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NEST ATTENTIVENESS IN HUMMINGBIRDS

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ABSTRACT.—With few exceptions, nest building, incubation, and care of young are the responsibilities of the female in hummingbirds (Trochilidae). The time females spent on these tasks (collectively defined as attentiveness) was determined for three species of hummingbirds nesting in southeastern Arizona and southwestern New Mexico, i.e., the Broad-billed (*Cynanthus latirostris*), Violet-crowned (*Amazilia violiceps*), and Black-chinned (*Archilochus alexandri*) hummingbirds. In addition to elucidating attentiveness, the data from my study also provide insights into the allocation of time for maintenance and other activities. This information, combined with that from other studies, shows a remarkable uniformity in attentiveness in the Trochilidae regardless of the taxa or geographic areas involved.
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With few exceptions, nest building, incubation, and care of young are the responsibilities of the female in hummingbirds, with males rarely participating in reproduction beyond copulation. In addition to carrying out these responsibilities, female hummingbirds must also tend to their own needs, such as food procurement, plumage maintenance, and predator avoidance. The allocation of time to this array of tasks is also influenced by a number of other factors, including the availability of resources, weather conditions, and interactions among individuals and taxa. With such factors and the demands of non-reproductive activities in mind, I examined nest attentiveness in nesting Broad-billed (*Cynanthus latirostris*), Violet-crowned (*Amazilia violiceps*), and Black-chinned (*Archilochus alexandri*) hummingbirds in southwestern New Mexico and southeastern Arizona. My focus was on determining the time allotted by individual females to the tasks of nest building, incubation, and care of young. These findings are presented along with comparisons to hummingbird attentiveness in other studies. In general, hummingbirds show similar attentiveness patterns, particularly as regards incubation and to lesser degrees with other stages of the reproductive cycle.

STUDY AREAS AND METHODS

Three areas were selected for this study; all lacked artificial food sources such as hummingbird feeders or extensive areas of cultivated plants. The first and largest of these was Guadalupe Canyon, situated along the United States-Mexico border in southwestern New Mexico (Hidalgo Co.) and southeastern Arizona (Cochise Co.). Hummingbirds regularly nesting in this area include the Broad-billed, Violet-crowned, and Black-chinned, while Costa's Hummingbird (*Calypte costae*) nests occasionally (Baltosser 1986b, 1989a, 1989b) and the Lucifer Hummingbird (*Calothorax lucifer*) has nested at least once (Scott 1994).

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The second area was a segment of Rucker Canyon which lies on the west side of the Chiricahua Mountains in Cochise Co. in southeastern Arizona. Black-chinned Hummingbirds were the primary species at this site, with a few Magnificent Hummingbirds (*Eugenes fulgens*) also nesting (Baltosser 1986b). The third and most northern of the areas was along the Gila River near the town of Cliff, Grant County, New Mexico (Baltosser 1986a). The Black-chinned Hummingbird was the only hummingbird to nest at this site (for map and extensive description of each area see Baltosser 1986b).

I recorded periods of attentiveness in nesting female hummingbirds during 209 h of observation in the summer of 1976. My data sets are based on six nests and 17.5 h of observation for Broad-billed Hummingbirds, five nests and 26.1 h for Violet-crowned Hummingbirds, and 46 nests and 165.6 h for Black-chinned Hummingbirds (25 nests and 67.4 h for Guadalupe Canyon, 11 nests and 50.5 h for Rucker Canyon, and 10 nests and 47.7 h for Cliff). Only sessions (attentive periods) and recesses (periods away from nest) thought to have begun and ended spontaneously have been included in my study in order to eliminate unnaturally short or long intervals (see Skutch 1962). Nests were randomly selected for intensive study (stratified random sampling) and they were monitored from vantage points far enough away to prevent my interfering with natural events. Events were timed using a stopwatch and chronicled with the aid of a tape recorder.

My periods of observation were 1–4 h, and I stratified these into morning (06:00–10:00), mid-day (11:00–16:00), and evening (17:00–20:30) segments to gather data when ambient temperatures were lowest (morning hours), highest (mid-day), and intermediate (evening). Observations scheduled in this manner also allowed me to gather data for the period following the nocturnal fast (morning) and prior to the onset of fasting (evening). A tally of the hours that I devoted to each period by species and area was maintained, so that the observer effort would be similar for each.

Observations of nest attentiveness were further broken down by stage of the nesting cycle, which I categorized as (1) nest construction, (2) incubation, (3) care of smaller young, and (4) care of larger young. My reason for having two categories for the care of young was to allow for the detection of any differences in attentiveness due to differences that might exist in the energy needs of the chicks. Small young in my study are defined as nestlings of approximately 1–7 days in age, whereas large young are defined as nestlings in excess of seven days of age.

In this study, I depict nest attentiveness in terms of the average duration (data pooled) of sessions and recesses for each stage, species, and area. These data have in turn been standardized to compare the frequency of the females' arrivals and departures (number on/off bouts) on an hourly basis (collectively referred to as their activity budget). Diurnal fluctuations in attentiveness (e.g., morning vs evening) are based on the duration of sessions and recesses during morning, mid-day, and evening periods. Data within these three periods were averaged and then ranked for each species, stage of nesting, and area. Rankings show the relative duration of sessions and recesses throughout the day (e.g., morning sessions the shortest of the day, afternoon sessions the longest, and evening sessions of intermediate duration). The frequency of "unscheduled" disruptions (e.g., sudden presence of a conspecific, another species, predator, or a passing vehicle near the nest) and their influence upon attentive patterns was enumerated via direct observation.

Statistical comparisons were made using nonparametric analyses of variance (Kruskal-Wallis), coupled with multiple comparison tests (see Day and Quinn 1989). Modified nonparametric Student-Newman-Keuls' multiple range tests (SNK) and Tukey's honestly significant difference tests (HSD) were used because they represent the extremes in performance of *a posteriori* multiple comparison methods (Pimentel and Smith 1990). SNK tends to form too many nonsignificant subsets (high error rate) and HSD too few (lower error

TABLE 1

DURATION (MIN) OF SESSIONS (ON) AND RECESSES (OFF) OF HUMMINGBIRDS IN GUADALUPE CANYON FOR ALL STAGES OF NESTING[a]

	Broad-billed (A)		Violet-crowned (B)		Black-chinned (C)		Significance among species (*)		
Stage	On	Off	On	Off	On	Off	Species	On	Off
Construction	N = 1		N = 1		N = 8				
Mean	1.5	1.1	0.6	0.5	1.2	3.0	A-B	—	—
SD	2.1	0.7	0.2	0.04	0.7	2.7	A-C	—	—
Effort	6.1	3.2	42.2	29.6	194.6	480.8	B-C	*	*
Incubation	N = 3		N = 2		N = 16				
Mean	17.3	4.7	15.1	5.6	9.1	3.8	A-B		
SD	7.6	1.9	8.2	1.5	5.8	2.4	A-C	*	
Effort	435.0	125.4	247.9	101.3	1274.8	520.1	B-C		
Small young			N = 1		N = 4				
Mean	—	—	10.2	7.1	5.5	9.9	A-B	—	—
SD	—	—	4.4	0.5	2.8	6.8	A-C	—	—
Effort	—	—	165.5	126.2	314.0	405.1	B-C		
Large young	N = 2		N = 3		N = 5				
Mean	2.2	17.9	0.8	22.8	1.8	26.7	A-B		
SD	2.0	5.5	0.3	10.4	1.7	9.8	A-C		
Effort	49.9	209.7	24.7	658.2	45.2	475.2	B-C		

[a] N = Number of nests sampled, Effort = total observation time (minutes).

rate). I used SNK to gauge the results of HSD and, of 72 comparisons, the two methods differed in only 14 instances (19%). The 14 differences were distributed among the four stages as follows: construction (12%), incubation (4%), small-young (3%), and large-young (0%). I have been conservative in that my findings are based on Tukey's HSD, with the level of significance set at $P < 0.05$.

RESULTS

Duration of Alternating Bouts

Hummingbirds in Guadalupe Canyon.—During nest construction a rapid pace of sessions and recesses occurs (Table 1), punctuated by extended recesses. Black-chins completed an average of 10 on/off bouts averaging 1.2 and 3.0 minutes, respectively, before taking recesses that averaged 15.8 min. Violet-crowns completed an average of 14 on/off bouts before recesses averaging 9.2 min were taken. Data for Broad-bills are limited, but additional observations (untimed) suggest that attentiveness in nest construction is similar to the above. Attentiveness among species for the remaining stages of the nesting cycle showed generally similar patterns (Table 1). The only significant differences in incubation were in the length

TABLE 2

DURATION (MIN) OF SESSIONS (ON) AND RECESSES (OFF) OF BLACK-CHINNED HUMMINGBIRDS AMONG THREE AREAS FOR ALL STAGES OF NESTING[a]

	Guadalupe (G)		Rucker (R)		Cliff (C)		Significance among areas (*)		
Stage	On	Off	On	Off	On	Off	Area	On	Off
Construction	N = 8		N = 1		N = 2				
Mean	1.2	3.0	0.9	2.4	0.5	0.5	G-R		
SD	0.7	2.5	0.4	1.6	0.3	0.01	G-C	*	*
Effort[a]	194.6	480.8	11.4	21.5	16.4	24.5	R-C	*	
Incubation	N = 16		N = 10		N = 7				
Mean	9.1	3.8	8.9	3.9	17.1	7.0	G-R		
SD	5.8	2.4	4.9	2.2	10.4	3.0	G-C	*	*
Effort[a]	1274.8	520.1	863.8	339.0	545.9	224.9	R-C	*	*
Small young	N = 4		N = 3		N = 5				
Mean	5.5	9.9	13.1	17.0	11.7	12.8	G-R	*	*
SD	2.8	6.8	6.8	9.0	4.1	5.3	G-C		
Effort[a]	314.0	405.1	268.8	421.4	356.2	392.4	R-C		
Large young	N = 5		N = 2		N = 3				
Mean	1.8	26.7	0.8	13.5	0.7	25.9	G-R		
SD	1.7	9.8	0.1	1.2	0.3	6.0	G-C		
Effort[a]	45.2	475.2	8.2	149.1	15.0	605.5	R-C		

[a] N = Number of nests sampled, Effort = total observation time (min).

of sessions between Broad-bills and Black-chins. For both the small-young and large-young stages, there were no significant differences among species.

Black-chinned Hummingbirds.—I found no significant differences among stages between Guadalupe and Rucker canyons, except for the small-young stage (Table 2). In this case, sessions and recesses were shorter in Guadalupe Canyon. Comparisons between Guadalupe Canyon and Cliff showed significant differences in the construction and incubation stages. Sessions/recesses were longer in Guadalupe Canyon during construction, whereas they were longer during incubation at Cliff. Between Rucker Canyon and Cliff, significant differences existed between construction and incubation. Construction sessions were longer in Rucker Canyon (recesses did not differ between the two areas), while on/off bouts during incubation were significantly shorter in Rucker Canyon.

Activity Budgets

Nest construction.—Female Broad-billed Hummingbirds spent 59.8% of each hour on the nest, while the remaining 40.2% was spent away

TABLE 3

COMPARISONS AMONG STAGES OF NESTING SHOWING THE PERCENTAGE OF TIME NESTING FEMALE HUMMINGBIRDS SPENT ON AND OFF NESTS AND THE ASSOCIATED NUMBER OF BOUTS (SCALED FOR 1-H INTERVALS)

Stage	Broad-billed Guadalupe	Violet-crowned Guadalupe	Black-chinned Guadalupe	Black-chinned Rucker	Black-chinned Cliff
Construction					
On	59.8	56.4	29.2	28.0	47.6
Bouts	23.4	56.4	14.8	19.0	59.0
Off	40.2	43.6	70.8	72.0	52.4
Bouts	23.0	56.0	14.0	18.4	59.0
Incubation					
On	84.3	76.6	75.0	74.0	76.7
Bouts	2.9	3.0	4.9	4.9	2.7
Off	15.7	24.4	25.0	26.0	23.3
Bouts	2.0	2.6	4.0	4.0	2.0
Small young					
On	—	64.7	36.6	43.7	57.3
Bouts	—	3.8	4.0	2.0	2.9
Off	—	35.3	63.4	56.3	42.7
Bouts	—	3.0	3.9	2.0	2.0
Large young					
On	10.8	3.8	9.0	6.9	3.5
Bouts	3.0	3.0	3.0	5.0	3.0
Off	89.2	96.2	91.0	93.1	96.5
Bouts	3.0	2.5	2.1	4.1	2.2

(Table 3). They averaged 23.4 attentive bouts (mean duration 1.5 min, Table 1) and 23.0 inattentive bouts (mean 1.1 min, Table 1) per hour (Table 3). Violet-crowned Hummingbirds were similar to Broad-bills but they differed from syntopic Black-chins in that the latter spent less time at the nest and had fewer bouts. Black-chins in Rucker Canyon were similar to those in Guadalupe Canyon, whereas those at Cliff were intermediate between these two populations and Broad-bills and Violet-crowns in Guadalupe Canyon (Table 3).

Incubation.—Attentiveness for this stage of the nesting cycle was similar for all species and areas in my study. Black-chins in Guadalupe and Rucker canyons and Violet-crowns spent virtually the same percentage of time on and away from nests, but this was achieved through different strategies (Table 3). Black-chins exhibited a greater frequency of on/off bouts (Table 3), and these were of shorter duration than those of Violet-crowns (Table 1). Broad-bills spent more time on their nests than either of the above species, were away less, and had fewer bouts (Table 3). Black-chins at Cliff were similar to all other species, although the frequency of on/off bouts was most like Broad-bills (Table 3).

Small young.—In one segment of Guadalupe Canyon, I was able to observe a Violet-crowned nest and a Black-chinned nest simultaneously. The Black-chinned under surveillance was generally present when the Violet-crowned was away and absent when it was present. Additionally, the Violet-crowned was on its nest about the same average time that Black-chins in the canyon were away and vice versa (Table 3). Black-chins at Rucker and Cliff spent more time on their nests and were away for shorter periods than Black-chins in Guadalupe Canyon. Black-chins at all three sites had shorter sessions and longer recesses than Violet-crowns (Table 3).

Large young.—All species in Guadalupe Canyon showed similar attentiveness patterns, although Violet-crowns averaged less time on the nest than Black-chins and Broad-bills (Table 3). Attentiveness in Black-chins in Rucker Canyon was similar to that in this species in Guadalupe Canyon, except that the former had shorter recesses (Table 1 and Table 2) and thus more bouts (Table 3). Black-chins at Cliff differed from those in Guadalupe and Rucker canyons in terms of the number of bouts and in total time spent on and away from nests. In these respects, this population was more like Violet-crowns than other Black-chinned populations.

Feeding young.—The time females spent feeding young did not differ significantly among species or areas. Feeding sessions in Broad-bills averaged 44 sec (N = 13, SD = 19.3), which is the same as in Violet-crowns (N = 46, SD = 18.1). Black-chins in Guadalupe and Rucker canyons had the same average time, which amounted to 51 sec (N = 30, SD = 20.4 and N = 20, SD = 23.2, respectively). The feeding sessions in Black-chins at Cliff averaged 43 sec (N = 29, SD = 16.3).

Diurnal Patterns

Hummingbirds in Guadalupe Canyon.—Attentiveness during incubation was shortest in the morning, longest during mid-day, and intermediate during the evening (Fig. 1). Recesses for all species were longest in the evening, which is the period preceding the nighttime fast. Violet-crowns differed from Broad-bills and Black-chins (morning recesses shortest and intermediate during mid-day) in that their recesses were of intermediate duration during mornings and shortest during mid-day.

Data for Broad-bills during the small-young stage are limited to casual observations, and thus comparisons are restricted to Black-chins and Vi-

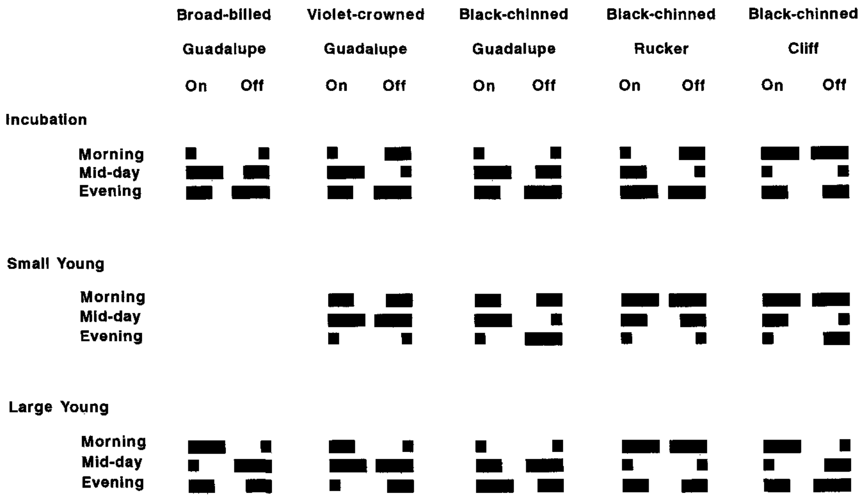

FIG. 1. Diurnal patterns in attentive behavior among species and areas for different stages of nesting; duration of bouts shortest (smallest polygon), duration intermediate in length (medium polygon), and duration longest (largest polygon; bout duration based on morning, mid-day, and evening averages).

olet-crowns (Fig. 1). Sessions were shortest during evening hours, longest during mid-day, and of intermediate length during mornings, which is the first opportunity to renew energy levels following nocturnal fasting. Recesses for both species were of intermediate length during morning hours. They were longest for Violet-crowns during mid-day and for Black-chins during the evening.

When large young were present, each of the three species exhibited a different pattern with regard to the duration of sessions (Fig. 1). However, all species exhibited the same pattern for recesses in that they were shortest in the morning, longest during mid-day, and of intermediate duration during evening periods. Comparisons among species show no other shared patterns *within* stages of nesting, and relatively few patterns were the same when comparisons were made *among* stages (Fig. 1).

Black-chinned Hummingbirds.—Comparisons among areas reveal that a number of patterns were similar in this species (Fig. 1). For example, incubation sessions in Guadalupe and Rucker canyons were shortest during mornings, which was in marked contrast to Cliff where they were longest (response to lower ambient temperature?). Recesses were shortest during mid-day in Rucker Canyon and Cliff, whereas they were longest during evening hours in Guadalupe and Rucker canyons.

The single feature in common among areas was during the small-young stage (Fig. 1), with sessions shortest during evening hours (the last opportunity to renew energy reserves prior to nocturnal fasting). At Rucker Canyon and Cliff, sessions and recesses were longest during morning hours (first opportunity after the nighttime fast to renew energy levels). Mid-day recesses were of intermediate duration in Rucker Canyon and shortest in Guadalupe Canyon and Cliff.

When large young were present, sessions in Rucker Canyon and Cliff were shortest during mid-day, longest in the morning, and of intermediate duration during evening hours (Fig. 1). In Guadalupe Canyon, sessions were shortest in the morning and longest in the evening. Recesses were shortest during mornings in Guadalupe Canyon and Cliff, but in Rucker Canyon they were longest. Recesses were of intermediate duration in the evening for Guadalupe and Rucker canyons (they were most lengthy at Cliff).

Nest Defense

Females often reacted to intrusions by other animals (even machinery) when these transgressions were into areas near their nests (Table 4). In some instances, this involved scolding or even attack by the female. Disruptions at other times resulted in the female disappearing for a brief period, whereas in other cases they evidenced "curiosity" at the intrusion. Conspecifics were the major cause of nest defense by Black-chins in Guadalupe and Rucker canyons. Black-chins rarely responded in this manner at Cliff, even though in several instances incubating females were within sight of each other. Interspecific intrusions were also the major cause of nest defense in Violet-crowns. In Broad-bills, nest defense was less frequent but it was elicited equally by incursions by conspecifics and other hummingbirds.

DISCUSSION

Diurnal Patterns

The incubation and small-young stages of the nesting cycle were most similar to one another (Table 1). By contrast, the construction and large-young stages had little in common and were each very different from the other two stages. These relationships (or lack thereof) can be interpreted in a number of ways. However, I assume that the similarity between the incubation and small-young stages was due, at least in part, to thermal constraints, small young being somewhat ectothermic after hatching. On the other hand, large young are farther along in their development and thus would not be expected to make the same demands upon the female as developing embryos or small young, which is also true of nest con-

TABLE 4

FACTORS THAT INDUCED FEMALE BROAD-BILLED (BB), VIOLET-CROWNED (VC), AND BLACK-CHINNED (BC) HUMMINGBIRDS TO LEAVE THEIR NESTS[a]

	Distractions/h by area and hummingbird species				
	Guadalupe Canyon			Rucker Canyon	Cliff
Source of distraction	BB	VC	BC	BC	BC
Cooper's Hawk (*Accipiter cooperii*)	—	—	—	0.02	—
American Kestrel (*Falco sparverius*)	—	0.04	0.02	—	—
Broad-billed Hummingbird (*Cynanthus latirostris*)	0.11	0.08	—	—	—
Violet-crowned Hummingbird (*Amazilia violiceps*)	0.17	—	0.02	—	—
Magnificent Hummingbird (*Eugenes fulgens*)	—	—	—	0.08	—
Black-chinned Hummingbird (*Archilochus alexandri*)	0.06	0.19	0.28	0.18	0.02
Hummingbird spp. (Trochilidae)	—	—	0.06	0.02	—
Acorn Woodpecker (*Melanerpes formicivorus*)	—	—	—	0.02	—
Gila Woodpecker (*Melanerpes uropygialis*)	—	—	0.02	—	—
Ash-throated Flycatcher (*Myiarchus cinerascens*)	—	—	0.06	—	—
Brown-crested Flycatcher (*Myiarchus tyrannulus*)	—	—	0.02	—	—
Cassin's Kingbird (*Tyrannus vociferans*)	—	—	0.05	—	—
Thick-billed Kingbird (*Tyrannus crassirostris*)	—	0.08	0.02	—	—
Gray-breasted Jay (*Aphelocoma ultramarina*)	—	—	0.05	—	—
Northern Mockingbird (*Mimus polyglottos*)	—	—	0.02	—	—
Summer Tanager (*Piranga rubra*)	—	0.04	0.05	—	0.02
Black-headed Grosbeak (*Pheucticus melanocephalus*)	—	—	—	0.02	—
Canyon Towhee (*Pipilo fuscus*)	—	—	0.03	—	—
Hooded Oriole (*Icterus cucullatus*)	—	0.04	0.12	—	—
Evening Grosbeak (*Coccothraustes vespertinus*)	—	—	—	0.02	—
Unknown bird species	—	—	0.02	0.04	—
Cattle (*Bos taurus*)	—	0.04	—	—	—
People (*Homo sapiens*)	0.06	—	0.03	0.02	0.06
Bumblebee (*Bombus* sp.)	—	—	—	—	0.02
Pipevine Swallowtail Butterfly (*Battus philenor*)	—	—	0.02	—	—
Unknown	0.06	0.04	—	—	—
Total number of distractions/hour	0.46	0.55	0.89	0.42	0.12

[a] Broad-billed observations based on six nests and 17.5 h of direct observation; Violet-crowned observations based on five nests and 26.1 h of direct observation; Black-chinned observations for Guadalupe Canyon based on 25 nests and 67.4 h, for Rucker Canyon 11 nests and 50.5 h, and for Cliff 10 nests and 47.7 h of direct observation.

struction. I have confined my discussion of diurnal patterns in attentive behavior (Fig. 1) to the incubation and small-young stages and, in turn, to hummingbirds in Guadalupe Canyon. This was done to avoid the confounding effects of differing selective pressures during other stages in the nesting cycle and among geographic areas.

Incubation.—A consistent pattern of nest attentiveness relative to time of day was evident among the hummingbirds in Guadalupe Canyon (Fig.

1). Morning sessions were shortest, which may well have resulted from the needs of females to feed themselves after the nocturnal fast, balanced against meeting the requirements of the developing embryos. Mid-day sessions were longest during incubation when temperatures were highest (average ambient temperatures [shade] of 32.6°C [SD = 0.8], with extremes of 31 to 38°C). This is contrary to many published expectations (e.g., Kendeigh 1952, 1963; von Haartman 1956; White and Kinney 1974) which suggest the existence of an inverse correlation between temperature and attentiveness. The intermediacy of evening sessions (Fig. 1) and the duration of evening recesses (longest of day for each species) are believed to represent periods of crop-filling anticipatory to evening fasting. Such an explanation is consistent with the feeding behavior of both free-living and captive hummingbirds (Beuchat et al. 1979, Wheeler 1980, Powers and Nagy 1988, Tiebout 1989, Powers 1991).

My findings regarding mid-day sessions might be interpreted as females shading their eggs (see Wolf 1964, Vleck 1981). However, female posture on the nest, and the fact that nests were not in direct sunlight, does not support this interpretation. Instead, the results might indicate that females remained on the nest as a way of minimizing energy expenditures or be a strategy for heat dissipation without excessive water loss (see Ricklefs 1971, 1974; Calder 1974). Another possibility is that females remained at the nest to foil ectothermic predators (e.g., snakes), many of which are most active during the warmer portion of the day.

Small young.—Attentive patterns of Violet-crowned and Black-chinned hummingbirds generally were similar (Fig. 1; data for Broad-bills lacking). Afternoon sessions were longest, which strengthens the argument that temperature and attentiveness were not inversely related. The intermediacy of sessions in both species during morning sessions contrasts with that for incubation when sessions were shortest. This may indicate that newly hatched young either (1) required more parental care than developing embryos or (2) that females expended less nighttime energy and could "afford" to remain at the nest longer. That evenings were used to "tank up" prior to fasting is supported in Black-chins by the fact that sessions were shortest and recesses longest during this stage (same pattern as in incubation).

Violet-crowned Hummingbird attentiveness during the evening period differed from that of Black-chins, being marked by the shortest sessions and recesses of the day. When the female was not at her nest, she was often perched in sight of it for relatively long periods. This might suggest that this period was not important for replenishing nectar supplies. However, plentiful and nearby Parry agaves (*Agave parryi*) were beginning to produce large quantities of nectar at this time (Baltosser 1989b), thus providing an abundance of food. This fact, plus the dominance of the Violet-crowned over Black-chinned and Broad-billed hummingbirds (Baltosser 1989b), may well have allowed the former to "refuel" more quickly (see Howell and Dawson 1954 for pertinent discussion).

Attentiveness Strategies

In most birds in which only one sex tends the eggs (excluding certain nidifugous species), the eggs are incubated 60–80% of the daylight hours (Skutch 1962). These levels of attentiveness curtail foraging, and under some circumstances, incubating birds may have difficulty finding enough food to maintain themselves (Skutch 1962, Walsberg 1983, Williams 1993). When levels fall below 60%, hatching may be retarded. However, an increase in levels above 70–80% does not necessarily shorten the incubation period (Skutch 1962).

In my study, the percentage of time hummingbirds covered their eggs during incubation was similar among the three species (Table 3). Black-chins and Violet-crowns in Guadalupe Canyon were very similar, as was the case for Black-chins among areas ($\bar{x}$ = 75.2%, SD = 1.4). However, despite the uniformity in overall time spent at the nest, the way in which it was partitioned varied among species. For example, Broad-billed and Violet-crowned hummingbirds had relatively few on/off bouts, which were relatively longer (Table 1). By contrast, Black-chinned Hummingbirds had shorter sessions and recesses (at least for Guadalupe and Rucker canyons) which resulted in more bouts.

Disruptions

Nest attentiveness during incubation and care of small young is clearly affected by what might be termed "intrinsic" considerations, e.g., thermoregulation, self-maintenance, and feeding of young. In addition, "extrinsic" considerations also affect attentiveness, the most important of which is intrusions into the nest area by other animals. Whether the intruders are potential competitors, predators, or neutral in intent, female hummingbirds can respond in one of two ways: passively or actively. Two opposing tendencies are thus exhibited by female hummingbirds while sitting on their nests: (1) to passively reduce interactions centered around the nest and (2) to actively defend the nest against intruders (Wolf and Wolf 1971, present study).

Comparative material is virtually lacking, but in the Purple-throated Carib (*Eulampis jugularis*), Wolf and Wolf (1971) found that nest defense was strongest against birds that posed the greatest source of danger; it declined as this potential diminished. Female Caribs often, though not inevitably, responded to intrusions by leaving the nest in pursuit. Large passerines were responsible for 51% of all disruptions, followed in descending order by small passerines (29%), conspecifics (12%), and other hummingbirds (9%).

Responses similar to those of the Purple-throated Carib were seen in my study when females were faced with intrusions by animals near their nests. However, compared to the Caribs, intrusions by conspecifics and other hummingbirds played a more prominent role (Table 4). Conspecifics were the major single source of disruption for Black-chins in both Guadalupe and Rucker canyons, amounting to 34% and 43%, respectively. The impact of other hummingbirds on this species was less in both areas, being only 9% and 24%, respectively. In Guadalupe Canyon, the impact of all other species on Black-chins was 57%, of which most were attributable to large passerines (Table 4). For Black-chins in Rucker Canyon, 34% of all interactions resulted from other non-hummingbird species, primarily large passerines. Black-chins were the only nesting hummingbird at Cliff, and despite the presence of an occasional migrant Broad-tailed (*Selasphorus platycercus*), Rufous (*Selasphorus rufus*), or Calliope (*Stellula calliope*), were not disrupted by these hummingbirds. Overall, disruptions at this site were minimal, with 50% being generally attributable to human interference.

Conspecific intrusions were not a factor for Violet-crowns, as the species was relatively rare and nests were widely dispersed. However, intrusions by Black-chinned and Broad-billed hummingbirds accounted for 50% of all cases in which Violet-crowns left their nest. Larger passerines were the other major source of disruption, accounting for 29% of the intrusions to which Violet-crowns responded. In Broad-billed Hummingbirds, conspecific intrusions accounted for 25% of the aggressive responses by this species. In addition, defense of the nest against other hummingbirds accounted for 50% of the responses of nesting Broad-bills.

The potential impact of intrusions around the nest can be examined by noting how frequently females left their nests and their fledging success. Comparisons of species nesting in Guadalupe Canyon show a significant inverse correlation between these parameters ($r = -0.996$, df $= 1$, $P < 0.05$), based on 6663 minutes (111 h.) of intensive observation at 36 nests (Baltosser 1986b). On average, fledging success for Black-chins was 44%, with nearly one intrusion/hour (Table 4), 60% for Violet-crowns with just over 0.5 intrusions/hour (Table 4), and 66.7% for Broad-bills with just under 0.5 intrusions/hour (Table 4). Black-chinned nesting success vs intrusion rate was not significantly correlated in Rucker Canyon or at Cliff.

Comparing attentiveness at successful nests vs those that were unsuccessful is another way of assessing the impact of intrusions around the nest. Because of limited sample size, this is possible only for Black-chinned Hummingbirds, and then only during incubation (stage with greatest mortality, see Baltosser 1986b). Attentiveness for Black-chins in Guadalupe Canyon that fledged averaged 75% (SD = 7.4, Range = 66–84%) and unsuccessful nests averaged 67% (SD = 10.7, Range = 50–81%). In Rucker Canyon, attentiveness was reversed, i.e., percentages for nests that fledged were lower ($\bar{x}$ = 71%, SD = 10.4, Range = 61–84%) than those which failed ($\bar{x}$ = 76%, SD = 3.9, Range = 71–81%). Black-chins at Cliff that were successful had greater attentiveness ($\bar{x}$ = 77%, SD = 7.2, Range = 68–86%) than those that were unsuccessful ($\bar{x}$ = 71%, SD = 5.8, Range = 67–75%).

Attentiveness in the Trochilidae

The data presented in this paper on nest attentiveness during incubation are compared with those on other hummingbirds in Table 5. In addition to studies already cited, this table includes data from Orr (1939), Skutch (1951, 1958, 1964, 1967), Calder (1971, 1975), Smith et al. (1974), and Montgomerie and Redsell (1980). Data are arranged by species and by the primary area in which each nests (i.e., temperate, subtropical, and tropical latitudes). Collectively, these data show that hummingbirds are similar in incubation attentiveness regardless of species and latitude. This suggests the existence of a fixed requirement for this stage of reproduction, which hummingbirds have been able to meet effectively throughout a wide variety of nesting habitats (Vleck 1981).

Aside from the present study, comparative data for other stages of the nesting cycle are generally unavailable for most hummingbirds. However, comparisons are possible based on Wolf and Wolf's study (1971) of the Purple-throated Carib and that of Bené (1940) on the Black-chinned Hummingbird. Female Caribs with small young spent 59.5% of each hour at the nest, compared to 57–59% for Black-chins in the study by Bené. These percentages are similar to my findings on Violet-crowned Hummingbirds in Guadalupe Canyon and nearly identical to Black-chins at Cliff (Table 2). Attentiveness in Black-chins in Guadalupe Canyon at this stage was only 36.6%, while that in Rucker Canyon was 43.7%.

For nests having large young, data from Wolf and Wolf (1971) shows attentiveness to average 8.5% (range 5.7–13.4%), based on three days of observation. This average is nearly the same as the 9% obtained for Black-chins by Bené (1940), and these are very similar to the 10.8% in Broad-bills and 9.0% in Black-chins I found in Guadalupe Canyon. In contrast, my figures were 3.8% for Violet-crowns, 3.5% for Black-chins at Cliff, and 6.9% for Black-chins at Rucker Canyon.

Wolf and Wolf (1971) found that feeding bouts for young in Purple-throated Caribs averaged 38 sec (SD = 11). This is similar to the 44 sec

TABLE 5

COMPARISONS AMONG TEMPERATE, SUBTROPICAL, AND TROPICAL NESTING HUMMINGBIRDS SHOWING UNIFORMITY IN ATTENTIVENESS DURING INCUBATION

Species of hummingbird	Average length (min.)		Percent attentive	Source
	Sessions	Recesses		
		Temperate		
Black-chinned Hummingbird	6.3	2.3	70	Vleck 1981
(*Archilochus alexandri*)	8.9	3.9	74	Baltosser, present study
	17.1	7.0	77	Baltosser, present study
	9.1	3.8	75	Baltosser, present study
Anna's Hummingbird	14.5	6.4	69	Calder 1975
(*Calypte anna*)	15.5	2.8	84	Howell and Dawson 1954
	8.5	2.2	79	Smith et al. 1974
	8.1	3.0	75	Vleck 1981
Costa's Hummingbird (*Calypte costae*)	15.8	2.4	83	Vleck 1981
Broad-tailed Hummingbird	7.7	2.1	78	Calder 1975
(*Selasphorus platycercus*)	—	—	72	Montgomerie and Redsell 1980
Allen's Hummingbird (*Selasphorus sasin*)	4.6	1.4	77	Orr 1939
Calliope Hummingbird (*Stellula calliope*)	7.3	2.0	77	Calder 1971
		Subtropical		
Violet-crowned Hummingbird (*Amazilia violiceps*)	15.1	5.6	77	Baltosser, present study
Broad-billed Hummingbird (*Cynanthus latirostris*)	17.3	4.7	84	Baltosser, present study
White-eared Hummingbird (*Hylocharis leucotis*)	9.1	4.0	70	Skutch 1962
		Tropical		
Violet Sabrewing (*Campylopterus hemileucurus*)	42.8	24.0	64	Skutch 1967
Purple-throated Carib (*Eulampis jugularis*)	—	—	69	Wolf and Wolf 1971
Violet-headed Hummingbird (*Klais guimeti*)	40.6	15.2	73	Skutch 1958
White-crested Coquette (*Lophornis adorabilis*)	11.9	6.4	64	Skutch 1962
Scaly-breasted Hummingbird (*Phaeochroa cuvierii*)	20.9	6.9	76	Skutch 1962
Little Hermit	24.7	11.7	67	Skutch 1951
(*Phaethornis longuemareus*)	40.7	16.4	71	Skutch 1962
	36.9	15.3	70	Skutch 1964

that I found in Broad-billed and Violet-crowned hummingbirds and to the 43 sec in Black-chins at Cliff. Black-chins in Guadalupe and Rucker canyons had bouts that averaged 51 sec, which is similar to what can be deduced for this species from Bené (1940).

SUMMARY AND CONCLUSIONS

Hudson (1920) and Woods (1927) were among the first to comment on the uniformity of general life-history traits among hummingbirds. Pitelka (1942) noted that this degree of uniformity is perhaps as extreme as that in any group of similar taxonomic rank. The data from the present study, coupled with those cited within, demonstrate considerable uniformity in nest attentiveness within the Trochilidae. This is best exemplified during incubation, but evidence of behavioral consistency is shown in all stages. This is remarkable, given the disparity among the species and latitudes from which comparative data were obtained.

The three hummingbird species that I studied in Guadalupe Canyon exhibited similar attentiveness during the incubation and small-young stages, i.e., stages of development when embryos and young were perhaps most vulnerable to thermal fluctuations. Anticipatory feeding was common and often characterized the behavior of female hummingbirds during hours immediately preceding the nocturnal fast. During morning hours when ambient temperatures were lowest, the need to replenish energy reserves depleted during the night was apparent in the behavior of nesting females. However, presumably because of thermoregulatory needs of embryos and newly-hatched young, attentive patterns seem to reflect a compromise between the female's needs and those of her brood.

Lengths of sessions and recesses can provide insight into resource availability and the competitive environment among hummingbirds. Factors that increase the comings and goings from a nest beyond those essential for self-maintenance, incubation, or the feeding of young may play a critical role. Success vs failure may hinge on extrinsic items that increase the number of unscheduled departures from the nest. For example, escalating the number of departures from a nest may increase predation through nest betrayal (Skutch 1949, 1962). Low constancy during incubation may also result in the death of embryos and young (e.g., Grant 1982) or prolong incubation (Pienkowski 1984) and, thereby, the risk of nest predation (Byrkjedal 1985).

Correlation is not the strongest form of inference (e.g., see Eberhardt 1970, Romesburg 1981), but results such as mine can provide valuable insights into biological processes. Given the potential data to be gained by focusing on interactions at the nest, it is surprising that more studies have not pursued this line of investigation. My research and that conducted by Wolf and Wolf (1971) demonstrate the need to investigate the extent to which female hummingbirds are induced by outside forces to leave their nests. The consequences of such disruptions (including frequency and duration) are potentially great and are a much overlooked aspect of the breeding biology of hummingbirds.

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