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

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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;

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 (428309N, 768279W). 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.

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 (6SE) insects/bolus ¹	18.1 6 1.7	18.9 6 2.8	18.4 6 2.4
Mean (6SE) mass (mg) ¹	24.1 6 1.6	25.3 6 2.8	23.2 6 2.1

¹ N 5 214 (McCarty and Winkler 1999a).

Food delivery during visits was based on analysis of 214 food boluses. Each bolus contained an average of 18.1 \pm 1.7 insects and averaged 24.1 \pm 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, $N \pm$ 206, R^2 , 0.01, $F_{1,204} \pm$ 0.04, $P \pm$ 0.85), nor the total



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

mass of the bolus increased significantly with nestling age (R^2 , 0.01, $F_{1,204}$ 5 0.12, P 5 0.73; Fig. 1a). Load size was not correlated with the size of the brood parents were feeding (N 5 210, number of items R^2 5 0.01, $F_{1,208}$ 5 2.17, P 5 0.14; bolus mass R^2 , 0.01, $F_{1,208}$ 5 1.25, P 5 0.27; Fig. 1b). Load size was not correlated with the date a sample was collected in the season (items R^2 5, 0.01, $F_{1,211}$ 5 0.70, P 5 0.40; mass R^2 , 0.01, $F_{1,211}$ 5 1.17, P 5 0.28).

Males and females collected equally large boluses of insects, both in terms of mass (t-test, t 5 0.61, P 5 0.54) and number of items delivered (t 5 0.15, P 5 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 5 1.16, P . 0.10) and bolus mass (F 5 1.06, P . 0.10).

The number of items delivered/trip was significantly higher at Unit One (20.2 \pm 2.0, N 5 179) than it was at Unit Two (6.7 \pm 2.0, N 5 31; t 5 2.83, P 5 0.005). However, bolus mass did not differ significantly between sites (Unit One 5 25.3 \pm 1.8 mg, Unit Two 5 17.0 \pm 3.6 mg; t 5 1.81, t 5 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 \pm 1.0 to 29.6 \pm 10.2 items/trip; ANOVA \pm 1.0 to 29.6 \pm 10.2 but the total load mass did not vary among nests (range 15.5 \pm 7.6 to 36.6 \pm 10.7 mg/trip; ANOVA \pm 1.11, \pm 5 0.37).

Overall feeding rate based on 195 focal nest observations was 14.5 6 0.6 visits per hour,

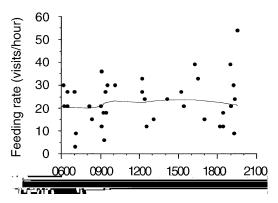


Fig. 2. Foraging intensity of Tree Swallows feeding young at different times of the day. Based on 30 min focal observations at 7 nests, each nest was observed 4–8 times on one day. Line is a LOWESS curve (Cleveland 1981; Wilkinson et al. 1992).

slightly lower than the rate at nests recorded on video. Females made a significantly larger share of the total visits to the nest $(62.5 \pm 5.5\%)$ than did males $(t \pm 2.29, P \pm 0.027)$. 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 $(t \pm 0.63, P \pm 0.53)$.

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 6 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*

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

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 (Rovama 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.

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