ABSTRACT.—We present the first record of territorial site-fidelity across multiple years by Purple-throated Caribs (Eulampis jugularis) on three different islands in the eastern Caribbean: St. Kitts, Dominica, and St. Vincent. Marked male Purple-throated Caribs were monitored throughout the flowering season of their main nectar resources, Heliconia caribaea (St. Kitts and Dominica) and H. bihai (St. Vincent), both native perennial herbs. Individual males were observed defending the same Heliconia patches for 3 years (St. Vincent), 4 years (St. Kitts), and 5 years (Dominica), and remained near these patches even when they were not in flower. The territorial behavior and resource dependence of Purple-throated Caribs on native heliconias likely have a key role in the coevolution of this specialized plant-pollinator interaction.


Territorial defense by hummingbirds may vary in duration from several hours a day (e.g., Stiles 1978, Cotton 1998) to several days, weeks or months per year (e.g., Temeles et al. 2005). Territorial defense by hummingbirds of the same areas over multiple years, however, has been rarely reported (but see Bassett and Cubie 2009). Specifically, territorial fidelity by hummingbirds, where the same individual uses the same plants for consecutive years, is undocumented.

Species in the Heliconia (Heliconiaceae) are primary sources of nectar for hummingbirds in the Neotropics, and territorial defense of Heliconia flowers by hummingbirds is common (Linhart 1973, Stiles 1975, Kress 1983, Dobkin 1984). Heliconias on the islands of the eastern Caribbean are a primary and predictable source of nectar for hummingbirds, especially the Purple-throated Carib (Eulampis jugularis) (Wolf and Hainsworth 1971, Wolf 1975, Temeles and Kress 2003, Gowda and Kress 2008). Only two native species of heliconias occur on the islands of the eastern Caribbean: H. bihai and H. caribaea. The flowering season of H. caribaea ranges from March to July with a peak in May, although rarely individual plants may produce single inflorescences from August to February. In contrast, H. bihai flowers all year with a peak in April (Gowda 2009). Male Purple-throated Caribs, depending on the island, defend feeding and/or breeding territories of either H. caribaea or H. bihai, or both, whereas female Purple-throated Caribs trapline-forage at undefended plants or rarely defend feeding territories (Wolf 1975; Temeles et al. 2005, 2006). Heliconia plants are long-lived (Berry and Kress 1991), and individual birds may use the same plants over successive years. We report on long-term territoriality and site-fidelity of Purple-throated Caribs of the same patches of heliconias over several years on St. Kitts, Dominica, and St. Vincent, three islands in the Lesser Antillean Archipelago of the Eastern Caribbean. We also report on additional food plants used by this species.

METHODS

Field Procedures.—Field work was conducted between 2003 and 2009 on St. Kitts (17° 20' N, 62° 45' W), Dominica (15° 25’ N, 61° 20’ W), and St. Vincent (13° 15’ N, 61° 12’W; Fig. 1).
The understory in tropical wet forests on these islands is dominated by abundant *H. bihai* and *H. caribaea*, although both species are usually allopatrically distributed within a given island. Plants in the genus *Heliconia* are long-lived (20 yrs), perennial, rhizomatous herbs in which each rhizome (genet) generates several ramets (clones; 2 to ≥ 100 ramets) in a given year (Berry and Kress 1991). Each ramet bears one multi-tiered inflorescence which consists of several sequentially opening flowers within a bract and several sequentially opening bracts within an inflorescence. Each flower within a bract lasts only a single day and flowers remain open from dawn to dusk (Temeles et al. 2005, Gowda and Kress 2008).

Purple-throated Caribs were banded at each site (Table 1) during March and April with unique color-coded darvic bands (www.avinet.com) and observed for 24 hrs (8 hrs/day × 3 days) per month in March, April, May, June, July, September, November, December, and January. These months represent both the peak (Mar to Jul) and the non-peak (Aug to Feb) flowering seasons of the two native heliconias (Gowda 2009) and also cover the breeding period of Purple-throated Caribs (Mar to Jul) (Wolf 1975, Temeles and Kress 2010). All observations of territoriality by Purple-throated Caribs on St. Kitts and Dominica were made at marked clumps of *H. caribaea* plants over multiple years. *H. caribaea* is very rare on St. Vincent (only 2 clumps found in the forest); thus, observations of territoriality by Purple-throated Caribs were conducted on marked clumps of *H. bihai*. We delineated the boundaries of territories by noting the point at which territorial males evicted intruders, which included both conspecific males and females, and heterospecifics (Temeles et al. 2005). We concluded that males were displaying ‘territorial fidelity’ if the same marked territorial bird was observed and recaptured at the same marked feeding plants for ≥2 yrs after first capture. We also recorded the number of flowers within the clump on each observation day to assess use of *Heliconia* patches by males in relation to flowering.

**RESULTS**

**Territoriality at Heliconia caribaea.**—We observed few visits (4–5 visits/day) by male Purple-throated Caribs to clumps of *H. caribaea* in the beginning of March when budding inflorescences were visible but no open flowers were available. Male Purple-throated Caribs on all islands, but especially on Dominica, increased their visitation frequency as the flowering season progressed (Fig. 2) and spent more time on the territory defending against incoming visitors to single flowering inflorescences or often even at inflorescences without flowers. Male Purple-throated Caribs rarely left the vicinity for more than a few hours a day or rarely for an entire day during the beginning of the flowering season of *H. caribaea*.

**TABLE 1.** Territorial defense of 11 male Purple-throated Caribs from three eastern Caribbean Islands. Number of individuals monitored per island = n, individuals displaying territoriality = T, and individuals displaying site fidelity = S.

<table>
<thead>
<tr>
<th>Island</th>
<th>Territorial durations (Obs yrs)</th>
<th>Territorial months on Heliconia</th>
<th>Territorial months on non-Heliconia plants</th>
</tr>
</thead>
<tbody>
<tr>
<td>St. Vincent* (n = 2, T = 2, S = 2)</td>
<td>3 yrs (2005–2008)</td>
<td>Apr–May</td>
<td>Unknown</td>
</tr>
</tbody>
</table>

*Heliconia caribaea* on St. Kitts and Dominica, and *H. bihai* on St. Vincent.
Only two male Purple-throated Caribs in Dominica were not observed on their territory on two separate days. Male Purple-throated Caribs showed aggressive territorial defense (Fig. 2A) by mid-April, the peak flowering season of *H. caribaea*, and allowed only females to feed within territories, which often consummated in a mating event. Conspecific females, males, and heterospecifics

![Diagram](image)

**FIG. 2.** Mean number of visits and observed chases by male Purple-throated Caribs at *H. caribaea* and *H. bihai* clumps on three islands in the eastern Caribbean Islands across a single flowering year. Columns represent visits (open) and chases (shaded) by male Purple-throated Caribs. Cross bars represent ± 1 standard error. The dotted line represents the mean number of flowers available each month across a single year. *Heliconia caribaea* on St. Kitts and Dominica, and *H. bihai* on St. Vincent."
Territorial defense at *H. caribaea* by male Purple-throated Caribs lasted from March to July on Dominica (Table 1). Territorial defense had higher temporal variation on St. Kitts and St. Vincent (Fig. 2B, C; Table 1). For example, on St. Kitts, an all-day territorial presence at *H. caribaea* clump by Purple-throated Caribs was observed only from March to May, whereas territorial defense by Purple-throated Caribs on St. Vincent was observed only in April and May and was further restricted within a day, between 0900 to 1500 hrs (Fig. 2C). Territorial defense by females was rare and only observed on St. Vincent where females chased conspecific females (4 times) and conspecific males (2 times). However, females chasing males could not be distinguished from their mating repertoire.

**Territorial Fidelity at Heliconia Patches.**—All marked males on the three islands were faithful to their feeding territories across multiple years (Table 1). Individual males remained faithful to their *Heliconia* patches for 3 years on St. Vincent, 4 years on St. Kitts, and 5 years on Dominica. Females did not show territorial behavior during the breeding season but the same female was recaptured in 2 years in the same feeding clump of *H. bihai* and *H. caribaea* on Dominica. Similarly, a banded, non-territorial female Purple-throated Carib was repeatedly observed at the same patch of *H. bihai* on St. Lucia over 2 years (EJT, unpubl. data) and in St. Vincent for 2 years. Thus, females may not defend territories, but they apparently exhibit site fidelity to *Heliconia* patches when traplining.

**Purple-throated Carib Territoriality and Site Fidelity in the Absence of Heliconias.**—Male Purple-throated Caribs exhibited territorial behavior around flowers of other plant species during times of the year when *H. caribaea* was not flowering. We observed the birds defending *Citrus* sp., *Costus* sp., *Gesneria cymosa*, *Heliconia psittacorum*, *H. wagneriana*, *Inga ingoides*, *Lobelia cirsiifolia*, *Marcgravia umbellate*, *Musa* sp., and *Wercklea tulipiflora*. Seven of nine resident males, despite the complete absence of flowers of *H. caribaea* from August to March, were observed in the general vicinity of their *H. caribaea* territory in September, November, December, and January on St. Kitts (2 of 3 birds) and Dominica (5 of 6 birds). One or more of the non-*H. caribaea* species was present within 200–1,000 m of *Heliconia* patches for all of these males. Male Purple-throated Caribs shifted their territorial defense to these plant species, although one of the marked birds was observed in a citrus farm >1 km distant.

**DISCUSSION**

Territoriality, foraging, and mate-selection in hummingbirds are behaviors strongly known to be influenced by local energy sources (Carpenter 1958, Gass et al. 1976, DeBenedictis et al. 1978, Gass 1978, Kodric-Brown and Brown 1978, Montgomerie et al. 1984, Gass and Sutherland 1985, Temeles and Kress 2010). The abundant heliconias in the eastern Caribbean Islands represent critical sources of nectar for hummingbirds due to the: (1) clonal habit of the plant that assures high density within a small radius (2 to 34 individuals/m²), (2) nectar rich flowers within the same inflorescence (up to 10 to 12/inflorcescence), and (3) long flowering season lasting several months (Apr to Jul) that assures a steady, dependable food source (Temeles et al. 2005, Gowda 2009, Temeles and Kress 2010). The presence of territoriality by Purple-throated Caribs throughout the flowering season of the heliconias and their associated multi-year site-fidelity confirms the two heliconias (*H. caribaea* in St. Kitts and Dominica, and *H. bihai* on St. Vincent) are critical nectar sources for Purple-throated Caribs. The presence of the same individuals at specific *Heliconia* clumps within a flowering season and across years suggests the Purple-throated Caribs on these islands have a long-term imprint of high-quality foraging sites that are not abandoned either within or between years. Hummingbirds use both fine (Miller et al. 1985, Sutherland and Gass 1995) and coarse-grained memory (Armstrong et al. 1987) to locate optimal food resources. Purple-throated Caribs likely use coarse-grained spatial memories to re-defend the same clump of *H. caribaea* year after year (Balda and Kamil 1989).

Our observations of Purple-throated Caribs in the general vicinity of their territorial sites during
the non-\textit{H. caribaea} flowering season suggest they may be aiding their spatial memory by maintaining site-fidelity even when heliconias are not in flower. On a broader level, many migratory North American hummingbird species have been recaptured at the same general locations between successive years (Bassett and Cubie 2009), and some lekking hummingbird species return to the same leks between years (Stiles and Wolf 1979). Long-term spatial memory may be a general characteristic of hummingbirds, although it may have evolved through a variety of different contexts (feeding, migration, and mating).

Our observation of strong fidelity to \textit{Heliconia} patches by Purple-throated Caribs has implications for coevolution between hummingbirds and \textit{Heliconia}. Bill morphology, body size, and energetics of male and female Purple-throated Caribs are closely related to one or the other species of \textit{Heliconia} on the islands of St. Lucia and Dominica (\textit{H. caribaea} with males; \textit{H. bihai} with females; Temeles et al. 2000, Temeles and Kress 2003). Close correspondence between hummingbirds and flowers suggests these islands are ‘hotspots’ (Thompson 2005) of reciprocal evolution. Thompson (2005) noted that gene flow among populations can dilute and weaken reciprocal adaptation. However, year-to-year fidelity by territorial male Purple-throated Caribs to the same patches of heliconias combined with territorial exclusion of intruding conspecifics and heterospecifics would reduce gene flow in both plants and hummingbirds, resulting in strong coevolution of Purple-throated Caribs with \textit{H. caribaea} through reciprocal selection for flower numbers and male size, and fighting ability (Temeles and Kress 2010). Similar fidelity by traplining females may also contribute to strong ecological interactions and evolutionary interactions with \textit{H. bihai} through flower size and shape and bill morphology (Temeles et al. 2009). Benkman et al. (2003) reported a case of coevolutionary interactions between a non-migratory population of Red Crossbills (\textit{Loxia curvirostra}) and lodgepole pine (\textit{Pinus contorta} spp. \textit{latifolia}) where reciprocal selection has largely shaped their bill morphology and seed defenses, respectively.

Our observations indicate that male Purple-throated Caribs continue to associate with patches of \textit{H. caribaea} even when these plants are not in flower. This raises the questions of whether males are defending and exhibiting fidelity to the \textit{Heliconia} species, or to the sites in which these plant species occur. We suggest it may be both and have no doubt that heliconias are the resource magnet that attracts hummingbirds to these sites. Our contention is supported by the observation that with the exception of introduced plants (e.g., bananas, citrus, and some ornamentals); we have found no native plant species on these islands that are as rewarding as heliconias in terms of overall nectar production (flowers of these heliconias produce 60 to 300 $\mu$L per day; Gowda and Kress 2008). Thus, fidelity to a long-lived, highly-rewarding resource, even when it is not in flower, may be a viable territorial strategy, especially if alternative low-quality resources are locally available. Once a territory is abandoned, it may be energetically more costly to re-establish it than to maintain it during times of low flower availability.

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