provisioning trip.

STATISTICAL ANALYSES

For each male studied at a given nesting stage, we compared the number of provisioning trips he made

TABLE 1. Number and total mass of provisions by male House Finches to their incubating mates or to their nestlings at three stages of the nesting cycle on Auburn University campus, Alabama, 1997–1998 (n = number of males). Young nestlings are 1 to 6 days old; older nestlings are 7 to 12 days old. Means are given ± SD. Values represent only those provisionings for which we were able to obtain accurate masses using an electronic balance, and do not represent total provisioning rates (see text).

Nest stage	Mean no. of provisions measured	Mean total mass (g) of provisions
Incubation (n = 22)	1.7 ± 1.3	0.9 ± 0.6
Young nestlings (n = 22)	2.4 ± 1.2	2.5 ± 1.9
Older nestlings (n = 24)	4.3 ± 2.8	5.4 ± 4.2

with the total mass of food provided in those trips. When we observed a male more than once in a single year at the same nesting stage (several males were seen to provision either an incubating female or their chicks at multiple nests over the course of the breeding season), we calculated the mean value of his measurements at that stage. When we had data from both years for a male at the same stage of the nesting cycle (e.g., data on provisioning behavior during incubation in both 1997 and 1998), we included in our dataset only those values from the year in which we observed the most provisioning trips by that individual.

To allow us to pool data from the two years of this study, we standardized all values to a mean of zero and a standard deviation of one. Because the data were not normally distributed, we used nonparametric Spearman rank correlation tests of the strength of the relationship between the number of provisioning visits and the mass of food delivered to the nest at each breeding stage. Because we suspected that the strength of this relationship might vary among the three breeding stages, we tested for significant differences between the relevant correlation coefficients using a z-transformation of the Spearman r-values; the resultant z-values are then used to calculate a test statistic which may be compared to the chi-square distribution (Zar 1999).

RESULTS

In the two years of our study we measured provisionings by 22 males during the incubation period, by 22 males feeding young nestlings, and by 24 males feeding older nestlings (Table 1). Eleven males were observed at all three stages of the nesting cycle, and an additional 23 males were observed during only one or two of the stages.

The number of provisioning trips by males was significantly correlated with the total mass of food provided during incubation (Fig. 1A), during the young nestling stage (Fig. 1B), and during the older nestling stage (Fig. 1C). The degree of correlation between the number of provisioning trips by the male and the mass of food provided increased significantly as the breeding cycle progressed ($\chi^2_2 = 8.7$, $P < 0.025$).

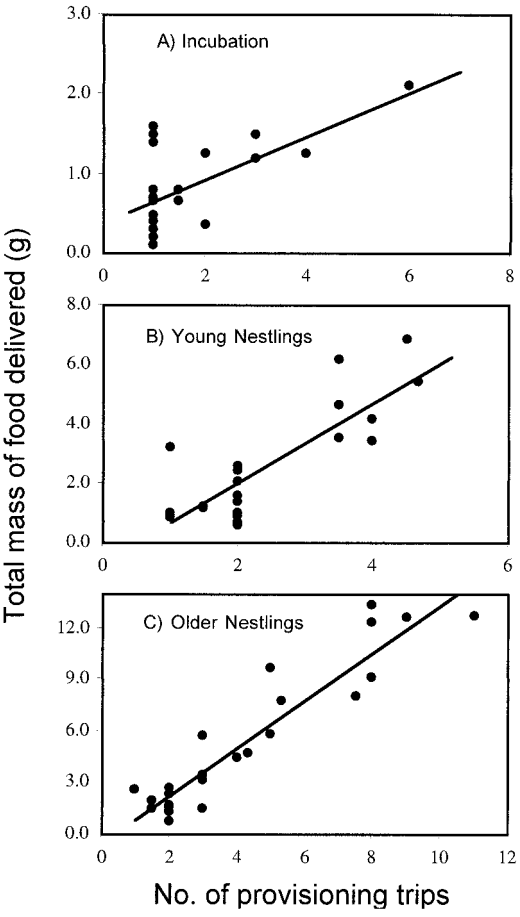

FIGURE 1. The relationship between the number of provisioning trips and the mass of food provided by a nesting male to: (A) incubating female ($r_s = 0.46$, $n = 22$, $P = 0.029$), (B) young chicks (days 1–6 after hatch; $r_s = 0.71$, $n = 22$, $P < 0.001$), and (C) older chicks (days 7–12 after hatch; $r_s = 0.89$, $n = 24$, $P < 0.001$). Each point represents one male; males with multiple nests in a given nesting stage are represented by mean values.

DISCUSSION

We compared the number of provisioning trips made by male House Finches with the mass of the food provided in those trips, and found that a simple count of the number of trips was significantly correlated with the mass of food provided. Additionally, we found that this relationship increased significantly in strength as the breeding cycle progressed. The technique we used in this study, combining videotaping of nesting behavior and measurement of provisioning masses with an electronic balance, is a powerful tool for detailed examination of avian reproductive strategies. However, its use, or that of similar arrangements, may not be necessary or even possible in many cases.

Ours is the first study of which we are aware that uses the mass data provided by electronic balances to test the validity of counting provisioning trips. Past research has used balances to measure foraging success (Wilkinson 1992), calculate total food intake (Grémillet et al. 1996), and follow body-weight changes under a variety of field and laboratory conditions (Jones 1987, Moreno 1989, Mulder and Swaan 1992). Perhaps most similar to our purpose, Prince and Walton (1984) and Szép et al. (1995) used electronic balances to compare provision size with time of day and provisioning rate, respectively. However, none of these studies reported data in a way that allowed comparison of the number of provisioning trips to the total mass of food delivered.

Our results indicate that simply counting provisioning trips to the nest may provide sufficient resolution to detect patterns in resource availability, foraging success, or parental care in House Finches. We should approach that conclusion with caution, however. We did not examine the role of females in provisioning the nestlings, and it is possible that provisioning rules differ between the sexes. Any assumption that the number of feeding trips is an adequate predictor of female provisioning will need further study. Also, foraging mode may influence the strength of the relationship between the number of feeding visits and the amount of food provided. The ability of birds of some species to carry relatively large loads in the bill or feet may increase variance in the size of food items brought to the nest, and therefore may decrease the correlation between the number of feeding trips and the amount of food provided (Carss and Godfrey 1996, Siikamäki et al. 1998). Therefore, estimating food delivery rate by counting provisioning trips may only be appropriate in those species of birds constrained somewhat by the size of their crop.

The possibility of a limit imposed by crop size may help explain the increasingly strong relationship between provision size and advancing age of the nestlings. Because there is an upper limit to the amount of food House Finches can carry in a single trip, the ability of the number of feeding trips to predict the mass of food provided should grow with the age of the chicks. Young nestlings require food often, but are able to handle only small amounts at a time. Therefore, in any one feeding trip they are unlikely to require or to accept the full amount of food that an adult is capable of carrying. By the time the nestlings are older, the provisioning trips of adult House Finches may begin more and more to reflect the maximum amount an individual can carry.

There are certainly other interpretations of our results, although further work will be necessary to distinguish between the possibilities. Male House Finches provided significantly more food per provisioning to older nestlings ($n = 24$) than they did to young nestlings ($n = 22$; $z = -2.6$, $P = 0.008$). This is consistent with the idea that the increasingly strong relationship between visitation rate and total amount of food provided may reflect an increase in the male's valuation of the brood, but is also consistent with a simple increase in food requirements as chicks get older.

Male House Finches do not defend territories (Hill 1993), so our study was not subject to the potentially confounding factors of seasonal changes in territory quality or intermale differences in territory quality. However, the strength of the relationship between the number of provisioning trips and the mass of food delivered could clearly be weakened in territorial species. The same concern applies to comparisons of provisioning trips made by males attending broods of different sizes. Nonetheless, even the weakest of the three relationships we report (between total mass of food provided and number of provisioning trips during incubation) is a strong one, allowing comparisons among male House Finches studied at similar points in the breeding cycle.

This research was supported by the Department of Zoology and Wildlife Science, by the College of Science and Mathematics, and by the Graduate School at Auburn University; also by the Alabama Agricultural Experiment Station and by grant IBN922171 from the National Science Foundation to GEH. We thank the BEERS discussion group, R. Morris, and an anonymous reviewer for helpful comments, P. Williams, L. Gunter, and J. van der Voort for assistance in watching videotapes, and S. Otis, S. Ducharme, and D. Filion for assistance in the field.

LITERATURE CITED

CARSS, D. N., AND J. D. GODFREY. 1996. Accuracy of estimating the species and sizes of Osprey prey: a test of methods. Journal of Raptor Research 30: 57–61.

GRÉMILLET, D., R. DEY, S. WANLESS, M. HARRIS, AND J. REGEL. 1996. Determining food intake by Great Cormorants and European Shags with electronic balances. Journal of Field Ornithology 67:637–648.

HILL, G. E. 1991. Plumage color is a sexually selected indicator of male quality. Nature 350:337–339.

HILL, G. E. 1993. House Finch (*Carpodacus mexicanus*). *In* A. Poole and F. Gill [EDS.], The birds of North America, No. 46. The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, DC.

JONES, G. 1987. The use of precision electronic balances to monitor short-term changes in the body mass of birds. Comparative Biochemistry and Physiology 87A:287–293.

KETTERSON, E. D., AND V. NOLAN. 1994. Male parental behavior in birds. Annual Review of Ecology and Systematics 25:601–628.

LEFFELAAR, D., AND R. J. ROBERTSON. 1986. Equality of feeding roles and the maintenance of monogamy in Tree Swallows. Behavioral Ecology and Sociobiology 18:199–206.

MORENO, J. 1989. Body-mass variation in breeding Northern Wheatears: a field experiment with supplementary food. Condor 91:178–186.

MULDER, J. L., AND A. H. SWAAN. 1992. Body-weight changes of egg-laying curlews *Numenius arquata*, as monitored by an automatic weighing system. Ardea 80:273–279.

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

PRINCE, P. A., AND D. W. H. WALTON. 1984. Automated

measurement of meal sizes and feeding frequency in albatrosses. Journal of Applied Ecology 21: 789–794.

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

SIIKAMÄKI, P., J. HAIMI, M. HOVI, AND O. RATTI. 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*. Behavioral Ecology and Sociobiology 22:447–453.

SZÉP, T., Z. BARTA, Z. TÓTH, AND Z. SÓVÁRI. 1995. Use of an electronic balance with Bank Swallow nests: a new field technique. Journal of Field Ornithology 66:1–11.

WILKINSON, G. S. 1992. Information transfer at evening bat colonies. Animal Behaviour 44:501–518.

WRIGHT, J., C. BOTH, P. A. COTTON, AND D. BRYANT. 1998. Quality vs. quantity: energetic and nutritional tradeoffs in parental provisioning strategies. Journal of Animal Ecology 67:620–634.

ZAR, J. H. 1999. Biostatistical analysis, 4th ed. Prentice Hall, Upper Saddle River, NJ.