"PROSTITUTION" BEHAVIOR IN A TROPICAL HUMMINGBIRD

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For an animal to survive, it must acquire sufficient energy to meet metabolic requirements. In many vertebrates a territory helps insure adequate energy for the resident (Brown 1964, Fisler 1969). The size and quality of the territory will depend on the spatial and temporal characteristics of the food supply and competition for the food (Holmes 1970, Wolf and Stiles 1970).

Most hummingbirds feed principally on nectar although they also eat small insects (Wagner 1946, Stiles 1971, Wolf and Hainsworth 1971). Male hummingbirds of many species defend groups of flowers from other hummingbirds, from other nectar-eating birds, and sometimes from insects. The ability of a male to maintain a territory depends on the relative dispersion of flowers and his dominance relationships with other species and individuals in the area (Brown 1964, Stiles and Wolf 1970, Wolf and Hainsworth 1971). In most hummingbirds that have been studied to date, males generally dominate females; there are a few exceptions (Wolf 1969). Male dominance over females may restrict the availability of energy to the female. Thus, when food is scarce or when the optimum resources can be controlled easily by the males, the subordinate females usually must exploit poorer nectar sources than the males.

Female hummingbirds of most species apparently are solely responsible for the nesting effort and there is no long-term pair-bond (Wagner 1954, Wolf 1964, Lack 1968), although males of some species may provide indirect aid (Wolf and Stiles 1970, Snow and Snow 1973). This means that even during the breeding season, females of most species are not able to cohabit or regularly to use an area defended by the male. In most species nesting females do not and probably cannot hold territories around flowers (Wolf and Wolf 1971, Stiles 1973) and they are forced to forage at energetically poor, undefended sites. Females whose behavior enables them to exploit food defended by males would seem to have a selective advantage in both the breeding and nonbreeding season. This report describes use of aspects of mating behavior in the nonbreeding season by female Purple-throated Carib Hummingbirds (*Eulampis jugularis*) to gain ready access to nectar supplies on male territories. Since sexual behavior in these cases is being used for an energetic benefit for the female, I term this "prostitution" behavior.

METHODS AND RESULTS

Eulampis jugularis is resident throughout most of the Lesser Antilles (Bond 1961) and is relatively common in the moister portions of most islands where it occurs. The sexes have the same coloration but have distinctly different bill shapes (male straight, female decurved; female longer than male) and slightly different weights (males average 9.9 g and females average 7.9 g). The observations reported here were made mostly in a cacao-banana plantation on Dominica, British West Indies, during January, March, and April 1969. In this plantation, territories were centered around banana flowers. Some females held poorer quality territories (either very large and hard to defend or with very few flowers) than the males, while others were not territorial and moved throughout the area foraging wherever they could find accessible flowers. In this area females were generally excluded from the richer energy sources by the territorial behavior of the males.

Eulampis breeds on Dominica from March through July, although there are local and annual variations in the onset and end of the breeding season depending on climatic conditions and flower availability (Wolf and Wolf 1971). In the study area the breeding season in 1969 started somewhat later than usual because of extreme drought and the resultant delay in onset of flowering of the principal native food plants. Males collected in and around the plantation in January had small testes (1.0–1.5 mm long), while males in early and mid-April had enlarged testes (6 mm). I am not sure if sperm are transferred at each mounting, but males in April probably were producing sperm. The small testes in January indicate that these males probably were not capable of fertilizing eggs (Williamson 1956). Females collected in this area had only slightly enlarged ovarian follicles by mid-April (follicles to 1.5 mm) and were not yet ready to lay eggs. Sperm storage for long periods is very unlikely to occur in female hummingbirds (Marshall 1961). Although the females apparently were unable sexually to reproduce, I observed mating behavior and copulations regularly in the nonbreeding season, as early as January.

The mating behavior that I observed in *Eulampis* can be divided into five stages, A to E, that usually were performed sequentially. The entire sequence rarely took more than five minutes.

Stage A was initiated when a female intruded into the territory of a male. She very quickly was chased from the territory by the resident male. The male often followed the female some distance away from the territory, especially late in stage A. Following the chase, the female very quickly returned to the territory and again was chased out by the male. The total number of such chases was quite variable, but often exceeded five. Near the end of stage A, the female might arrive back in the territory before the male and the male might sit in the territory a few seconds before chasing the female which normally was feeding at flowers defended by the male. Stage A ended when the male allowed the female to remain in the territory.

During stage B the female, now allowed in the territory, often sat or fed very close to the male with no apparent aggression by the male. For this report the critical part of late stage A and much of stage B is that the female was able to feed unmolested at the flowers otherwise rigorously defended by the male. Occasionally, the male performed a rocking arc display toward the female, who was usually more than five feet away at the time. In this display, he held one or both wings at about a 45° angle from the body, maintained the entire body horizontal on the perch, and swung his body back and forth in a horizontal arc. To me, this display was identical to one performed rarely by a female *Eulampis* sitting near her nest as another *Eulampis* flew over. One or both birds might also perform "jump-flights." These were apparently ritualized perch change flights, with exaggerated body and wing movements and wing crackling sounds during the flight. Jump-flights normally were followed by a short period of wing shuffling after the bird landed. The female during stage B was able not only to feed in the male's territory but also could, and did, regularly displace the male from occupied perches, including perches that were used regularly by the male before the female arrived. All behavior between the two birds at this stage indicated a reversal of dominance roles so that the female was now dominant to the male. Stage B ended when the two birds came together on a common perch.

Stage C was characterized by displays given by one or both individuals in close proximity to each other. The major type of display was hovering back and forth in front of the other bird, usually while the second bird was sitting. Either the male or female hovered, usually the male. The hoverer was at the same level or slightly below the sitting bird and about six inches away. The hoverer had its bill raised, exposing the iridescent throat. The sitting bird turned its head to follow position changes by the hoverer. Infrequently, when the female hovered, the male also gave a perched, horizontal arcing display as described for stage B. In addition to a single bird hovering, both sometimes hovered while facing each other eight inches or less apart. Usually the hovering pair circled in the air during this display. Other displays that could be performed at this time included the male flitting back and forth by the sitting female, landing alternately on one side of her and then the other. Stage C ended when the male, starting from a sitting position or hovering display, moved to the back of the female or attempted to make cloacal contact ventrally.

Stage D could take one of two forms, either mounting with the male on the back of the female or attempted cloacal contact with appressed abdomens. In the dorsal mounting, the male hovered around and settled onto the back of the female. Just before being mounted, the female sank lower onto the perch and assumed a horizontal posture. Each individual twisted its tail to one side making cloacal contact possible. The ventral approach required both birds to hang somewhat below the perch in comparison to the regular perch position. The birds were sitting adjacent to each other and the abdomens met while each was fluttering somewhat to maintain its position. This appeared to be a somewhat less certain position and often a ventral attempt was followed by a dorsal mounting. Stage D ended with the breaking of cloacal contact and the male flying away from the female.

Stage E, the postcopulatory period, could take several courses depending on the behavior of each sex. The female usually remained on the perch and fluffed her feathers and shook her wings. Following this, she either immediately left the territory or at-

TABLE 1. Ordering of first four stages in all courtship sequences observed in the nonbreeding season.

		Stage that followed				
		A	B	C	D	Total
Stage that preceded	A	0	6	3	1	10
	B	4	0	16	0	20
	C	4	7	5	11	27
	D	0	0	1	0	1
	Totals	8	13	25	12	58

TABLE 2. Ordering of first four stages in courtship bouts that ended in mounting.

		Stage that followed				
		A	B	C	D	Total
Stage that preceded	A	0	4	3	1	8
	B	1	0	10	0	11
	C	2	2	3	11	18
	D	0	0	1	0	1
	Totals	3	6	17	12	38

tempted to feed again at the male's flowers. The male, immediately after dismounting, either sat a short distance away or went off in a long circular flight accompanied by a *tsing* sound, probably vocally produced. If the female attempted to feed at the flowers in the territory, the male chased her immediately if he was sitting nearby or when he returned following the circular flight. In either case, the male appeared to chase the female as soon as he was aware that she was feeding. The female was not allowed to feed in the territory as during the initial stages of the courtship sequence. The territory was once again the exclusive domain of the male.

In table 1 I have indicated the sequence of stages in all courtship bouts observed during this study. It is evident that the ideal sequence was most frequent, but the order was sometimes changed somewhat. However, the copulation stage was very rarely followed by an earlier stage. Much of the lack of precision of the sequencing could be attributed to incomplete sequences that a short time later were started again, with initial or intermediate stages missing. For example, the sequence that moved from stage A directly to stage D probably involved a female who had interacted with the male a short time before, when the sequence had not been completed. The most common reversals of sequence were between adjacent stages among the first three. These reversals probably represented incomplete dominance shifts and possibly incomplete synchrony of stage progression in the male and female. The very short period of time, less than five minutes, in which the sequence normally occurred required precise synchrony of activities by the pair.

In table 2 are similar staging data for all sequences in table 1 that culminated in mountings or ventral abdominal contact. Comparing the two tables leads to the conclusion that there were no major differences in patterning of mating versus nonmating sequences, except for the obvious lack of stage D in nonmating sequences.

I saw 12 matings or attempts that went through stage D (table 2). Seven of the 12 included feeding in the territory prior to stage D. Only 4 of the 12 did not include feeding in the territory prior to mating and in each case I did not see the interaction until it had reached late stage B or stage C. In all four cases it was possible that feeding by the female in the male's territory occurred prior to the start of my observations. The last mating occurred in a situation where I could not be sure if the female had fed or not. Thus, it appeared very likely that most or all complete mating sequences included feeding by the female in the territory of the male.

Five courtship sequences progressed only to late stage B or stage C and did not culminate in mating. Three of the five included feeding by the female and her departure shortly thereafter. The male chased the female twice when she attempted to feed and the female finally left. One instance of feeding and one of nonfeeding occurred shortly after a completed mating sequence in the same territory and may have involved the same female. It seemed likely that some incomplete sequences involved females returning very quickly and being chased away with no feeding, in a manner similar to what occurred right after a mating if the female attempted to feed. Females may also not cooperate after feeding, but generally such episodes were followed fairly soon by a complete mating sequence. Most of these birds were not marked so I could not tell if it was the same female in complete and incomplete sequences, but I hypothesize that often this was the case.

I could see no differences between mating sequences that occurred during the nonbreeding period in this locality (January and probably March) and sequences that occurred just before or during the breeding season. Thus it appeared that both sexes engaged in reproductive display and mating behavior during a time of the year when females were not capable of being fertilized and at least some of the time when males were not able to fertilize females.

DISCUSSION

The very short time involved in the mating sequence necessitates essentially a complete dominance reversal to establish a pair relationship between two individuals who ordinarily interact during this season on the male's territory in a highly aggressive fashion. Since the predominant feature of the area being defended by the male is the supply of nectar contained in the flowers, the dominance reversal is presumably completed and made behaviorally obvious by the female foraging at the flowers in the territory during late stage A and early stage B. By stage B the male no longer responds to the female as an intruder, since she has become a potential sex partner.

Since all mating sequences I saw in January, and very probably those in March and April, occurred prior to nesting in this area, they were not immediately enhancing the reproductive fitness of the resident male. This leads to the possible conclusion that females used the mating sequence to gain access to the rich energy supply within a male's territory, essentially parasitizing the male (see also Zahavi 1971, for a similar phenomenon in wintering wagtails, *Motacilla*, in Israel). For the female this behavior is no longer useful after she has fed, and several sequences were stopped by the female flying off just before or during stage C. However, if males were able to learn the identity of individual females, it seems likely that a female must reinforce the male to continually gain access to a territory. This reinforcement is provided by allowing the mating sequence to proceed to completion even though the female is not ready to lay her eggs. Thus, mating behavior during the nonbreeding season could be a behavioral reinforcement to permit continued poaching by the female.

A male allows use of the energy within his territory, the defense of which is of some energetic expense to him (Brown 1964, Wolf and Hainsworth 1971). There are three possible explanations of why this should occur. First, a male who allows poaching by one or more females may control flowers that are distributed in such a way that the territory contains more energy than the male can use. Limited use of the nectar by the females might have no detrimental effect on the male and could be selectively neutral. This explanation seems unlikely since a male always chased or tried to chase other nectar-eaters from his territory, including the females with whom he mated, both just before and just after mating.

Second, it is possible that a male has not been able to divorce the mating patterns from hormonal controls even though this behavior is energetically disadvantageous. However, the small sample of males during January suggested that the testes were regressed at this season and probably were not producing the high androgen titer associated with the breeding season in other birds (Payne 1969). Furthermore, some mating sequences were interrupted by the participating male prior to actual mating, indicating that males are able to control the occurrence and extent of this behavioral pattern to some degree.

A third, and most likely explanation, is that poaching by a female is either energetically neutral or disadvantageous for a male depending on territory quality, but that there are positive selective forces related to the mating behavior. As the breeding season approaches, it is obviously advantageous for a male to mate with as many females as possible, on the chance that they are ready to be fertilized. Perhaps there is also some advantage for a male to establish individual recognition and dominance relations with females during the nonbreeding season to increase the probability of mating with them during the breeding season.

SUMMARY

Females of *Eulampis jugularis* use mating behavior during the nonbreeding season to gain access to rich food sources being defended by males. Periodic copulations reinforce the courtship response to an intruding female by the territorial male. The advantage of the behavior to the male is presently unclear.

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