

NESTING AND FEEDING HABITS OF BROWN-CHESTED MARTINS IN RELATION TO WEATHER CONDITIONS

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ABSTRACT.—Brown-chested Martins (*Phaeoprogne tapera*) at Guanare, Venezuela, have a clutch size of 4.0 ± 0.2 (SE) eggs, smaller than that reported for the Purple Martin (*Progne subis*), a temperate species. The eggs are incubated for 62.4% of the daylight hours; incubation periods are longer at low ambient temperatures. Nestling Brown-chested Martins do not lose weight near fledging; the growth rate constant is 0.284. On a biomass basis, Brown-chested Martins bring more dragonflies to the nest than reported for Purple Martins; relatively more dragonflies are brought as the nestlings grow. Cool, wet, and cloudy weather reduces feeding activity and the rate at which food is gathered by the tropical martin, as has been reported for the temperate species.

Among temperate hirundines, such as Purple Martins (*Progne subis*), Common House-Martins (*Delichon urbica*), and Barn Swallows (*Hirundo rustica*), bad weather and food scarcity reduce the frequency of feeding visits to the brood and the growth rate and survival of nestlings (Finlay 1971a, Rheinwald 1971, Bryant 1975, Turner 1980). Little is known, however, about the effects of weather on related aerial feeders in the tropics where, in contrast to high latitude sites (e.g., Finlay 1971a), cold weather is not usually experienced during the breeding season (for example, Ricklefs 1971). Tropical hirundines, however, feed less during heavy rainfall and hot weather (Moreau 1939, Ricklefs 1971).

My purpose was to see how the breeding and feeding ecology of a hirundine is affected by variations in weather and feeding conditions in an area of high ambient temperature. In my study, the ambient temperature varied from 23 to 35°C, whereas in Finlay's (1971a) for example, it ranged from 2 to 24°C. In this paper, I describe the breeding and feeding habits of Brown-chested Martins (*Phaeoprogne tapera*), and compare them with published information concerning Purple Martins, giving particular attention to the effects of weather and feeding conditions.

STUDY AREA AND METHODS

I studied Brown-chested Martins at Guanare, Venezuela (9°2'N, 69°44'W, elev. 183 m) from 12 April to 7 June 1981. The mean annual temperature there is 28.2°C and the annual rainfall is 1,465 mm. The dry season lasts from November to the end of March, although some rain falls in every month. The peak of the wet season is in July (Gonzalez 1948).

My study sites were bridges over streams and rivers roughly 1–20 km southwest of

Guanare along the main road into the town. I found 22 nest-sites at or near eight bridges, although only 12 nests were accessible. The martins fed close to the nest-sites (within roughly 1 km of them) over marsh, grassland, and natural savanna devoted to cattle grazing. The dominant plants were herbaceous with few trees, which were mostly under 20 m high. The ground was partially flooded in the wet season. Small areas of gallery forest extended along stretches of the rivers, but I never saw martins feeding there.

I monitored the nest attendance of incubating martins (sex unknown) at two nests (for eight 1-h periods over two days at one nest and 18 1-h periods over seven days at the other) and the feeding activity of adults at two other nests (one with three nestlings—for 25 1-h periods over eight days—and a second with four nestlings—for 24 1-h periods over 10 days). Observations began when both broods were seven days old and ended when they were 23 days old. Broods were aged by comparison with weights and wing-lengths of chicks of known age in another nest that was checked daily.

I determined what the birds ate from the remains (wings) of prey in droppings under a perch and in three nests. Although this method has been used in other studies of hirundines (Bryant 1973, Waugh 1979), it was not reliable for determining the size of dietary items such as Lepidoptera and Odonata, because only fragments of their wings remained. Hence, these groups are probably under-represented in my data. I also obtained food boluses from collared nestlings in two nests (not otherwise used for feeding studies). One brood was 7 days and the other 11 days old when bolus collection began; both were 23 days old when it ended. Collars were left in place for 24 2-h periods

over 16 days. Walsh (1978) noted that small items slipped past the collar on Purple Martins more than 21 days old, but I saw no evidence of this in my study. Boluses were collected mainly in dry weather; hence, the droppings may represent the overall diet of the martins better than the boluses. In order to determine how much food was brought to a chick per unit time, I measured the time taken for the parent to collect each bolus.

I observed feeding martins on 18 days for periods of 5–10 min each (60 periods between 07:00–11:00, 63 between 11:30–15:00, 74 between 15:30–19:00) and recorded the habitat and foraging height of the birds as follows: over open ground, waterside vegetation, water, or near trees; below 5 m, 5–50 m, or above 50 m. I also measured food abundance at these feeding sites using a fine mesh (<1 mm) hand net to sample flying insects (80 samples over 23 days): 50 strokes through the air 0.1–2 m above ground per sample. To estimate the density of rapidly flying insects, such as dragonflies, I set up 14 100-m transects at the same sites and counted the number of flying Odonata within 2 m of them over a period of 3 min.

At the beginning of each observation period, I noted the ambient temperature in the shade (T_a) and sunlight (T_s), windstrength, rainfall intensity (both rated on a scale of 1 to 5), and cloud cover. The latter was rated on a scale of 1 to 7: 1, clear sky; 2, > 0 ≤ 25% white cloud; 3, > 25 ≤ 50% white cloud; 4, > 50 ≤ 75% white cloud; 5, > 75 ≤ 100% white cloud; 6, ≤ 75% grey cloud; 7, > 75% grey cloud. Values of 6 or 7 occurred immediately before, during, or after it rained and such conditions are hereafter referred to as “wet”; values between 1 and 5 denote “dry” conditions.

Numbers throughout the text are means ± 1 SE.

RESULTS

BREEDING BIOLOGY

I found 2 nests in dead trees and 20 in holes in bridges. Five bridges had a single nest, two had three nests and only one (with 16 apparently suitable holes) had four active nests. Adults frequently fought at entrances to holes when more than one nest was present at a specific site.

The mean clutch size was 4.0 ± 0.2 eggs (range 3–5, $n = 10$). Six clutches were destroyed by predators or floods; in the other four, 7 of 14 eggs hatched.

The incubation period was 14–15 days. I saw only one member of each pair incubating. The eggs were covered for $62.4 \pm 2.6\%$ ($n =$

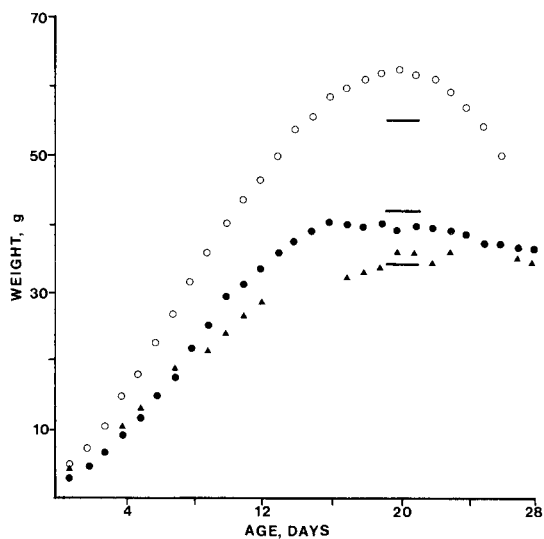


FIGURE 1. Growth curves for three species of hirundines: open circles, Purple Martin ($n = 11$; Allen and Nice 1952); closed circles, Gray-breasted Martin ($n = 11$; C. T. Collins, unpubl.); triangles, Brown-chested Martin ($n = 3$; this study); horizontal bars, adult weights (Finlay 1971a, french 1976, this study).

26 h of observation) of the 12 daylight hours daily. The attentiveness of the incubating parent was negatively correlated with T_s ($r = -0.57$, $P < 0.01$, 24 df). Incubation periods (between successive bouts of feeding) were 2–25 min in dry ($n = 29$) and 2–54 min in wet ($n = 39$) weather, but over 50% of them lasted 2–12 min (median = 11 min). Feeding periods were generally shorter, 60% being less than 8 min long (median = 7 min, range 1–18 min, $n = 73$). The longest period that a martin was away from its nest was during very heavy rain.

Nestlings in one nest reached a peak weight of 36.5 ± 0.61 g ($n = 3$, Fig. 1) at about 20 days of age; the growth rate constant, K , was 0.284 days^{-1} (calculated from Ricklefs' [1967] graphical method). They came to the entrance of the nest-hole to beg for food on day 18 and left the nest at approximately four weeks of age. Fledging success was 71% (10 of 14 nestlings fledged from six nests).

FEEDING ECOLOGY

On a numerical basis, Isoptera were the main constituent of the adult martins' diet, followed by Hymenoptera and Diptera (Table 1). The mean wing-length of the food items was 8.4 ± 0.1 mm ($n = 358$). Termites and ants were caught mainly in wet weather and also formed a higher proportion of items in the droppings than in the boluses. (Table 2). The composition of the boluses indicates that the chicks' diet consisted of (1) significantly ($P < 0.001$) smaller insets in wet (48.1 ± 6.6 mg,

TABLE 1. Percent occurrence (by numbers) of insect taxa in the diet of adult Purple and Brown-chested martins.

Taxon	Purple Martin ^a	Purple Martin ^b	Brown-chested Martin ^c (n = 389)
Isoptera	0	0	62.5
Orthoptera	1.1	trace	0
Odonata	15.1	0-1	6.7 ^d
Hemiptera	14.6	2-28	1.6
Lepidoptera	9.4	0-14	1.3 ^d
Diptera	16.1	3-20	10.8
Hymenoptera	23.0	2-35	15.2
Coleoptera	12.5	32-68	2.1

^a From gizzards (Beal 1918).^b From gizzards (Johnston 1967).^c From droppings (this study).^d Probably underestimated since these were fragmented in the droppings.

$n = 56$ insects) than in dry (103.2 ± 3.3 mg, $n = 167$ insects) weather, and (2) fewer dragonflies when it was wet (36% vs. 63% in wet and dry weather, respectively, $\chi^2 = 6.43$, $P < 0.05$). Diptera, Hymenoptera, and small Lepidoptera were the major food items in their first two to three weeks. Throughout the nestling period, the proportion of dragonflies in the diet increased and in dry weather was positively correlated with nestling age ($r = 0.66$, $P < 0.05$, 9 df). The mean dry weight of prey items in the boluses was 89.0 ± 3.4 mg ($n = 223$).

Each nestling was fed on average 2.82 ± 0.33 times per hour ($n = 24$ h of observation) in a brood of three and 2.88 ± 0.24 times per hour ($n = 25$ h of observation) in a brood of four. In dry weather, nestlings in the latter brood were fed more frequently as they grew ($r = 0.62$, $P < 0.01$, 15 df); the same was not true for the brood of three ($r = 0.18$, 16 df). Feeding frequency was correlated with T_s and cloud cover (Table 3). During very heavy rain, the parents ceased feeding the nestlings.

The dry weight of food boluses (overall mean 133.4 ± 2.9 mg, $n = 149$) was not correlated with the weather, but the time taken to collect them was (Table 3): food was gathered more

TABLE 2. Percent occurrence (by numbers) of insect taxa in the droppings and food boluses of nestling Brown-chested Martins.

Taxon	Droppings (n = 115)	Boluses (n = 223)
Isoptera	43.5	8.5
Odonata	15.7	54.7
Hemiptera	0	0.4
Lepidoptera	11.3	22.9
Diptera:	4.3	6.3
Brachycera	2.6	1.3
Syrphidae	0.9	4.9
Calypterae	0.9	0
Hymenoptera:	25.2	7.2
Formicoidea	11.3	0.4
Aculeata	3.5	6.7

TABLE 3. Correlations between the feeding ecology of Brown-chested Martins, insect abundance, and weather.

Dependent variable	Ambient temperature in sunlight	P	Cloud cover	P	n
Meals h ⁻¹ nestling ⁻¹	0.42	0.01	-0.32	0.05	49 ^a
Bolus dry weight, mg	0.16	N.S.	-0.14	N.S.	24 ^a
Bolus collection time, min	-0.85	0.001	0.73	0.001	24 ^a
Food-gathering rate, mg min ⁻¹	0.75	0.001	-0.66	0.001	24 ^a
Dragonfly numbers along transects	0.94	0.001	-0.83	0.001	14
Log ₁₀ dry weight of net samples	0.39	0.001	-0.23	0.05	80

^a The number of 1- or 2-h periods over which measurements were made.

quickly in warm and dry than in cool and wet weather (Table 4, Fig. 2). In this context, the number of dragonflies and the size of the net samples were both correlated with T_s and cloud cover (Table 3).

In dry weather, martins fed mainly at low and medium heights over waterside vegetation and around trees, but in wet weather they fed more at medium heights (Table 5).

DISCUSSION

BREEDING BIOLOGY

Purple Martins in North America usually nest in (artificially) large groups in martin houses, within which each male maintains a territory (Brown 1979). Brown-chested Martins are territorial, but nest singly or in small groups in natural cavities; in Argentina, for example, they use old furnariid and termite nests (Hudson 1920). Gray-breasted (*Progne chalybea*), Southern (Galapagos) (*P. elegans modesta*), and Caribbean (*P. dominicensis*) martins also nest in crevices among rocks or in man-made structures (Hartley 1917, Hudson 1920, Beebe 1924, French 1976).

In common with many genera of birds (Lack 1947), tropical and insular species of *Progne* and *Phaeoprogne* have smaller clutches than their temperate counterparts. For example, the Purple Martin has a clutch of 4.8 eggs in Alberta (Finlay 1971b), 4.9 in Michigan (Allen and Nice 1952), and 4.6 in Texas (Brown 1978), the range being three to eight eggs. In contrast, the clutch size of the Caribbean Martin is only two in Tobago and up to six elsewhere in the West Indies (French 1976); Gray-breasted Martins produce two to five eggs in northern South America (Hartley 1917, French 1976, Collins, unpubl.) and five in Argentina (Hudson 1920); the Brown-chested Martin, four

TABLE 4. Differences in the feeding ecology of Brown-chested Martins in wet and dry weather. Values in the table are means \pm SE (*n*) for the number of 1- or 2-h periods over which observations were made.

Variable	Dry weather	Wet weather	<i>P</i>
Meals h ⁻¹ nestling ⁻¹	3.3 \pm 1.3 (35)	1.7 \pm 1.1 (14)	0.001
Bolus dry weight, mg	129.6 \pm 20.4 (16)	118.5 \pm 34.3 (8)	N.S.
Bolus collection time, min	4.3 \pm 1.2 (16)	9.1 \pm 2.7 (8)	0.001
Food-gathering rate, mg min ⁻¹	30.7 \pm 11.8 (16)	14.2 \pm 4.7 (8)	0.001

(Hudson 1920, this study); and the Southern Martin on the Galapagos Islands only 1.9 eggs (Beebe 1924).

Incubation periods are similar among the members of this group: 15–18 days for Purple and Gray-breasted martins (Hartley 1917, Allen and Nice 1952, Finlay 1971b), and 14–15 days for the Brown-chested form in my study. Only female Purple and Gray-breasted martins incubate (Hartley 1917, Allen and Nice 1952).

Weather conditions influence incubation behavior in both Purple and Brown-chested martins. The Purple Martin incubates for 81% of daylight hours when the ambient temperature is 14.4°C, but only 69% at 19.8°C (Allen and Nice 1952). The Brown-chested Martin spent less time on eggs (62%) than the Purple Martin does, but incubated at a higher average ambient temperature of 27.6°C.

Purple Martins usually spend 4–15 min at a time on the eggs, but sometimes over 30 min, especially in bad weather; their inattentive periods generally last less than 12 min (Allen and Nice 1952, Kendeigh 1952). Finlay (1971a), however, noted that the female spends a long time away from the nest in very inclement weather. Brown-chested Martins also have short inattentive periods, and long spells at the nest in cool, cloudy weather.

Egg losses were much higher for Brown-

chested Martins (82%) than has been reported for Purple Martins (8% lost, 4% infertile; Brown 1978). Nest failures are common, however, in tropical altricial species (Ricklefs 1969.)

Nestling Purple Martins gain weight until they exceed the average adult weight (Fig. 1) before diminishing as water is lost from maturing tissues (Ricklefs 1968). Gray-breasted and Brown-chested martins do not exhibit such marked peaks followed by weight recession (Fig. 1). The growth rate constant of Brown-chested Martins (0.284 days⁻¹) was lower than that reported for Purple and Gray-breasted martins (0.384 and 0.395 days⁻¹, respectively; Ricklefs 1976).

The nestling periods of Purple and Brown-chested martins are both about four weeks (Finlay 1971b, this study), whereas that of the Gray-breasted form has been reported as only 22 days (Hartley 1917), as well as 28 days (Collins, unpubl.). Fledging success (as a percentage of nestlings hatched) of Brown-chested (71%) and Purple martins (70% in Alberta [Finlay 1971b]; 84% in Texas [Brown 1978]) is similar. Allen and Nice (1952), however, gave a lower figure of only 46% for Purple Martins in Michigan during inclement weather.

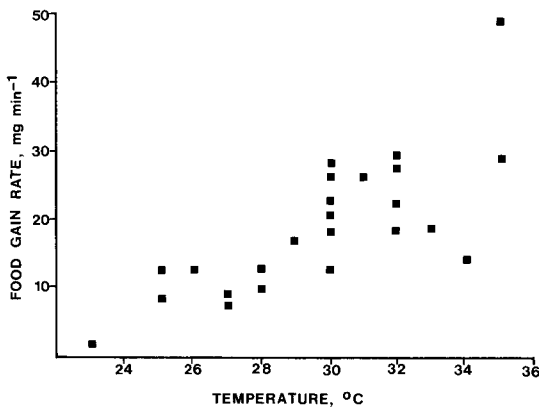


FIGURE 2. The rate of food-gathering by Brown-chested Martins in relation to the ambient temperature in the sun. Each point represents a 2-h period.

TABLE 5. Density of Brown-chested Martins at various feeding stations. Values in the table are numbers of martins observed at each station expressed as a percentage of the total number of martins observed at all feeding stations.

Feeding site	Feeding height (m)	Dry weather (<i>n</i> = 129)	Wet weather (<i>n</i> = 68)	All weathers (<i>n</i> = 197)
Open ground	<5	0	0	0
	5–50	6.2	0	4.1
	>50	0	0	0
Trees	<5	14.7	23.5	19.3
	5–50	34.1	39.7	32.0
	>50	0	0	0
Waterside	<5	31.0	0	20.3
	5–50	6.2	47.1	20.3
	>50	0	0	0
Over water	<5	6.2	0	4.1
	5–50	0	0	0
	>50	0	0	0
Niche breadth ^a		4.72	2.30	4.76

^a Niche breadth $B = 1/\sum p_i$, where p_i is the proportion of observations in category i (Levins 1968).

TABLE 6. Percentage occurrence (by weight) of insect taxa in the diet of nestling Purple and Brown-chested martins.

Taxon	Purple Martin ^a	Brown-chested Martin ^b (n = 223)
Isoptera	0	0.3
Odonata	30.2	69.9
Hemiptera	2.5	trace
Lepidoptera	17.1	20.6
Diptera	27.3	2.5
Hymenoptera	7.0	4.9
Coleoptera	2.8	0

^a From Walsh (1978).^b This study.

FEEDING ECOLOGY

Adult Brown-chested Martins feed mainly on termites, a group that is unavailable to Purple Martins, which reportedly feed on a wider variety of prey (Table 1). The weather, however, affected the diet of Brown-chested Martins because rain stimulates termites to swarm (Kirkpatrick 1957), and these insects are not always otherwise available; larger prey, such as dragonflies and moths, were taken in dry weather.

Nestling Brown-chested Martins were fed more dragonflies and fewer Diptera (by weight) than has been reported for nestling Purple Martins, at least in Canada (Walsh 1978, Table 6). The small quantity of Diptera brought to the former may reflect the relative scarcity of large flies in this area (Turner 1983). I have no information about the relative availability of Odonata in Venezuela and Canada. Chicks of both martins, however, were fed proportionately more dragonflies and fewer syrphids as they grew (Finlay 1971b, Walsh 1978, this study). Since the tropical dragonflies averaged three times larger than the syrphids in the birds of my study (mean dry weights of 93.1 and 32.5 mg, respectively), it may have been more profitable for the adults to collect them, rather than syrphids, once the nestlings were large enough to swallow.

Adult and nestling Southern, Gray-breasted, and Caribbean martins commonly consume Odonata and Lepidoptera (Beebe 1924; French 1976; Collins, unpubl.; Turner, unpubl.). This is in marked contrast to other smaller hirundines which eat few large insects, relying instead mainly on Diptera and Hymenoptera (Beal 1918; Waugh 1979; Turner 1983). Since dragonflies are scarce in cool, cloudy weather (this study), martins then consume other, often smaller, prey. Syrphids are also less active in cloudy weather, which probably explains why they form 24% of the nestling diet of Purple Martins under sunny conditions, but only 3% under cloudy conditions (Spice

1972). Thus, the diet of all species of *Progne* and *Phaeoprogne* is probably affected by bad weather.

Other aspects of feeding ecology also depend on weather conditions and nestling age at least in some hirundines. The size of boluses extracted from immature Brown-chested Martins did not change as the chicks grew and the number of feeding visits per hour increased at only one nest. In contrast, the bolus size of young Purple Martins increases until they are at least three weeks old, especially during the first 10 days after hatching, and the number of feeding visits per hour increases during the first 8–10 days (Finlay 1971b, Walsh 1978). In Finlay's study, feeding rates decreased after day 14, but larger food items were then brought to the nestlings. For British hirundines, the frequency of feeding is also fairly constant after the first one to two weeks of the nestling period (Bryant and Gardiner 1979, Turner 1980). Thus, the daily food intake varies little after an initial period of rapid increase.

Among Purple Martins, parents feed their chicks less frequently during rain, overcast skies, and temperatures below 13°C (Finlay 1971b). Brown-chested Martins also made fewer feeding visits and took longer to collect a bolus of food in bad weather, although daytime temperatures in my study did not fall below 23°C. The low feeding frequency of both species is probably due to the scarcity of food in bad weather at Guanare and in temperate areas (Turner 1980, this study). Wet weather also reduced the number of feeding sites used by Brown-chested Martins as it does in British hirundines (Waugh 1978).

Weather, and consequently feeding conditions, thus influence the incubation behavior and feeding ecology of both temperate and at least one tropical species of martin despite the warmer temperature of the tropical site.

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RECENT PUBLICATIONS

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