ENERGETIC ASPECTS OF REPRODUCTION BY THE CLIFF SWALLOW

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ABSTRACT.—Energy budgets were constructed for the Cliff Swallow during the nest building, incubation, and nestling periods using time budgets and aerodynamic theory. Mean daily energy expenditures during these periods were 1.55, 1.23, and 1.28 watts respectively, with required food harvest rates of at least 3.95, 4.42, and 4.07 watts. The cost of constructing an average size nest (600 g) was approximately 122 kilojoules expended over about 7 days, but the multiple use of the nest makes the cost per brood considerably less than this. The ecological advantages accruing from the nest apparently are related primarily to physical protection from predators and reduction of intraspecific aggression, rather than microclimatic conditions established within the nest.—
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Accepted 25 March 1976.

THE complexity of most avian nests indicates the central role of this structure to reproductive success, but the energetic cost of building a nest cannot be determined directly and no accurate data are available. Collias and Collias (1967) used time budgets and the meager data then available for the metabolic cost of flight to estimate the cost of different activities of the Village Weaver (*Textor cucullatus*). Utter and LeFebvre (1973) utilized D_2O^{18} studies and time budgets to estimate the daily energy expenditure of Purple Martins (*Progne subis*) raising nestlings.

The present study quantifies the cost of nest construction by time budget analysis and the application of recent aerodynamic theory (Pennycuick 1969, Tucker 1973) and assesses the advantages gained from the nest for the Cliff Swallow *Petrochelidon pyrrhonota* Vieillot.

The natural history of the Cliff Swallow has been described by Bent (1942) and Emlen (1952, 1954). The birds build gourd-shaped nests of mud, usually under overhanging rock formations, bridges, or eaves of buildings. Cliff Swallows reoccupy and repair old nests, and establish new colonies in suitable places near sources of mud and food. The clutch size is 3 to 6, the incubation period is 12 to 14 days, and 2 or 3 broods are raised per year.

The few microclimatological studies of bird nests (Stoner 1936, Kendeigh 1961, Ricklefs and Hainsworth 1969, White et al. 1975) have indicated a degree of thermal stability and high humidities within nests, but the gaseous environment of bird nests has not been studied previously.

METHODS

The Cliff Swallows in this study were a colony of about 40 adults nesting under the eaves of two buildings at Jalama Beach, Santa Barbara County, California. They foraged principally over a nearby estuary and collected mud from the creek bank about 90 m from the nesting sites.

The swallows were studied continuously over 24-hour periods during nest construction (13–14 April), the incubation period (7–8 May), and the period with nestlings (21–22 May, 1975). A daily time budget was constructed for each of these periods. Hourly censuses were made of the numbers of swallows seen at the nests, collecting mud at the creek, and foraging over the estuary. To calculate daily flight time it was assumed that the swallows did not perch except at the nest sites. Foraging flights of individual swallows from about 10 nests were timed with a stopwatch over periods of 20 to 30 min. The time required to collect a mud pellet, carry it to the nest, and pack it into the nest walls was measured, and the flight velocity was determined over a 90 m course.

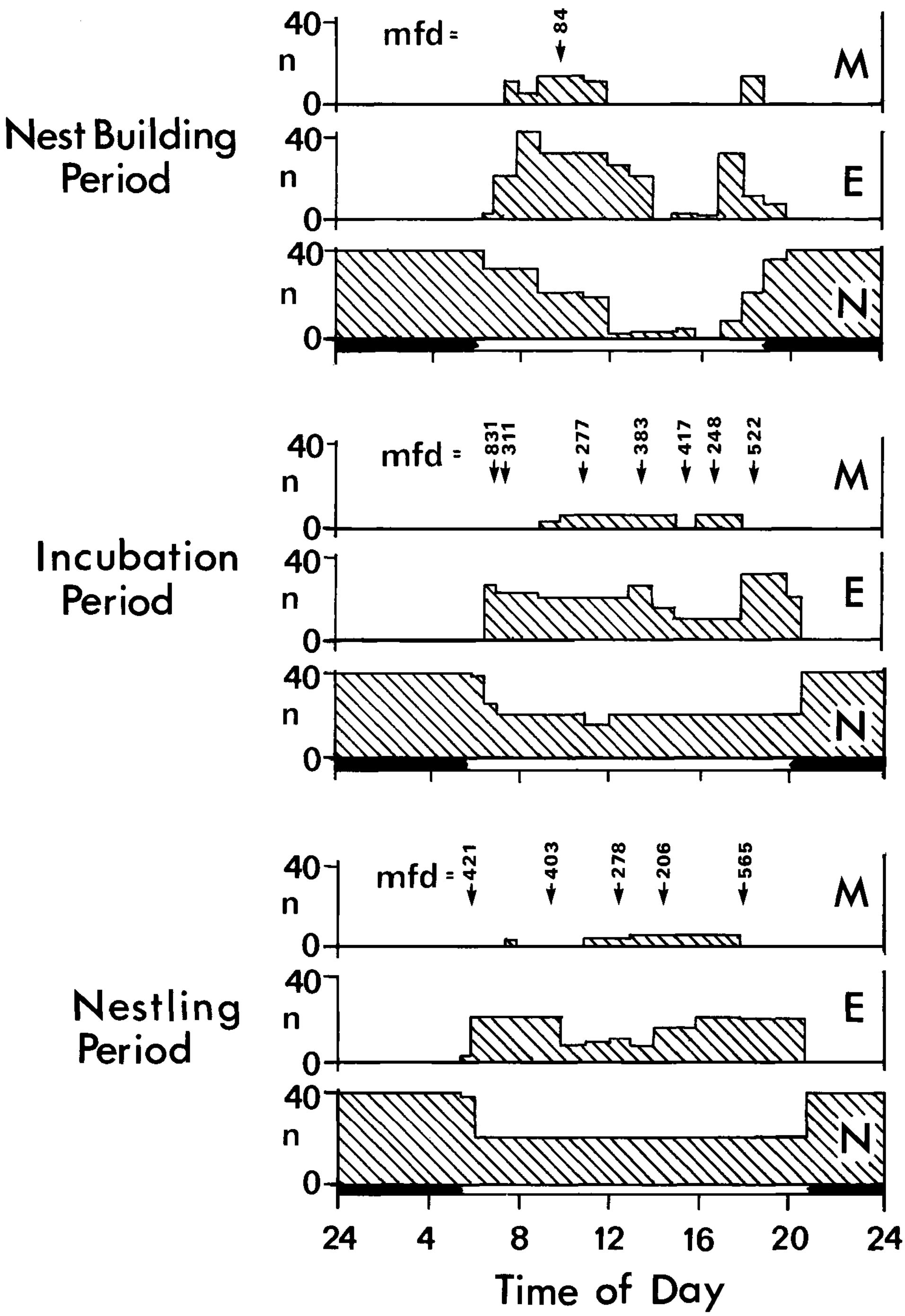

Fig. 1. The number (n) of Cliff Swallows observed at the mud collecting sites (M), estuary (E), and nest site (N), and photoperiod during nest building, incubation, and foraging periods; mfd = mean flight duration (seconds).

TABLE 1

DAILY TIME AND ENERGY BUDGETS OF CLIFF SWALLOWS DURING NEST CONSTRUCTION, INCUBATION, AND NESTLING PERIODS[1]

	Nest construction		Incubation		Nestlings	
	Hrs	kJ	Hrs	kJ	Hrs	kJ
Foraging	9.5	92.1	6.8	65.3	7.5	78.9
Nest construction	3.0	15.9	0.4	2.5	0.2	0.8
In nest	11.5	26.0	16.8	38.1	16.3	36.8
TOTAL	24.0	134.0	24.0	105.9	24.0	110.5
Harvest rate (TOTAL/h foraging; W)	3.91		4.36		4.07	
Daily energy expenditure						
$W (g)^{-1}$	0.063		0.050		0.052 (0.43)[2]	
× SMR	3.67		2.92		3.05 (3.02)[2]	

[1] Conversion of time to energy assumes flight cost = 2.69 W, cost of mud collecting and packing = 0.84 W, and existence metabolism = 0.63 W.
[2] Data for Purple Martin (Utter and LeFebvre 1973).

Mud samples were collected from the creek bank used by the swallows and from the nests, and were oven-dried for 36 hours at 250°C to determine the water content. An average-sized nest and a large nest were collected and the mud portion weighed. Adult swallows were captured with a mist net and released after their weight, wing span, and wing length were measured.

Temperature, humidity, and the concentration of CO_2 were measured within the nests, above the occupants. A 30-gauge thermocouple (Bailey Instruments), a humidity probe (Thunder Scientific), and a short length of glass tubing connected to a glass syringe were introduced about 10 cm into the nest chamber. The concentration of CO_2 in the air sample was immediately determined with a Scholander 0.5 cc gas analyser.

Standard metabolic rate (SMR) was predicted for the Cliff Swallow from the equation of Lasiewski and Dawson (1967) and the energetic cost of flight was estimated from aerodynamic theory of flapping flight (Pennycuick 1969, Tucker 1973).

All statistics are expressed as mean ± SD with the number of observations in parentheses. All units are S.I., and the conversion factors are 1 watt (W) = 0.860 kcal/h and 1 kilojoule (kJ) = 0.239 kcal.

RESULTS

Daily time budgets of the Cliff Swallows differed markedly during the nest construction, incubation, and nestling periods (Fig. 1). The total number of birds counted was about 40 except during the period of nest construction when the swallows foraged in the foothills near the coast. The mean flight duration during nest construction, incubation, and the nestling period is correlated with the periods of mud collection (Fig. 1). Standard deviations of mean flight duration were about 20% of the mean value.

Mud the swallows collected contained 23.8% water and was at field capacity (could hold no more water) whereas air-dried mud pellets from nests contained 3.8% water. The weight of individual air-dried pellets from nests were 0.425 ± 0.029 g (N = 10) which corresponds to a mean wet weight of 0.516 g. The air-dried weight of the average-sized nest was 596 g and of the large nest 672 g.

The weight, wing span, wing length, and wing disc load (body weight per area of wing disc with diameter equal to wing span) were:

body weight = 24.6 ± 2.3 g (N = 10)
wing span = 29.2 ± 0.6 cm (N = 10)
wing length = 13.6 ± 0.6 cm (N = 10)
wing disc load = 0.0367 ± 0.0034 $g(cm)^{-2}$ (N = 10)

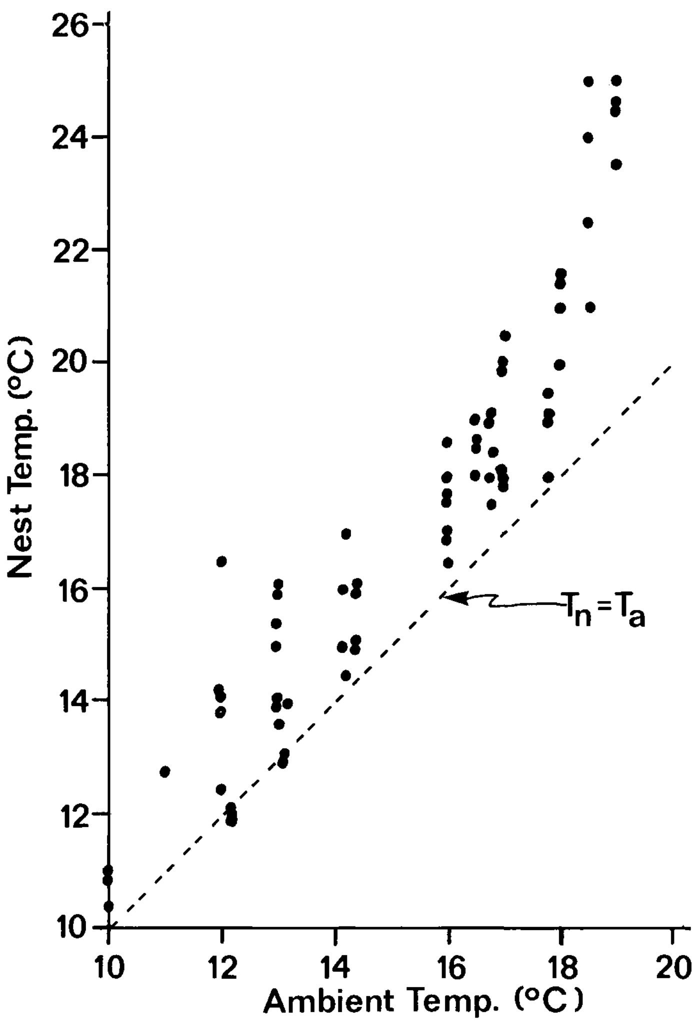

Fig. 2. Temperatures in Cliff Swallow nests (T_n) as a function of ambient temperature (T_a).

The flight velocity was determined to be approximately 8.7 m per sec (ca. 23 mph) and the metabolic cost of flight at this velocity for a 24.6 g bird is predicted to be 2.69 W or 6.4 SMR (Tucker 1973). No correction was made for ambient wind velocity. The metabolic cost of collecting mud from the creek bank and packing it into the nest was assumed to be 2 SMR (0.84 W) and the mean existence metabolism in the nest was assumed to be 1.5 SMR (0.63 W). A 50% error in either of the latter assumptions results in only a 7% error in the mean daily energy expenditure because of the large contribution of flight relative to nonflight activities. The daily energy expenditures of Cliff Swallows during the nest construction, incubation, and nestling periods were 0.063, 0.050, and 0.052 W $(g)^{-1}$ (Table 1).

The temperature gradient between the inside and outside of the nest was between 0 and 7°C (Fig. 2) and unoccupied nests were 0 to 4°C above ambient during the day because of the solar heat load. Relative humidity was variable inside the nest (Fig. 3)

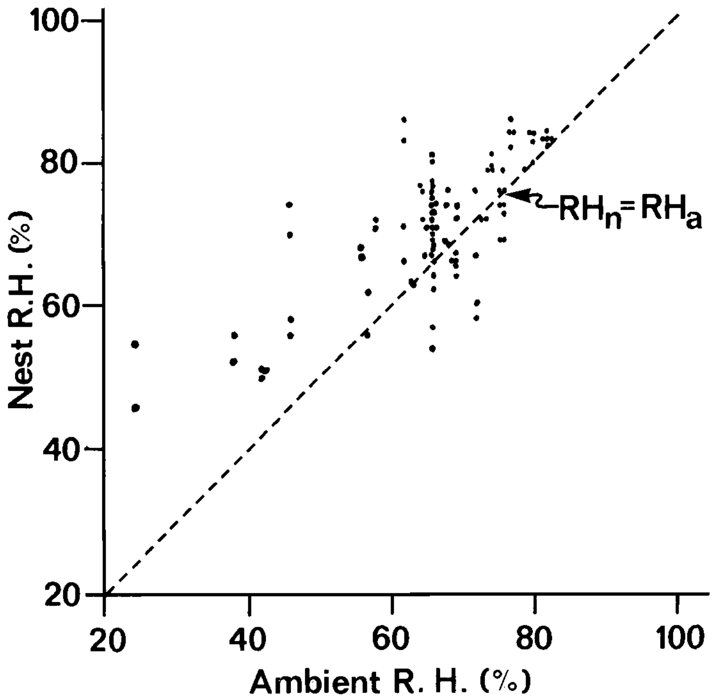

Fig. 3. Relative humidity in Cliff Swallow nests (RH_n) as a function of ambient relative humidity (RH_a).

but absolute humidity was invariably greater inside the nests (11.39 ± 2.5 mm Hg, N = 61) than outside (9.03 ± 1.1 mm Hg, N = 18).

The concentration of CO_2 within nests was 0.10 ± 0.007% (N = 8) during nest construction, 0.20 ± 0.007% (N = 18) during incubation, and 0.32 ± 0.01% (N = 15) during the nestling period. There was no apparent diel cycle in the concentration of CO_2 within the nests except during nest construction when the swallows were absent from the nests for long periods and the concentrations of CO_2 were low.

DISCUSSION

The time and energy expended upon construction of a nest by a bird contributes to its reproductive success through behavioral, physiological, and physical advantages accruing from the nest. The time devoted to nest construction can be obtained from

TABLE 2

INTERDEPENDENCE OF MEAN FLIGHT DURATION AND MUD COLLECTION DURING THE NESTLING PERIOD[1]

	Mean flight duration	T_n (°C)	RH_n (%)	AH_n (mm Hg)
Unoccupied nest	—	19.0	56	9.23
Nest 8 (no fresh mud)	333 (n = 3)	19.0	58	9.56
Nest 7 (fresh mud)	115 (n = 9)	19.5	70	11.90
Nest 9 (fresh mud)	119 (n = 5)	20.0	77	13.53
Ambient (shade)	—	16.0	70	9.54

[1] Mean flight duration in seconds; n = number of flights observed; T_n = nest temperature; RH_n and AH_n = relative and absolute humidity in nest.

time budget studies, but the actual cost of nest construction has not been determined for any avian species. Such a measurement must be undertaken through indirect means such as energy budgeting, and the Cliff Swallow is an ideal subject for such a study because it builds an elaborate mud nest and temporally separates nest construction from other activities.

The metabolic cost for a 24.6 g Cliff Swallow flying at 8.7 m $(sec)^{-1}$ is predicted to be 0.109 W $(g)^{-1}$ from aerodynamic theory (Tucker 1973). Carrying a 0.516 g pellet of mud adds about 1% of this value to the cost of flight, and is ignored in subsequent calculations. The observed flight velocity of 8.7 $m(sec)^{-1}$ is similar to the velocity predicted for minimum cost of transport (v_{mr}) of 8.2 $m(sec)^{-1}$ (Tucker 1973).

The number of trips required to complete construction of a 600 g nest is about 1,400 (600 ÷ 0.425). Emlen (1952) estimated from the nest surface area that each nest contained about 900 to 1,200 pellets. The flight time for a round trip between the nest and the creek bank was, for the swallows observed in this study, about 20 sec, with 10 sec to pick up the mud pellet and 30 sec spent in the nest. The mean metabolic rate during such a 60-sec cycle is therefore 3.47 SMR $= (^1/_6 \times 2) + (^1/_3 \times 6.4) + (^1/_2 \times 2)$, and the total cost of nest construction is

3.47	× 0.420	× 1,400	× 60.0 = 122 kJ
mean cost (× SMR)	SMR (W)	# trips	sec

If the Cliff Swallows maintain the observed intensity of nest construction of 3 h per day, a 600 g nest would require 7.8 days for completion. The reported period for nest construction is 5 to 14 days depending upon the weather conditions (Bent 1942, Emlen 1952), but this time probably depends directly upon the distance between the nest and the source of mud.

The daily energy expenditure of Cliff Swallows was greater during nest construction than for the incubation or nestling periods, but the required food harvest rates were similar (Fig. 1). Some of the time designated as foraging is spent in social encounters, especially during the courtship period, and so the harvest rates would be somewhat greater than the values presented in Table 1.

The added energetic demands of the nestlings must require a greater harvest rate than the calculated 4.07 W (Table 1). No data are available for the metabolic requirements of developing Cliff Swallows, but minimum estimates can be obtained from the growth rates of nestlings of a similar size species, the Barn Swallow *Hirundo rustica* (Stoner 1935). Assuming a caloric equivalent of 6.28 $kJ(g)^{-1}$ wet weight and a mass specific metabolic rate equal to that of the adult (Ricklefs 1974), the extra energy required per nestling during development is from 0.10 to 0.48 W, or 8 to 10% of the energy expenditure of the adult. Adults occasionally extended their foraging time during the nestling period by leaving the nest unattended for short periods.

The energetic demands of building a nest are similar to the demands of incubation, but are less than those of raising nestlings. The major cost of nest construction is therefore the time spent collecting the mud and building the nest (about 24 hours for a 600 g nest) rather than the energy expenditure of transporting and working the mud pellets.

Nests of Cliff Swallows are typically more than 3 m above the ground and afford valuable protection against most predators (Bent 1942). The construction of a gourd-shaped nest diminishes the territorial area that must be defended to the narrow nest entrance. Intraspecific aggression at the nest site is high, and the territorial boundaries (narrow entrance and nest walls) are required for successful breeding (Emlen 1954).

Cliff Swallow nests provide little homeostasis of nest temperature unlike many nests (Stoner 1936, Ricklefs and Hainsworth 1969, White et al. 1975), but offer protection against radiative heat loss to the night sky (Calder 1974), wind chill, and rain.

The relative humidity within Cliff Swallow nests was variable at high ambient humidities but was high at low ambient humidities (Fig. 3). Absolute humidity was invariably greater within the nest because of the pulmocutaneous water loss of the nest occupants and/or evaporation of water from recently collected mud pellets. The swallows collected mud during the warmer periods of the day while they were incubating or had nestlings (Fig. 1). This was apparent from the presence of swallows at the creek bank and the decreased duration of flights from the nest (Fig. 1). The relative and absolute humidities were high when mud was collected (Table 2). The reason for prolongation of mud collecting is unclear, but it may be routine nest maintenance. Birds rapidly repaired any damage to the exterior of the nest. Alternatively, the swallows may actively maintain a high humidity within the nest or use evaporation of water from mud pellets to cool the nest in a manner similar to the use of fecal sacs by Cactus Wrens, *Campylorhynchus brunneicapillus* (Ricklefs and Hainsworth 1969).

The concentrations of CO_2 within Cliff Swallow nests were highest during the nestling period (0.20 ± 0.01%), but are unlikely to stress either the adults or nestlings. Hatchability of eggs is probably not affected by concentrations of CO_2 less than 1% (Lundy 1969).

The present study describes some temporal and energetic aspects of nest building and reproduction by the Cliff Swallow, and demonstrates the role of physical measurements and aerodynamic theory in the construction of energy budgets. The close agreement of data from the present study with accounts of natural history of Cliff Swallows (Bent 1942, Emlen 1952, 1954), data for the Purple Martin (see Table 1), and data for other species (King 1974) is gratifying. As nests of Cliff Swallows are usable for a number of years and 2 or 3 broods are raised per year, the cost of building the nest is considerably less than 122 kJ, surprisingly low in view of the number of advantages accruing from the nest.

ACKNOWLEDGMENTS

I am greatly indebted to Patricia Roesler for assistance with data collection in the field. I thank P. L. Timko for reading the manuscript and preparing the figures, and G. A. Bartholomew, G. E. Walsberg, and D. F. Hoyt for constructive criticism of the manuscript. The study was supported by a University of California Student Patent Fund Grant to the author and NSF grant GB 32947 to G. A. Bartholomew.

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