

SHORT COMMUNICATIONS

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HABITAT SEPARATION AND ARTHROPOD RESOURCE USE IN THREE LESSER ANTILLEAN HUMMINGBIRDS¹

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The main processes governing hummingbird guild organization in specific geographical areas appear to be diffuse coevolution between hummingbird and hummingbird-pollinated flowers, and interspecific competition for floral nectar resources (Grant and Grant 1968, Stiles 1975, Feinsinger 1976, Kodric-Brown et al. 1984, Brown and Bowers 1984). Hummingbird species in the same geographical area exhibit morphological patterns reflecting evolutionary adaptations for competitive interactions with other hummingbirds and for mutualistic interactions with bird-pollinated flowers (Kodric-Brown et al. 1984). Mutualistic interactions of hummingbirds with flowers are considered at least as important (Kodric-Brown et al. 1984, Brown and Bowers 1985) or more so in some communities (Snow and Snow 1972, Stiles 1975) than interspecific competition in determining organization of hummingbird communities.

Habitat separation in hummingbird assemblages is influenced by species' morphological traits, such as body size and bill length and size. Hummingbirds in different size categories can coexist and have overlapping geographical and habitat distributions, while co-occurring species of similar size tend to segregate altitudinally and by habitat (Lack 1973, 1976; Kodric-Brown et al. 1984). Spatial arrangement of sympatric species may be on a more local scale such as different heights within the same habitat (Stiles and Wolf 1970, Snow and Snow 1972, Martin 1988), different portions or layers of vegetation (Feinsinger 1976), or specific flower species or feeding substrates (Stiles 1975, Feinsinger 1976). All resource and habitat partitioning studies, however, involve hummingbirds' use of nectar sources.

Habitat and food resource use of three sympatric hummingbirds in Dominica, West Indies feeding pri-

marily on arthropods were studied. The objective was to quantify habitat and resource partitioning among these species, including pairs of similar and different size and bill morphologies, while feeding on what has been considered a secondary resource in hummingbird diets (Feinsinger 1976, Wolf et al. 1976, Feinsinger and Colwell 1978).

Hummingbird communities in Lesser Antillean islands are generally limited to two species, one large and one small (Lack 1973, 1976; Kodric-Brown et al. 1984). On Dominica, however, three species were encountered in the same areas and elevations. Two species, the Green-throated Carib (*Sericotes holosericeus*) and Purple-throated Carib (*Eulampis jugularis*), have curved bills of similar length (culmen in *Eulampis* = 23.59 mm, *Sericotes* = 22.74 mm, Brown and Bowers 1985) and differ slightly in size (*Eulampis* = 127 mm, *Sericotes* = 120 mm, Bond 1985) but more so in weight (*Eulampis* = 8.67 g, *Sericotes* = 5.60 g, Brown and Bowers 1985). The third species, Antillean Crested Hummingbird (*Orthorhynchus cristatus*), is considerably smaller (89 mm, Bond 1985), lighter (2.70 g, Brown and Bowers 1985), and has a straight bill approximately half the length (culmen = 10.72 mm) of that of the other two species. The Green-throated Carib is distributed on all Lesser Antillean islands in forest clearings and in lowland areas (Lack 1973). The Purple-throated Carib is present in all mountainous islands of the Lesser Antilles except Grenada and occurs regularly in the rain forest and thickets (Lack 1973). The Antillean Crested Hummingbird is the most widespread species of all, occurring on all islands and elevations from sea level to highland areas (Lack 1973).

STUDY AREA AND METHODS

Field work was conducted at the Archbold Tropical Research Center, Springfield Field Station on Dominica, West Indies, between 25 May and 15 June, 1991. The Springfield Field Station is located on the western side of the island spanning 360 to 620 m elevation. The dominant vegetation is lowland rainforest (Bullock and Evans 1990). Distinct arboreal species of this forest

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TABLE 1. Percent of observations of different hummingbird species in different habitats at the Archbold Tropical Research Center, Dominica.

	Habitat (%)			(n)
	Forest	Field	Edge	
<i>Orthorhyncus cristatus</i>	80	4	16	(25)
<i>Eulampis jugularis</i>	100	0	0	(20)
<i>Sericotes holosericeus</i>	0	15	85	(20)
Expected values	62	7	31	

are *Rhyticocos amara* and *Coccoloba venosa* with *Pithecellobium*, *Swartzia*, *Andira*, *Cedrela*, *Myrcia*, *Calophyllum*, and *Bucherevia* as characteristic genera (Nicolson 1991). Interspersed within the dominant primary forest vegetation are patches of secondary forest, including citrus, banana, and coffee orchards, and horticultural plots. Some orchards and horticultural plots were abandoned for several years and were overgrown with vines and other secondary invaders.

Four sites were selected for observation of hummingbird feeding activity: primary forest, a forest gap, an old abandoned field, and the edge area between an old field and primary forest. All sites were located at elevations between 460 and 500 m. The forest site had an average canopy height of 13 m and >95% canopy cover. Visibility at the forest site was limited to 15 m. The forest gap was an 8 × 10 m area of open canopy within the forest, and was dominated by *Heliconia*. The old field was approximately 100 × 150 m with >95% ground cover of vines and other invaders reaching less than 1.5 m in height. Because the highest point in this site was in the middle of the field, only half the field could be observed at any one time. The edge habitat comprised a 50 m area of forest and 5 m into the previously described field. For the purpose of this study the gap was considered edge habitat, and data from the edge and gap sites were combined.

Hummingbird foraging activity was observed for periods of 1–2 consecutive hours between 08:00–11:00 and between 12:00–17:00 e.s.t. for a total of 43 hr, between 25 May and 15 June 1991. Within each site all hummingbird foraging attempts observed were recorded as to location on canopy (upper, middle, bottom, and interior), food (nectar or arthropod), height of foraging (in 3 m categories), and substrate from which food was taken (flower, leaf, branch or trunk, air). To minimize biases introduced by individual birds perhaps temporarily specializing on a specific substrate or prey item, no more than three feeding attempts were recorded for any individual hummingbird. Whether the same individual returned to the observation site at a later time is not known. Territorial *Eulampis* were observed in the study area but were not present at the study sites selected.

The three species were compared using a χ^2 test and where significant differences were found, χ^2 comparisons were made between all species pairs.

RESULTS

During the 43 hours of observation, 18 *Sericotes*, 20 *Eulampis*, and 25 *Orthorhyncus* were observed for a

TABLE 2. Percent usage of foraging substrate by each hummingbird species (number in parentheses is number of observations).

	(n)	Foraging substrate in %			
		Flowers	Leaves	Branches or trunks	Air
<i>Orthorhyncus cristatus</i>	(29)	48	28	21	3
<i>Eulampis jugularis</i>	(26)	62	23	0	15
<i>Sericotes holosericeus</i>	(22)	0	5	9	86
Expected values		39	20	20	31

total of 83 observations, with 33, 23, and 27 for *Orthorhyncus*, *Sericotes*, and *Eulampis* respectively. All three species took nectar only on a few occasions, and fed on arthropods on 86%, 88%, and 100% of feeding attempts in *Orthorhyncus*, *Eulampis*, and *Sericotes*, respectively. Possible explanations for this feeding scheme are presented in Chavez-Ramirez and Dowd (1992). All hummingbirds observed feeding appeared to be trapliners, moving rapidly through the study sites with the exception of two *Sericotes*. The two *Sericotes* observed feeding continuously from a single perch directed their foraging attempts at insect swarms flying near their perch. On each foraging sally between one to five prey items were taken. Neither of the two *Sericotes* behaved territorially in the presence of other hummingbirds.

Differences in habitat use among species were highly significant (Table 1, $\chi^2 = 55.96$, $df = 4$, $P < 0.005$). *Eulampis* was the most selective of the three species and was observed using only forest, while *Sericotes* was observed in open canopy sites (edge and field). *Orthorhyncus* was the only species seen in all three habitats, but it was observed most frequently in forest.

Significant differences were observed between *Sericotes* and the other two species with respect to feeding substrates (Table 2; $\chi^2 = 52.72$, $df = 6$, $P < 0.005$). *Sericotes* took arthropods mainly from the air. They initiated foraging attempts from a perch and then sallied and sally-hovered (Remsen and Robinson 1990) at target prey. *Orthorhyncus* and *Eulampis* took prey by gleaning from plant substrates, primarily flowers. In all pairwise comparisons of species, substrate use was significantly different ($P < 0.005$).

Foraging heights were not significantly different among species but each species foraged preferentially at certain heights. *Orthorhyncus* and *Eulampis* overlapped in their preference for feeding under 3 m, while *Sericotes* fed primarily between 4–6 m.

No significant differences were observed among species in regard to feeding location on canopy of plants ($\chi^2 = 10.6$, $df = 6$, $P < 0.5$). *Orthorhyncus* foraged in all canopy locations but predominantly in the interior of plants. When foraging on or near plants ($n = 5$) *Sericotes* foraged only in the middle and upper portions of the canopy while the *Eulampis* foraged in all locations except the upper canopy.

DISCUSSION

The preferred foraging substrate of *Orthorhyncus* and *Eulampis* was flowers. The fact that the *Orthorhyncus*

and *Eulampis* foraged primarily on *Heliconia* flowers explains why they fed preferentially below 3 m. *Heliconia*, which was the most common flowering plant observed in the forest and gap sites during the study period, has inflorescences approximately 1.5 m in height. *Sericotes* took flying arthropods primarily between 4 and 6 m in height. It is not known if flying insects are more common at certain heights or if *Sericotes* has an easier time feeding at this height.

The two caribs, similar in size and bill morphology, did not overlap in occurrence by habitat. *Orthorhyncus*, which is expected to compete less with either carib species, overlapped in habitat with both, but appeared to prefer forest, thereby overlapping to a greater extent with *Eulampis*. The overlap by *Orthorhyncus* with the two caribs was not unexpected since its smaller size and different bill morphology should allow it to coexist with the two larger species. Similar choice and use of plant substrates by *Orthorhyncus* and *Eulampis* may indicate possible competition for arthropod resources between these two species. It is not known if each species was taking different types or species of arthropods from the same plant substrates.

The two caribs, due to their similar size and bill morphology, are expected to compete intensely for floral nectar and hence show habitat separation through interspecific competition. The habitat separation observed between *Sericotes* and *Eulampis* during this study, despite foraging primarily on arthropods, suggests interspecific competition may be occurring. In other Caribbean islands the diet of sympatric hummingbird species has diverged during nectar shortages while converging at times of nectar abundance (Feinsinger et al. 1985). In some areas, overlap in hummingbird diets has varied widely over different seasons (Wolf 1970).

On tropical islands significant differences have been reported in densities and species of arthropods present in open and closed canopy sites. Foliage arthropods are significantly more abundant in number of species, individuals, and biomass in forest understory sites than in open areas such as abandoned pastures and secondary vegetation (Janzen 1973). Both *Orthorhyncus* and *Eulampis* foraged primarily on plant substrates. Both species also showed similar patterns of substrate use (flowers > leaves > branches and air) perhaps indicating differential densities of prey species in these substrates within the forest. *Sericotes*, found exclusively in open sites, fed almost exclusively by sallying for flying insects. The preference for aerial arthropods suggests flying insects may be the most abundant, or most easily taken, arthropod type in open canopy sites. Specialization of each carib to forage on plant substrates or flying insects may predispose each species to remain in habitats with the greatest density of arthropods on which each has adapted to feed on, as an alternative to floral nectar. Further study is necessary to determine if habitat separation and differential arthropod use by the caribs is a result of continued interspecific competition, or of alternative specialized strategies for arthropod foraging, which in turn could be an outcome of previous competition.

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RELATIVE ABUNDANCE AND SEASONAL DISTRIBUTION OF SEABIRDS IN THE CANAL DE BALLENAS, GULF OF CALIFORNIA¹

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Key words: *Sea of Cortez; Gulf of California; distribution; Gavia; Podiceps; Oceanodroma; Puffinus; Phaethon; Pelecanus; Sula; Fregata; Larus; Sterna; Synthliboramphus.*

The Gulf of California is a 1,000 km long subtropical sea with relatively high primary productivity and extremely dynamic oceanography (Alvarez-Borrego 1983). It is the northern range limit in the eastern Pacific and adjacent waters for five species of tropical Pelecaniformes, and the southern range limit for several temperate seabird species and one family, Alcidae. Furthermore, 70-98% of the world population of six seabirds breed in the Gulf of California (Black Storm-Petrel *Oceanodroma melania*, Least Storm-Petrel *O. microsoma*, Craveri's Murrelet *Synthliboramphus craveri*, Yellow-footed Gull *Larus livens*, Heermann's Gull *L. heermanni*, and Elegant Tern *Sterna elegans*) (Anderson 1983, Velarde 1989, Tobón-G. 1992, Torresillas-B. 1992).

Despite the interesting biogeography of the Gulf of California and its importance to seabird populations, there are few publications on the distribution and abundance of seabirds there. Grinnell (1928) and Wilbur (1986) summarize information on the range of seabirds and specific sighting records, Anderson et al.

(1976) and Anderson (1983) provide information on breeding seabirds, and Helbig (1983) made counts on three ferry crossings in the lower gulf.

None of these publications provide data on the seasonal distribution of seabirds at sea in the Gulf of California. Therefore, we made counts of seabirds during a study on cetaceans (Tershy et al. 1990) in Canal de Ballenas, central Gulf of California. Our aims were to determine (1) which species of seabirds used the study area, and (2) their relative abundance during each season in 1985-1986.

STUDY AREA AND METHODS

The study area was a 20 × 40 km section of the Canal de Ballenas (29°00'N, 113°20'W) including Bahía de los Angeles and Bahía de las Animas (see Tershy et al. 1990, 1991a for a detailed description). It is characterized by (1) three main habitat types: shallow sandy bays, rocky points and islands, and nearshore pelagic waters over 1,500 m deep; (2) extreme temporal habitat variability with temperature water conditions (<15°C) and prevailing northwest winds in winter and spring, and tropical water conditions (>26°C) with southeast winds in the summer and fall; and (3) strong tidal currents (>3 m/sec) which cause extensive vertical mixing and sustained year round primary productivity comparable to major upwelling zones (Rodén 1964, Alvarez-Borrego 1983).

On 167 days between April 1985 and April 1986, we conducted 1,378 hr of offshore observations in a 4.5 m skiff and counted all seabirds within a 100-m radius. We used a consistent but non-random search method (Tershy et al. 1990, 1991a) and attempted to cover all three major habitat types on a weekly basis. Counts were made only when visibility was greater than 5 km and wind speed less than 11 km/hr (Beaufort 2 or less). Therefore, we did not correct for differences in weather or interspecific differences in sightability. We attempted to count birds which followed the boat

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