J. Field Ornithol. 73(1):9–14, 2002

The number of visits to the nest by parents is an accurate measure of food delivered to nestlings in Tree Swallows

John P. McCarty[1]

Cornell University, Department of Ecology and Evolutionary Biology, Ithaca, New York 14853 USA

Received 28 July 2000; accepted 20 February 2001

ABSTRACT. The number of visits parents make to their nest during chick rearing is a commonly used measure of the amount of food delivered to nestlings and an index of the quality of parental care. Use of the number of visits for these purposes assumes that parents feed nestlings when they visit and that there are no systematic differences in the amount of food delivered on each visit. These assumptions were tested in Tree Swallows (*Tachycineta bicolor*) breeding in nest boxes near Ithaca, New York. Video observations of parents inside their nest boxes showed that parents feed nestlings on 95–98% of visits to the nest. An average visit delivered 18.1 insects with a total dry mass of 24.1 mg, usually to a single nestling. Although females visited more frequently, the load they carried on each visit was not different than that carried by males. Load size did not differ with nestling age, brood size or the date of the feeding. Overall, there were few systematic differences in load size among nests. Therefore, the number of visits to the nest is a good measure of food delivery and parental care in Tree Swallows.

SINOPSIS. **El número de visitas al nido por los padres es una medida exacta del alimento llevado a los pichones en *Tachycineta bicolor***

El número de las visitas de padres a su nido durante la crianza de los pichones se utiliza comunmente como medida de la cantidad de alimento llevado a los pichones y como un indice de la calidad parental. El usar el número de visitas para estos propósitos asume que los padres alimentan los pichones cuando los visitan, y que no hay diferencias sistemáticas en la cantidad del alimento llevado en cada visita. Se examinaron estas aseveraciones en individuos de *Tachycineta bicolor* anidando en cajas cerca de Ithaca, en Nueva York. Observaciones de video de los padres dentro de las cajas con nidos mostraron que los padres alimentan los pichones en 95% a 98% de las visitas a los nidos. Una visita promedio traia 18.1 insectos con una masa seca total de 24.1 mg, usualmente a un solo pichón. Aunque las hembras hicieron visitas más frecuentemente, su carga en cada visita no fué diferente de la llevada por los machos. El tamaño de la carga no difirió con la edad del pichón, el tamaño de la camada o la fecha de la comida. En general, hubo pocas diferencias sistemáticas en el tamaño de las cargas entre nidos. Por lo tanto, el número de visitas al nido es una buena medida de la distribución de alimento y del cuidado parental en *Tachycineta bicolor*.

Key words: feeding rate, load size, parental care, *Tachycineta bicolor*, tree swallow

The rate at which parents deliver food to dependent offspring is critical to understanding a wide range of questions about behavior, ecology, and life history strategies (e.g., Lack 1954; Royama 1966; Davies et al. 1992; Freeman-Gallant 1996; Dickinson and Weathers 1999; Hunt et al. 1999; Bishop et al. 2000). Field studies typically monitor the number of visits parents make to the nest and implicitly assume that parents deliver food in similar amounts on each visit. For many species where interactions between parents and offspring at the nest are clearly visible, this assumption may be tested through simple observations. However, for cavity nesting birds such as Tree Swallows (*Tachycineta bicolor*), it is difficult to tell from a distance if parents are carrying food and what parents do once they enter a nest is not generally known. Numerous studies of the behavior and ecology of Tree Swallows assume that the number of visits to the nest accurately reflects the amount of food parents deliver and that males and females deliver similar amounts of food on each visit (e.g., Williams 1988; Lombardo 1991; Whittingham et al. 1993; Winkler and Allen 1995; Leonard and Horn 1998; Bishop et al. 2000)

I examined the assumption that the number of visits to the nest is an indicator of parental feeding rate. First, I examined whether parents actually fed nestlings when visiting the nest by

[1] Current address: Department of Biology, University of Nebraska at Omaha, Omaha, NE, 68182-0040 USA. Email: <tachycineta@yahoo.com>

videotaping interactions between parents and nestlings in nestboxes. Second, I collected samples of the food parents brought nestlings to look for systematic differences in the amount of food delivered during each visit. Finally, I monitored the daily cycle of feeding activity to determine if the time of day when visits are measured influenced activity rates.

METHODS

I studied Tree Swallows breeding in nest-boxes at two sites near Ithaca, New York (42°30′N, 76°27′W). These sites, Unit One and Unit Two, are part of the Cornell University Experimental Ponds Facility (see McCarty and Winkler 1999a,b). Nests were visited every one to two days during the breeding season to determine brood size and nestling age. Adults were captured using nest traps. Sex was determined by the presence or absence of a brood patch and by plumage color (Hussell 1983). Males and females were banded with different combinations of color bands prior to release. The sex of parents visiting the nest was determined either by observing their color bands or plumage characters.

The reliability of using the number of visits to the nest as a measure of nestling feeding activity was evaluated by video-taping the interior of nest-boxes during parental visits (Lombardo 1991). A Super VHS camera was placed to tape a side-view of the interior of a modified nest box. Observations were distributed throughout the nestling period. A visit was scored as a confirmed feeding visit if the parent's bill was inserted in the mouth of a nestling. If the parent lowered its head to a nestling and appeared to be feeding but the actual contact was blocked from view, the visit was classified as a probable feeding, and if contact was not observed and the parent did not behave as if it were feeding, the visit was considered a non-feeding visit.

Adult Tree Swallows collect a bolus of insects before returning to feed their nestlings. Insect boluses were obtained from adults captured as they returned to the nest (McCarty and Winkler 1999a) and by using an artificial nestling puppet (McCarty and Winkler 1991). All insect samples were stored in 70% ethanol. Insects were later identified and measured, and the number of insects converted to dry mass (McCarty 1995; McCarty and Winkler 1999a). At a subset of nests adults were captured multiple times during the nesting season, and for some of these, multiple food samples were available, allowing me to compare variation in load size within and among nesting pairs.

Visitation rate was measured using information from focal nest observations conducted in 1990–1992. Observation periods lasted 15–60 min. Calculations of visitation rate by sex include only those observations where the sex of the visiting parent was known. Comparisons between Ponds Units are based on breeding pairs as the unit of analysis, and all observations are included, even if the sex of the visiting parent was unknown.

The daily cycle of foraging activity was investigated in 1993 using focal observations of nests containing nestlings 10 or 11 d old. Each nest was observed for between 4 and 8 periods of 30 min each. During observation periods the number of visits to the nest by the parents was recorded. Observations spanned the entire period of foraging activity, from approximately 06:00 to 20:00.

Results are reported as mean ± SE. Lines on scatterplots are LOWESS curves, a method using locally weighted regression to smooth scatterplots (Cleveland 1981), calculated using SYSTAT (Wilkinson et al. 1992).

RESULTS

Behavior of Tree Swallows inside the nestbox was recorded on videotape at a five nests over 16 observation periods (Table 1). Observation periods averaged 29 ± 2.6 min. The sex of the visiting parent could be identified at four of the five nests totaling 10 observation periods. Nestling age at the time of observation ranged from day 4 to 20 ($\bar{x}$ = day 12.6 ± 1.1). A total of 132 nest visits was recorded during the observation periods, giving a visitation rate of 18.2 ± 2.0 visits/h. Feeding was confirmed for 126 visits, and was probable for an additional three visits (Table 1). The three visits when feeding did not occur were all recorded at the beginning of a single observation period. The parents at this nest were agitated by the presence of the video camera, and in at least two of the three non-feeding visits they were carrying food but left the nest without feeding nestlings. Later observations of this nest showed that the parents were feeding normally.

Table 1. Feeding behavior of Tree Swallows at five nests as recorded on video during 16 recording periods. The sex of the parents visiting could be determined for 10 of the recording periods. The sex of the parent delivering the bolus was known for 198 of the samples.

	All Adults	Males	Females
Feeding confirmed	126	22	41
Feeding probable	3	0	2
No feeding	3	1	2
Mean (±SE) insects/bolus[1]	18.1 ± 1.7	18.9 ± 2.8	18.4 ± 2.4
Mean (±SE) mass (mg)[1]	24.1 ± 1.6	25.3 ± 2.8	23.2 ± 2.1

[1] $N = 214$ (McCarty and Winkler 1999a).

Food delivery during visits was based on analysis of 214 food boluses. Each bolus contained an average of 18.1 ± 1.7 insects and averaged 24.1 ± 1.6 mg dry mass (Table 1). Based on these data, the average dry mass of an insect in the diet is 1.33 mg or approximately 750 dry insects/g. Neither the number of items delivered (Linear Regression, $N = 206$, $R^2 < 0.01$, $F_{1,204} = 0.04$, $P = 0.85$), nor the total mass of the bolus increased significantly with nestling age ($R^2 < 0.01$, $F_{1,204} = 0.12$, $P = 0.73$; Fig. 1a). Load size was not correlated with the size of the brood parents were feeding ($N = 210$, number of items $R^2 = 0.01$, $F_{1,208} = 2.17$, $P = 0.14$; bolus mass $R^2 < 0.01$, $F_{1,208} = 1.25$, $P = 0.27$; Fig. 1b). Load size was not correlated with the date a sample was collected in the season (items $R^2 = <0.01$, $F_{1,211} = 0.70$, $P = 0.40$; mass $R^2 < 0.01$, $F_{1,211} = 1.17$, $P = 0.28$).

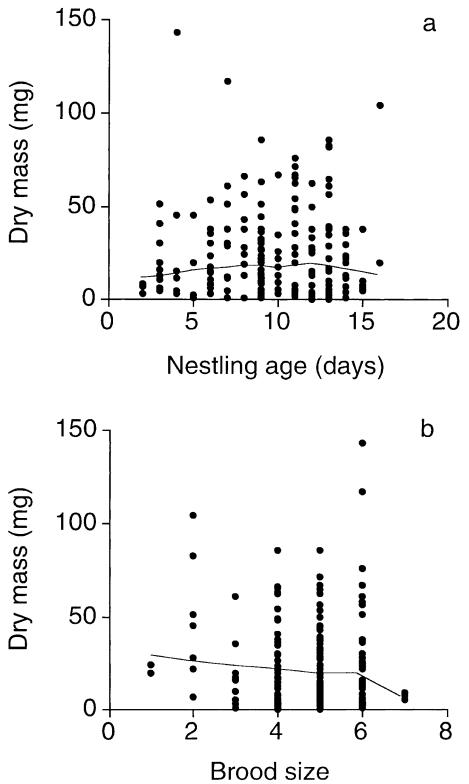

Fig. 1. Insect biomass delivered/visit to nestling Tree Swallows. Lines are LOWESS curves (Cleveland 1981; Wilkinson et al. 1992).

Males and females collected equally large boluses of insects, both in terms of mass (*t*-test, $t = 0.61$, $P = 0.54$) and number of items delivered ($t = 0.15$, $P = 0.88$; Table 1). The degree of variation in load size was also similar for males and females. An *F*-test on the variance in load size did not detect a difference in variance between males and females for the number of items ($F = 1.16$, $P > 0.10$) and bolus mass ($F = 1.06$, $P > 0.10$).

The number of items delivered/trip was significantly higher at Unit One (20.2 ± 2.0, $N = 179$) than it was at Unit Two (6.7 ± 2.0, $N = 31$; $t = 2.83$, $P = 0.005$). However, bolus mass did not differ significantly between sites (Unit One = 25.3 ± 1.8 mg, Unit Two = 17.0 ± 3.6 mg; $t = 1.81$, $P = 0.07$).

Adults at different nests could be delivering different amounts of food per trip. At seven nests, four or more diet samples were collected during a single nesting attempt. The average number of items delivered/trip varied among these nests (range in means 2.4 ± 1.0 to 29.6 ± 10.2 items/trip; ANOVA $F_{6,50} = 2.77$, $P = 0.02$) but the total load mass did not vary among nests (range 15.5 ± 7.6 to 36.6 ± 10.7 mg/trip; ANOVA $F_{6,50} = 1.11$, $P = 0.37$).

Overall feeding rate based on 195 focal nest observations was 14.5 ± 0.6 visits per hour,

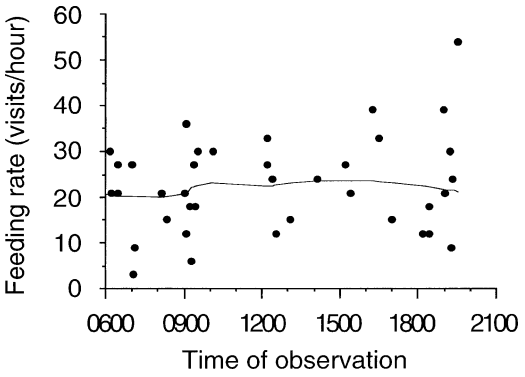

Fig. 2. Foraging intensity of Tree Swallows feeding young at different times of the day. Based on 30 min focal observations at 7 nests, each nest was observed 4–8 times on one day. Line is a LOWESS curve (Cleveland 1981; Wilkinson et al. 1992).

slightly lower than the rate at nests recorded on video. Females made a significantly larger share of the total visits to the nest (62.5 ± 5.5%) than did males ($t = 2.29$, $P = 0.027$). Feeding rate was similar at the two sites: the mean for 147 nests at Unit One was 14.8 ± 0.7, while 48 nests at Unit Two averaged 13.8 ± 1.3 visits/h ($t = 0.63$, $P = 0.53$).

Day-long focal observations were conducted at eight nests. Intensity of Tree Swallow foraging activity was variable, but showed no obvious pattern with time of day (Fig. 2). Mean visitation rate during these visits was 22.7 ± 1.7 trips/h, with a maximum of over 50 trips/h (Fig. 2). Intensity of foraging was usually highest after 10:00, but intensities of 60–80% of peak activity were regularly observed before 08:00.

DISCUSSION

Parents were observed feeding nestlings on 95.5% of visits to the nest (126 confirmed feedings out of 132 visits; Table 1) and feeding was likely to have occurred on an additional 2.3% of visits (3 of 132 visits). This is in contrast to Cliff Swallows (*Petrochelidon pyrrhonota*) where colonies act as information centers and adults that are unsuccessful at foraging return to their nest without food, in order to follow successful neighbors as they leave to forage (Brown 1986). Part of this difference in behavior probably lies in the fact that Tree Swallows at Ithaca routinely forage within sight of their nest-box (and their foraging neighbors), while Cliff Swallows feeding nestlings travel to concentrations of insects up to 1 km away (Brown and Brown 1996; McCarty and Winkler 1999a).

Adult Tree Swallows feed at a high rate throughout the nestling period, reaching a peak of over 20 visits/h, and capturing over 6000 insects/d (McCarty 1995). The range in feeding rate observed at Ithaca is similar to that reported for other studies of Tree Swallow foraging rates (Leffelaar and Robertson 1986; Quinney 1986; Williams 1988; Lombardo 1991; Winkler 1991). This rate of visitation is generally greater than that observed in Cliff Swallows, although brood size in Cliff Swallows tends to be smaller than that of Tree Swallows (Brown and Brown 1996).

Load size did not vary with the age of nestlings being fed or the number of nestlings being fed (Fig. 1). The average bolus mass found at Ithaca (24 mg) is similar to the mean of 28 mg reported for Tree Swallows in Ontario (Quinney 1986) and 30 mg per bolus at an upland site in Michigan (Johnson and Lombardo 2000). However, the mass of boluses delivered was larger in Alberta, ranging from 37–54 mg (Dunn and Hannon 1992), suggesting that additional attention to this variable is needed when comparing sites that differ in food availability. At Ithaca, variation in mass of food boluses between sites was not significant. For studies comparing behavior at different sites collection of food boluses is a straightforward way to check this assumption. Alternatively, differences in nestling mass gain over short time periods could be substituted as an index of parental care to avoid assumptions of equal load size (Hussell 1988; McCarty and Winkler 1999b).

Male and female parents delivered similar amounts of food during each feeding visit. The lack of a difference in load size between males and females reported here confirms results from Ontario where males and females delivered similar load sizes (Quinney 1986). The larger number of visits made by females in this and other populations represents a larger contribution to feeding of offspring and is not a result of a trade-off between frequency of visits and load size (Lombardo 1991; Dunn and Robertson 1992). In contrast to the female-biased care seen here, several studies in Ontario have re-

ported equal feeding rates by males and females (Leffelaar and Robertson 1986; Quinney 1986; Dunn and Robertson 1992). This difference may be related to the quality of foraging habitat available, with males decreasing their care when food becomes more abundant (Lombardo 1991; Dunn and Robertson 1992).

The lack of a strong temporal pattern in foraging activity (Fig. 2) suggests that the time of day when the observations were made did not have a strong influence on the results, relative to other factors that might have influenced feeding rate. Likewise, the lack of change in load size over the course of the breeding season suggests that the number of visits can be compared between early and late nests.

Differences among pairs in insect biomass delivered/trip were small relative to other sources of variation. However, pairs did differ in the number of items delivered. These differences appear to reflect different foraging strategies among groups of adults. Pairs at Unit Two tended to deliver fewer but larger insects on each visit (especially odonates; McCarty 1995) while those at Unit One delivered larger numbers of smaller insects, so that the total biomass delivered/visit was similar at the two sites. While there were no significant differences between the two sites in either biomass delivered/load or the number of visits/h, growth rates of nestlings at Unit Two tended to be slightly greater than those at Unit One (McCarty 2001).

The rate of food delivery to nestlings has two components; 1) the number of feeding visits made by the parents, and 2) the amount of food delivered on each visit or load size (Royama 1966; Brown and Brown 1996). In field studies of cavity nesting birds such as Tree Swallows, the number of visits is typically used as an index of parental care and food delivery (e.g., Hussell 1988; Wiggins 1990; Lombardo 1991; Wheelwright and Dorsey 1991; Dunn and Robertson 1992; Whittingham et al. 1993; Winkler and Allen 1995; Leonard and Horn 1998). This assumes first that food is actually delivered with each visit, and second that no systematic differences in load size are present. The results presented here show that while variation in load size may introduce variation into estimates of biomass delivered, in most cases the use of visitation rates as a measure of the amount of food parents deliver is justified.

ACKNOWLEDGMENTS

This research was supported by grants from the North American Bluebird Society, the American Museum of Natural History F. M. Chapman Fund, and the Cornell Laboratory of Ornithology. I thank Nelson Hairston, Jr. and Bob Johnson for making the Cornell Ponds Facility an enjoyable and productive place to work. I gratefully acknowledge comments on earlier drafts of this paper provided by S. T. Emlen, M. P. Lombardo, D. W. Winkler, and L. L. Wolfenbarger.

LITERATURE CITED

Bishop, C. A., P. Ng, P. Mineau, J. S. Quinn, and J. Struger. 2000. The effects of pesticide spraying on chick growth, behavior and parental care in Tree Swallows (*Tachycineta bicolor*) nesting in an apple orchard in Ontario, Canada. Environmental Toxicology and Chemistry 19: 2286–2297.

Brown, C. R. 1986. Cliff Swallow colonies as information centers. Science 234: 83–85.

———, and M. B. Brown. 1996. Coloniality in the Cliff Swallow. University of Chicago Press, Chicago.

Cleveland, W. S. 1981. LOWESS: a program for smoothing scatterplots by robust locally weighted regression. American Statistician 35: 54.

Davies, N. B., B. J. Hatchwell, T. Robson, and T. Burke. 1992. Paternity and parental effort in Dunnocks *Prunella modularis*: how good are male chick-feeding rules? Animal Behaviour 43: 729–745.

Dickinson, J. L., and W. W. Weathers. 1999. Replacement males in the Western Bluebird: opportunity for paternity, chick-feeding rules, and fitness consequences of male parental care. Behavioral Ecology and Sociobiology 45: 201–209.

Dunn, P. O., and S. J. Hannon. 1992. Effects of food abundance and male parental care on reproductive success and monogamy in Tree Swallows. Auk 109: 488–499.

———, and R. J. Robertson. 1992. Geographic variation in the importance of male parental care and mating systems in Tree Swallows. Behavioral Ecology 3: 291–299.

Freeman-Gallant, C. R. 1996. DNA fingerprinting reveals female preference for male parental care in Savannah Sparrows. Proceedings of the Royal Society of London, Series B 263: 157–160.

Hunt, K. E., T. P. Hahn, and J. C. Wingfield. 1999. Endocrine influences on parental care during a short breeding season: testosterone and male parental care in Lapland Longspurs (*Calcarius lapponicus*). Behavioral Ecology and Sociobiology 45: 360–369.

Hussell, D. J. T. 1983. Age and plumage color in female Tree Swallows. Journal of Field Ornithology 54: 312–318.

———. 1988. Supply and demand in Tree Swallow broods: a model of parent-offspring food-provisioning interactions in birds. American Naturalist 131: 175–202.

Johnson, M. E., and M. P. Lombardo. 2000. Nestling Tree Swallow (*Tachycineta bicolor*) diets in an up-

land old field in western Michigan. American Midland Naturalist 144: 216–219.

LACK, D. L. 1954. The natural regulation of animal numbers. Clarendon Press, Oxford.

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.

LEONARD, M. L., AND A. G. HORN. 1998. Need and nestmates affect begging in Tree Swallows. Behavioral Ecology and Sociobiology 42: 431–436.

LOMBARDO, M. P. 1991. Sexual differences in parental effort during the nestling period in Tree Swallows (*Tachycineta bicolor*). Auk 108: 393–404.

MCCARTY, J. P. 1995. Effects of short-term changes in environmental conditions on the foraging ecology and reproductive success of Tree Swallows, *Tachycineta bicolor*. Ph.D. dissertation. Cornell University, Ithaca, NY.

———. 2001. Variation in growth of nestling Tree Swallows across multiple temporal and spatial scales. Auk 118: 179–193.

———, and D. W. WINKLER. 1991. Use of an artificial nestling for determining the diet of nestling Tree Swallows. Journal of Field Ornithology 62: 211–217.

———, and ———. 1999a. Foraging ecology and diet selectivity of Tree Swallows feeding nestlings. Condor 101: 246–254.

———, and ———. 1999b. The relative importance of short term fluctuations in environmental conditions in determining the growth rates of nestling Tree Swallows: an investigation of natural variation using path analysis. Ibis 141: 286–296.

QUINNEY, T. E. 1986. Male and female parental care in Tree Swallows. Wilson Bulletin 98: 147–150.

ROYAMA, T. 1966. Factors governing feeding rate, food requirement and brood size of nestling Great Tits *Parus major*. Ibis 108: 313–347.

WHEELWRIGHT, N. T., AND F. B. DORSEY. 1991. Short-term and long-term consequences of predator avoidance by Tree Swallows (*Tachycineta bicolor*). Auk 108: 719–723.

WHITTINGHAM, L. A., P. O. DUNN, AND R. J. ROBERTSON. 1993. Confidence of paternity and male parental care: an experimental study in Tree Swallows. Animal Behaviour 46: 139–147.

WIGGINS, D. A. 1990. Food availability, growth and heritability of body size in nestling Tree Swallows (*Tachycineta bicolor*). Canadian Journal of Zoology 68: 1292–1296.

WILKINSON, L., M. HILL, S. MICELI, P. HOWE, AND E. VANG. 1992. SYSTAT version 5.2. SYSTAT Inc., Evanston.

WILLIAMS, J. B. 1988. Field metabolism of Tree Swallows during the breeding season. Auk 105: 706–714.

WINKLER, D. W. 1991. Parental investment decision rules in Tree Swallows: parental defense, abandonment, and the so-called Concorde Fallacy. Behavioral Ecology 2: 133–142.

———, and P. E. ALLEN. 1995. Effects of handicapping on female condition and reproduction in Tree Swallows (*Tachycineta bicolor*). Auk 112: 737–747.