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FACTORS ASSOCIATED WITH THE INTERVAL BETWEEN FEEDING VISITS IN BROOD-REARING CHIMNEY SWIFTS

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Chimney Swifts (*Chaetura pelagica*) forage almost exclusively by hawking insects from the air. During brood-rearing, adult swifts of both sexes periodically bring food to their nestlings. During our studies on Chimney Swift behavior and ecology (Zammuto and Franks 1978, 1979a, 1979b, 1981a, 1981b, Blodgett and Zammuto 1979), we noticed daily differences in the duration of time adults spent outside the nest-chimney between feeding visits. This led us to relate several environmental factors (hour of day, nestling age, and brood size) to the interval of time between feeding visits. Only Fischer (1958) and Dexter (1969) have provided in-depth information on Chimney Swift nesting activity, but neither specifically studied the effects of environmental factors or nestling characteristics on feeding rate.

STUDY AREA AND METHODS

The study area in Macomb, Illinois is described elsewhere (Zammuto and Franks 1979a, 1981a). During the 1977 breeding season, we located nests by watching selected groups of chimneys for swifts entering or departing and by checking for active nests in chimneys that had had roosting flocks (Zammuto 1978, Zammuto and Franks 1979a, 1981a). Feeding activity at 14 nest-sites without nest helpers (Dexter 1952) was randomly studied at several times of day. During nest-site observation, we recorded the time elapsed between one adult's departure to the subsequent entrance of either parent (henceforth referred to as "time out"), the ambient temperature, wind speed (using a Dwyer wind meter, held 1.5 m above ground near nest-site), approximate percent cloud cover (eye estimate to nearest 5%), and hour (CDT). Nestling age (see Fischer 1958) and brood size were periodically recorded for 6 accessible broods.

Correlation and regression analyses (Nie et al. 1975) were performed for all nests combined to assess the association of time out to temperature, wind speed, cloud cover (with arcsine transformation to correct for normality, Poole 1974, Zar 1974), nestling age, and brood size (only 6 nests for latter 2 variables). When a nest-site was observed for at least 15 "time out" periods with rain and/or hazy skies, the effect of sky haziness (present or absent) and precipitation (present or absent) on time out was analyzed with t-tests.

RESULTS AND DISCUSSION

Interval between feeding visits.—The mean (±SD) time elapsed between a total of 398 feeding visits involving 14 nests was 14.6 ± 9.3 min. This is substantially shorter than the 35 min found by Fischer (1958) in New York or the 24 min found by Kendeigh (1952) in Ohio. The Vaux Swift

(*Chaetura vauxi*) averaged 18 min (Baldwin and Zaczkowski 1963), and the Common Swift (*Apus apus*) averaged 29 min (Lack and Lack 1951).

Temperatures.—Swifts spent significantly more time away from nests between feeding visits during warmer temperatures (Tables 1 and 2). This may indicate that swifts have more difficulty obtaining insects at warmer temperatures. Glick (1939, 1957) demonstrated that temperature was the most important factor controlling numbers of flying insects. In his studies, numbers of flying insects were highest at 25°C, becoming fewer above and below this temperature. The length of time spent away from the nest in our study was shortest from 21–24°C, becoming significantly ($P < 0.001$) longer above and below these temperatures (Table 2). Koskimies (1950), Lack and Lack (1951), Bryant (1975), and Finlay (1976) found similar relationships among temperature, numbers of flying insects, nestling growth rate, and/or nest-entrance-departure activity for other avian insectivores.

On many occasions, our adults remained in the nest-chimney for a "rest" (>5 min) before departing when temperatures were above 35°C. Glick (1939, 1957) found 66% fewer flying insects at 35° than at 25°C. Resting may become more advantageous as the food supply reaches some lower threshold.

Wind speed.—Swifts spent significantly more time away from nests between feeding visits during higher wind speeds (Tables 1 and 2). In studies by Glick (1939, 1957), numbers of flying insects decreased at wind speeds above and below 9 km/h but this reduction was more demonstrable at higher wind speeds. Our data suggest that swifts catch more insects when the wind is calmer (Table 2). Lack and Lack (1951) found higher nestling growth rates on calmer days for the Common Swift.

Most nesting swifts flew straight paths while approaching or leaving the nest-chimney, but during high winds (>12 km/h) their paths were irregular. Presumably, winds also may have hindered their hawking precision so that the interval between feeding visits may increase with increased wind speed regardless of insect abundance.

Cloud cover, sky haziness, and precipitation.—Percent cloud cover was not associated ($P > 0.05$) with the interval between feeding visits (Table 1). Koskimies (1950) felt that cloudiness had little effect on Common Swift activity. The literature concerning flying insect abundance with respect to cloudiness shows no trends (McClure 1938, Glick 1939, 1957).

Haziness significantly ($P < 0.05$) shortened the interval between feeding visits (13.3 min for hazy skies, vs 15.6 min for clear skies; $t = 2.43$, df = 353). To our knowledge, no researcher has studied the effects of sky haziness on insect abundance. Perhaps insects become more visible with the softened light, or perhaps more are in flight with the reduced solar stress.

Rain significantly ($P < 0.01$) lengthened the interval between feeding visits (12.5 min in rain, vs 8.1 min with no rain; $t = 2.85$, df = 121). McClure (1938) always captured fewer insects during rain. The interval between feeding visits immediately decreased after the rain stopped.

TABLE 1. Equations, correlations, and elasticities showing the relationships of factors (X's) to time elapsed between feeding visits (Y).

Independent variable	No. records	Equation[1]	Correlation[2] coefficient	Elasticity[3]
Temperature (°C)	398	Y = −1.81 + 0.62X	0.24***	1.12
Wind speed (km/h)	398	Y = 13.34 + 0.19X	0.11*	0.08
Cloud cover (%)	398	Y = 13.61 + 0.02X	0.09	0.07
Nestling age (days)	275	Y = 23.56 − 0.73X	−0.52***	−0.62
Brood size	275	Y = 26.93 − 3.26X	−0.23***	−0.85

[1] Where Y is the time elapsed between one adult's departure and the subsequent entrance of either parent and X is the independent variable listed.
[2] Significance levels: $*P < 0.05$; $***P < 0.001$.
[3] Percentage change in Y associated with a 1% change in X measured from the mean of each variable (Wesolowsky 1976:73).

Hour of day.—Nesting swifts were active during early morning and in unfavorable weather, but non-breeders were not (see Zammuto and Franks 1981a). As indicated by shorter time outs, adults fed their nestlings more frequently between 0500–0600 (CDT) and 1701–2000 (Table 3). Numbers of flying insects were probably high during these periods (McClure 1938, Glick 1939, 1957). An evident trend emerging from these data is a successive hourly increase in time out from 0500–0800, then a successive decrease until 1300, another increase in mid-afternoon, and a decrease until dusk (Table 3). This trend corresponds to some degree with information on flying insect abundance (McClure 1938, Glick 1939, 1957) and to the feeding rates of other insectivorous nestlings (Koskimies 1950, Walsh 1978).

Nestling age and brood size.—As the nestlings grew older they were fed significantly more often (Tables 1 and 4). Perhaps older nestlings need more food and stimulate more frequent feeding visits by parents. In contrast, Fischer (1958) found that the interval between feeding visits lasted 30 min for one-week-old Chimney Swifts and 45 min for those

TABLE 2. Relationships of ambient temperature (°C) and wind speed (km/h) to the interval between feeding visits for 14 nests.

Ambient temperature	Mean ± SD min time out	Sample size	Wind speed	Mean ± SD min time out	Sample size
18.1–21.0	16.5 ± 8.8	15	0.0–3.0	12.3 ± 10.8	84
21.1–24.0	10.1 ± 8.4	110	3.1–6.0	14.7 ± 8.7	162
24.1–27.0	15.3 ± 9.5	93	6.1–9.0	16.1 ± 8.6	48
27.1–30.0	15.9 ± 8.5	116	9.1–12.0	15.2 ± 9.0	80
30.1–33.0	16.5 ± 8.8	46	12.1–24.0	16.5 ± 8.8	24
33.1–36.0	21.3 ± 9.3	16			
36.1–39.0	32.0 ± 11.3	2			
Total		398			398

TABLE 3. Relationship of hour of day (CDT) to the interval between feeding visits for 14 nests.

Hour of day	Mean ± SD min time out	Sample size
0500–0600	6.5 ± 3.8	15
0601–0700	14.6 ± 9.6	16
0701–0800	21.9 ± 9.7	10
0801–0900	19.8 ± 10.5	10
0901–1000	18.8 ± 4.3	9
1001–1100	16.8 ± 10.8	23
1101–1200	15.0 ± 8.1	48
1201–1300	14.0 ± 6.8	52
1301–1400	15.6 ± 9.2	52
1401–1500	14.7 ± 10.3	33
1501–1600	17.9 ± 8.1	26
1601–1700	18.9 ± 10.2	23
1701–1800	10.4 ± 10.0	35
1801–1900	10.1 ± 8.4	36
1901–2000	12.0 ± 10.2	10

2 weeks old. Nestling age was the only factor that accounted for more than 25% ($P < 0.001$) of the variance in time out.

Larger broods were fed significantly more often than smaller broods (Tables 1 and 4). This trend was even more evident for the Common Swift (Lack and Lack 1951). In our study, broods of 4 nestlings were fed significantly ($P < 0.001$) more often than those of 3 ($t = 8.61$, df = 234) or 5 ($t = 4.74$, df = 179). Perhaps a brood size of 4 is the optimum for maximal feeding efficiency.

SUMMARY

The mean time elapsed between 398 feeding visits for 14 Chimney Swift nests was 14.6 ± 9.3 min. Significantly more time elapsed between feeding visits with increasing temperature, wind speed, and precipitation, but significantly less time elapsed with increasing sky haziness, nest-

TABLE 4. Relationships of nestling age (days) and brood size to the interval between feeding visits for 6 nests.

Nestling age	Mean ± SD min time out	Sample size	Brood size	Mean ± SD min time out	Sample size
1–3	24.2 ± 7.5	18	3	20.1 ± 9.0	94
4–7	16.6 ± 7.6	61	4	10.3 ± 8.2	142
8–11	19.2 ± 10.2	63	5	17.3 ± 7.7	39
12–15	13.8 ± 8.6	41			
16–19	12.5 ± 7.4	43			
20–24	5.6 ± 5.6	49			
Total		275			275

ling age, and brood size. Cloud cover was not associated with the time elapsed between feeding visits. Hour of the day and all the environmental factors reported to effect an increase in flying insect abundance were concomitantly associated with a shorter interval between feeding visits.

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