

Notes on the displays and mounting behaviour in the Purple-throated Carib Hummingbird (*Eulampis jugularis*)

by

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Since 1975 we have been studying the population dynamics, foraging strategies and reproduction biology of hummingbirds living on several islands in the Lesser Antilles, West Indies. Here, we summarize our observations made on Guadeloupe (Riflet), Dominica (Freshwater Lake, Morne Trois Pitons) and on St. Lucia (Edmond Forest Reserve, Mt. Gimie) of the displays and mounting behaviour of the Purple-throated Carib Hummingbird (*Eulampis jugularis*), the largest species in the guild of Lesser Antillean trochilids (average body mass: 8.7 g, n = 19). Behavioral observations were also made on captive *Eulampis jugularis* kept in Bonn. Although some details on the displays and nesting habits of this species have been described (Bond 1941, Schuchmann 1977, Wolf 1975, Wolf & Wolf 1971) we will augment this published information and present some ideas on the adaptiveness of certain behaviours.

The reproduction period

The reproduction cycle of *Eulampis jugularis* falls into the months of January (earliest nesting date 3rd January 1978, Micoud, St. Lucia, pers. observation) to July (latest record for Dominica, Wolf & Wolf 1971). Wolf (1975) reported that males collected in January on Dominica had small testes (1.0–1.5 mm long), and concluded that these males were incapable of sperm transfer (also see Williamson 1956). In mid-April, during the peak of the breeding season, Wolf (1975) found males to have enlarged (6.0 mm) and sperm producing testes.

On St. Lucia, where most of our studies were conducted, we frequently noted considerable yearly variation in the onset and the end of the breeding period. This variation coincided with nectar availability (mainly from flowers of *Heliconia caribea*) at higher, moisture altitudes, where this species is generally found (Bond 1961).

By mid-July males, females and immature birds disperse into lowland areas and are often found foraging for nectar in the flower gardens of coastal villages. Also during this period, on Guadeloupe and on St. Lucia, Purple-throated Caribs were observed in semi-dry and even in xerophytic habitats along the shore-

line, collecting nectar from cacti (*Opuntia* sp., *Melocactus* sp.). The dispersal pattern of this species during the non-breeding season is poorly known and warrants further study.

Sexual differentiation

Male and female *Eulampis jugularis* show only slight differences in their plumage (Bond 1961). Generally, the iridescent green wings and the deep purple red gorget are more brightly coloured in males than in females. However, these characters are only useful for birds in the hand. The most reliable and easiest way to distinguish the sexes is by the more elongated and pronounced curved beak in the female. The male's bill is distinctly shorter and almost straight (average in males: 24 mm, $n = 12$; average in females: 30 mm, $n = 7$). It should also be noted that the sexes differ in body mass (average in males: 9.6 g, $n = 12$; average in females 7.8 g, $n = 7$; values were obtained from St. Lucia). Immature birds have distinctly shorter bills and orange gorgets which are sometimes deep-red with conspicuous orange mottling. Based on these characters, immatures and adults can normally be distinguished in the field.

Male *Eulampis jugularis* occupy and defend feeding territories almost year round (Wolf & Wolf 1971). Females hold feeding territories, centred around flowers, only during the post-breeding period, but will defend the area near the nest against avian intruders. We can confirm the observations of Wolf & Hainsworth (1971) that male *Eulampis* are dominant over all other sympatric hummingbird species, including females.

Display and mounting behaviour

The courtship display sequence of *Eulampis jugularis* has already been described (Schuchmann 1977, Wolf 1975). Therefore, we only outline the main stages, leading to synchronization of sexual behaviour (sequences A to E below) and present additional notes if our observations differ from previous descriptions. The entire mating sequence normally takes less than 4 to 5 minutes.

A — A female intrudes into a male's territory. Generally, she is chased from the territory by the resident male, but continues to return until the male will permit her to perch within the defended territory.

B — Almost immediately after the female is "accepted" the pair performs the "arc-display". During this display the iridescent green wings are stretched at about 25° to 45° from the body. In that position both birds swing their entire bodies side to side, like a pendulum. The wing-lifting behaviour seems to depend upon the intensity of the performed "arc-display". While "arcing" the male produces a series of shrill calls (Fig. 1). During this ritualized phase both sexes often reach synchrony in their "arcing" actions.

C — Thereupon, perch change flights were observed and wing shuffling after the pair landed. According to Wolf (1975) at this stage the female often displaces the male from occupied perches, indicating "a reversal of dominance roles". We

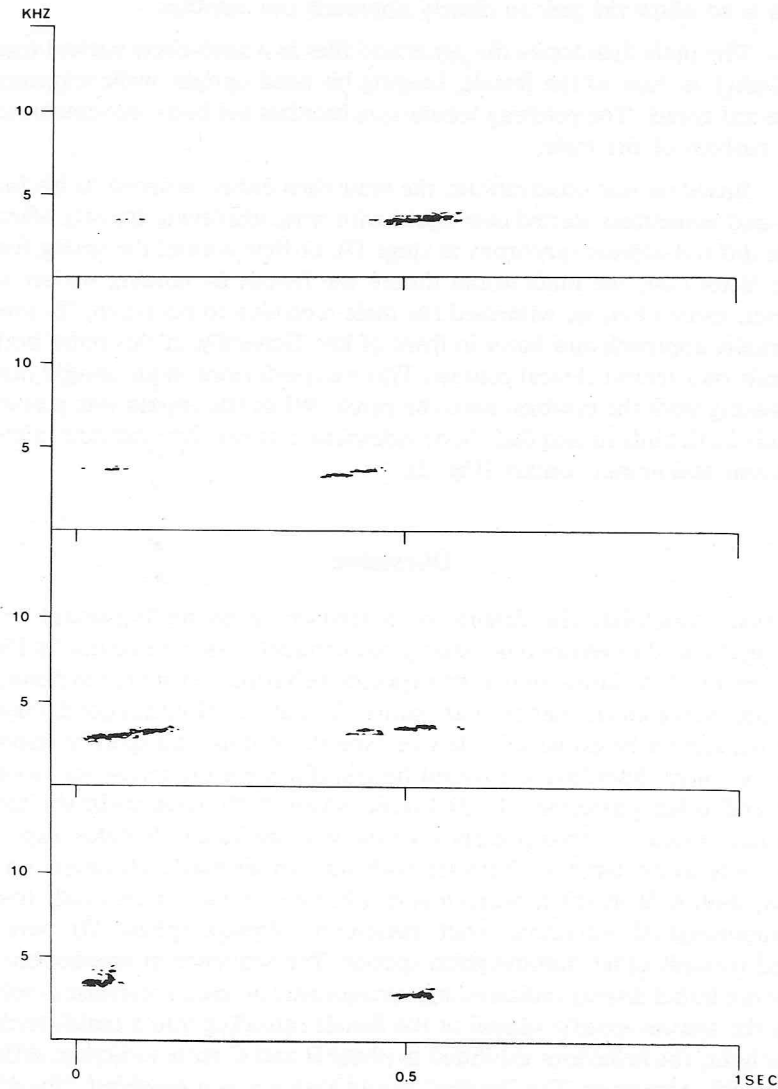


Fig. 1: Sound spectrograms of male vocalizations ("song") of *Eulampis jugularis* representing the typical pattern of each call. This "song" is given by males only. The individual calls sound like a sharp whistle to the human ear. All tracings were made from original spectrograms.

assume that these close-distant flights serve as motoric actions to relieve antagonistic drives; for if the display is interrupted at that stage the female is promptly chased off the male's territory. Females will often stop these perch change flights and start the sequence over again with an "arc-display". The result of these flights is to allow the pair to closely approach one another.

D — The male then leaves the perch and flies in a semi-circle pattern (pendulum flight) in front of the female, keeping his head upright while exposing the purple-red gorget. The perching female synchronizes her body movements to the flight pattern of the male.

E — Based on our observations, the male then either returned to his former perch and sometimes started over again with wing displaying (mostly when the female did not achieve synchrony at stage D), or flew around the sitting female. In the latter case, the male would mount the female by landing on her back. However, more often we witnessed the male returning to his perch, fly towards the female, approach and hover in front of her. Generally, at this point both individuals had ventral cloacal contact. This was performed in an upright posture by lowering both the position onto the perch. While the copula was performed frontally both birds turned their body sideways crossing their rectrices, allowing maximum abdominal contact (Fig. 2).

Discussion

In many trochilids the defense of a territory plays an important role in allowing the bird to secure daily energy requirements. As pointed out by Pitelka (1942), most of the intra- and/or interspecific behaviours exhibited in hummingbirds are antagonistic rather than sexual in nature. Hummingbird displays, therefore, cannot be explained solely as "specific stimuli and specific response" actions as often described in estrildid finches (for literature review see Goodwin 1982) and other passerines. In *Eulampis*, where both sexes maintain feeding territories at least for several months of the year, males and females respond to almost any avian territory intruder with an "arc-display". However, on Dominica, Wolf & Wolf (1971) noted that this behaviour was directed only towards non-hummingbird intruders, while pendulum displays (phase D) were performed towards other hummingbird species. The sequence of interactions that follow the initial display indicates that antagonistic or sexual response is selected for by the species specific stimuli of the female intruding into a male's territory. In this light, the behaviour exhibited in phase B and C serve as keys to differentiate specific responses. The "arcing" would then act as a modified "fly at" behaviour. Then, depending on the response of the intruder, the territory owner decides whether to react antagonistically or sexually. These reactions are presumably irreversible (displacement behaviour), even when the partner does not continue to produce additional stimuli. In our laboratory birds, we often wit-

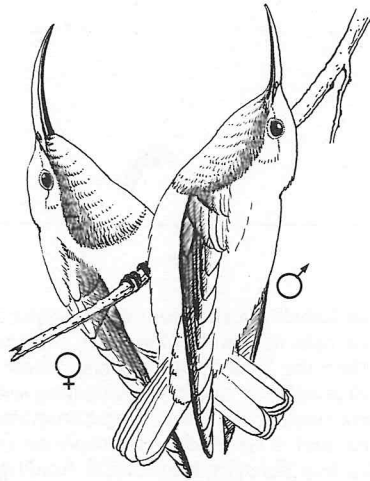


Fig. 2: Ventral mounting in a pair of *Eulampis jugularis*. Shaded areas represent iridescent parts of the plumage. Drawing: W. Hartwig.

nessed such distinct, canalized behaviour. Even when the female had left the perch at phase D, the male would continue to display in front of the place the female had been sitting and would finally copulate with the perch.

The function of calls or phrases of the poorly developed song in *Eulampis jugularis* have not been satisfactorily investigated. However, this is the case in almost all vocal behaviour communication in hummingbirds. In *Eulampis*, we recorded one type of "song" which was heard only from territorial males. This "song", which is unknown from females, was repeated up to 9 to 17 times from a preferred perch within the feeding territory (core area). However, females give calls similar, but more modulated in structure, to the terminal portion of the male song (Fig. 3), when chasing intruders from the feeding or nesting territories. The vocal repertoire in males and females may well be an acoustic signal, indicating an occupied feeding territory. During the first stages of display (A, B) the male "song" may act as an additional selective filter to sort out antagonistic or sexual responses. We observed males singing at intruders prior to "arc-display" and prior to chasing. Normally, intruding food competitors of the hummingbirds reacted upon the "singing at" behaviour of the defender with "flying by". Thus, the territory owner could judge the next course of action.

We only observed dorsal mounting in 3, out of 19 cases, and ventral copulation seems to be the common position in *Eulampis*. Why such a mating behaviour is performed can only be a matter of speculation. Perhaps the reduction of the feet (including claws and toes) might serve as a partial explanation for ventral mating. In many bird species the feet play an important role in balance

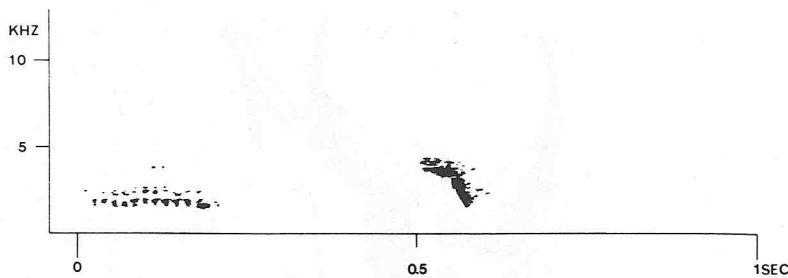


Fig. 3: Sound spectrograms of female vocalizations of *Eulampis jugularis*. This is the only but frequently heard series of calls in females. Each call sounds like a shrill whistle but is performed much louder than the "song" of the male. These low frequency calls can be heard by females and occasionally by males when chasing avian intruders from occupied territories. Tracings were made from original spectrograms recorded with a Uher 4000 Report L tape recorder and a Sennheiser microphone (model MD 421 N). Recordings were analyzed with a Kay Sonagraph Spectrum Analyzer with a wide-band pass filter.

and help the male's approach to the female when alighting dorsally. In hummingbirds the feet are often so small (except trochilids living at high altitudes) that they only serve for perching. In the large *Eulampis* ventral mounting might therefore be a more effective means of sperm transfer.

It is interesting to note that we recently observed ventral mounting in the large South American hummingbird *Topaza pella* (average body mass: 14.0 g, n = 6) kept in our aviaries. Based on morphology, Schuchmann (1980) suggested a close relationship between the Lesser Antillean *Eulampis* and the South American *Topaza*. Whether similar mounting behaviour of these two genera was achieved independently or reflects a shared primitive condition warrants further study.

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Summary

Eulampis jugularis is the largest hummingbird species in the guild of Lesser Antillean trochilids (average body mass: 8.7 g). The reproduction period of *Eulampis* falls into the

months of January to July. While males occupy feeding territories year-round, females exhibit such a behaviour only during the non-breeding period. The courtship display in *Eulampis* can be divided into 5 main stages. A — A female intrudes into a male's territory (visual contact). B — When the female is accepted the pair performs "arc-display" with wings stretched from the body. C — Perch change flights by both sexes, allowing a close approach one another. D — Pendulum flight of the male in front of the female, exposing his purple-red gorget. E — Ventral mounting. Because of a pronounced reduction of the feet, ventral mounting in the large *Eulampis* might be a more effective means of sperm transfer. The South American hummingbird species *Topaza pella*, even larger than *Eulampis jugularis*, exhibits ventral mating as well. Besides these common behaviour patterns, they also share similar morphological characters. Thus, a common phylogenetic origin might be possible.

Zusammenfassung

Die Brutzeit von *Eulampis jugularis*, der größten Trochilidenart der Kleinen Antillen, fällt in die Monate Januar bis Juli. Nur die ♂ dieser Art besetzen das ganze Jahr über Nahrungsterritorien, die sie gegen intra- und interspezifische Konkurrenten verteidigen. Territoriale Verhaltensweisen zeigen dagegen ♀ nur außerhalb der Brutzeit. Trotz der geringen Unterschiede im Gefieder beider Geschlechter erlaubt die Schnabelform und -länge eine unmittelbare geschlechtsspezifische Zuordnung im Freiland (♂ Schnabel gerade, Länge 24 mm, n = 12; ♀ Schnabel stark gekrümmt, Länge 30 mm, n = 7). Das Balzverhalten von *Eulampis jugularis* umfaßt 5 gut differenzierbare Phasen. A — ♀ dringt in das Territorium eines ♂ ein (visuelle Kontaktaufnahme). B — Wird das ♀ im Territorium geduldet, beginnt das ♂ sitzend Drehbewegungen mit dem Körper auszuführen, wobei die irisierend grünen Flügel ca. 25° bis 45° vom Körper abgewinkelt werden. C — Danach fliegen sie nacheinander in kurzen Intervallen auf und nähern sich einander durch gegenseitigen Standortwechsel. D — Sobald sich beide gegenüber sitzen, beginnt das ♂ unmittelbar vor dem ♀ einen Pendelflug auszuführen, wobei es seinen purpurroten Brustlatz präsentiert. E — Daraufhin erfolgt in der Regel eine ventrale Kopulation.

Die beobachteten Schlüsselreize während der Balz von *Eulampis jugularis* werden agonistischen und geschlechtlichen Stimuli zugeordnet und in ihrer Eigenschaft als Filtermechanismen diskutiert.

Da bei dieser relativ großen Trochilidenart die Beine sehr stark verkürzt sind und somit nur wenig Halt bei einer dorsalen Vereinigung gewährleisten, ist vermutlich eine ventrale Kopula beim Spermientransfer günstiger. Eine ähnliche ventrale Kopulation konnte bisher nur noch bei der südamerikanischen Kolibriart *Topaza pella* beobachtet werden. Da *Topaza* und *Eulampis* darüber hinaus in einigen morphologischen Merkmalen übereinstimmen, liegt ein gemeinsamer stammesgeschichtlicher Ursprung beider Gattungen nahe.

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