

BRONZY SUNBIRDS TOLERATE INTRUSION ON FORAGING TERRITORIES BY FEMALE GOLDEN-WINGED SUNBIRDS THAT PERFORM "BEGGING" DISPLAY

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Abstract.—Female Golden-winged Sunbirds (*Nectarinia reichenowi*) are subordinate to both sexes of Bronzy Sunbirds (*N. kilimensis*). Nevertheless, they were often able to avoid being evicted from foraging territories of Bronzy Sunbirds by using a wing-quivering, tail-spread display strongly evocative of food-begging displays. The female Golden-winged Sunbirds appeared to be exploiting communication that functions in the reproduction of Bronzy Sunbirds.

NECTARINA KILIMENSIS TOLERA LA INVASIÓN DE SU TERRITORIO DE FORRAJEO POR PARTE DE HEMBRAS DE *N. REICHENOWI* QUE EXHIBEN CONDUCTA DE PEDIR ALIMENTO

Sínpsis.—Las hembras de *Nectarina reichenowi* se subordinan a ambos sexos de *N. kilimensis*. No obstante, muchas veces evitan ser expulsadas del territorio de forrajeo de la última, haciendo temblar sus alas y replegando el rabo, evocando la conducta de pedir alimento. *N. reichenowi* parece estar explotando aspectos de conducta de comunicación que son parte funcional de la reproducción de *N. kilimensis*.

Some social behavior "manages" (Owings and Hennessy 1984) or "manipulates" (Krebs and Dawkins 1984) the behavior of others. I have observed female Golden-winged Sunbirds (*Nectarinia reichenowi*) that are otherwise subordinate to Bronzy Sunbirds (*N. kilimensis*) use displays to overcome the defense of a foraging territory by Bronzy Sunbirds. These displays may exploit the Bronzy Sunbirds' responses either to food begging by juveniles or solicitation of courtship feeding by a mate.

SUBJECTS AND STUDY SITE

Bronzy Sunbirds and Golden-winged Sunbirds were sympatric at the study site near the south shore of Lake Naivasha, Kenya, at an altitude of 1900 m. Bronzy Sunbird males divided a dense stand of leonotis (*Leonotis nepetifolia*) growing on irrigated land into foraging territories. Golden-winged sunbirds sometimes entered these territories. Both species' bills conform closely to the shape of the leonotis flower, and both species feed from the flowers efficiently (Gill and Wolf 1978).

Bronzy Sunbirds socially dominate Golden-winged Sunbirds (Gill and Wolf 1979, pers. obs.). Male Bronzy Sunbirds defended their territories by flying directly at intruders, most of which fled immediately. When an intruder did not flee, the Bronzy Sunbird male landed 10–15 cm from it, then moved closer until the intruder left. The occasional aggressive approaches by female Bronzy Sunbirds or Golden-winged Sunbirds took the same form.

Bronzy Sunbirds breed throughout the year in east Africa. Most re-

production occurs in late March through April (Brown and Britton 1980). There were no nests on any of the territories I studied, but two Bronzy Sunbird males consistently tolerated a particular banded Bronzy Sunbird female while evicting all other female Bronzy Sunbirds.

During March and April 1984, Golden-winged Sunbird females were observed in four of eight territories defended by color-banded Bronzy Sunbird males. These eight territories were observed for a total of 1341 min, in 1009 of which the males were present. Only one territory was observed at a time. Observations were made on one banded and at least one unbanded Golden-winged Sunbird female.

RESULTS

Golden-winged Sunbird females interacted a total of 63 times with territorial Bronzy Sunbird males, 10 times with Bronzy Sunbird females resident in territories, and six times with Golden-winged Sunbird females temporarily occupying a territory in the absence of the territorial Bronzy Sunbird male. On 21 occasions intruding Golden-winged Sunbird females, which are readily distinguished from Bronzy Sunbird females in all plumages by yellow-edged wing and tail feathers, responded to aggressive approaches by male or female Bronzy Sunbirds with a display. Each such display was performed by a female Golden-winged Sunbird perched on the vertical stalk of a *leonotis* plant. The display began with the female spreading her feet apart on the stalk. She turned her body to a 90° angle to the stalk and fanned her tail feathers. The extent of this fanning varied greatly, even in the same individual. She spread her wings to varying degrees, but they were never more than about half extended. Frequently she fluttered or quivered her wings slightly. Sometimes she rotated her body so that her belly was turned partially up. There was no indication that she vocalized. I never observed female Bronzy Sunbirds displaying similarly. Following this display, the aggression was terminated on 20 of the 21 occasions, and the female Golden-winged Sunbird was able to resume foraging. The aggression was never terminated without a display.

At least two different Golden-winged Sunbird females displayed a total of 18 times to Bronzy Sunbird males and were tolerated after each display (16 of those 18 displays were by one banded Golden-winged Sunbird female to one Bronzy Sunbird male). Golden-winged Sunbird females displayed three times to Bronzy Sunbird females and were tolerated twice. In contrast, they displayed four times to other Golden-winged Sunbird females and were never tolerated.

The Golden-winged Sunbird females appeared to benefit from the displays, especially when they were directed at Bronzy Sunbird males. The duration of the Golden-winged Sunbird female's time in the territory was recorded after each of 18 encounters with either a Bronzy Sunbird male or female in which the Golden-winged Sunbird female displayed. The average duration of the Golden-winged Sunbird female's time in the territory after a display was 314 s in the 17 timed encounters with a Bronzy Sunbird male and 300 s in the one timed encounter with a Bronzy

Sunbird female. In the course of a longer-than-average intrusion, the resident Bronzy Sunbird aggressively approached the intruder every few minutes, whereupon the intruder again displayed and again was tolerated. In the 33 encounters with a Bronzy Sunbird male in which a Golden-winged Sunbird female did not display, the average duration of her stay was 10 s, and in the seven such timed encounters with Bronzy Sunbird females the average duration was 21 s. This data set involved pooling, and so was not suitable for significance tests using inferential statistics. The data did suggest, however, that the display benefited the Golden-winged Sunbird females: they fed continually while in the territory.

DISCUSSION

I propose that the tail-fanning, wing spreading display induces a dominant Bronzy Sunbird to tolerate a subordinate Golden-winged Sunbird in the Bronzy sunbirds' territory. An alternative interpretation is that the Golden-winged Sunbird female dominated the Bronzy Sunbird male by this display and remained in the territory as a dominant. I doubt this alternative interpretation. Male Golden-winged Sunbirds were present in low numbers at this site but never held a territory, and no male Golden-winged Sunbird was ever in a Bronzy Sunbird's territory for more than a few seconds before being evicted. Perhaps the Golden-winged Sunbird females were not asserting dominance but signalling that they would defend themselves against aggression, thus disuading the Bronzy Sunbirds via a generalized aggressive passerine signal. This interpretation seems unlikely for two reasons: 1) when the aggressive bird continued to press after the display, the Golden-winged Sunbird always left and never retaliated; and 2) of all the sunbirds of both sexes of several species removed from territories, only Golden-winged Sunbird females gave this display.

When in a Bronzy Sunbird's territory during its absence, intruding female Golden-winged Sunbirds occasionally repelled other intruders. A Golden-winged Sunbird female resident in a Bronzy Sunbird male's territory displaced Variable Sunbird (*Nectarinia venusta*) males twice and Malachite Sunbird (*Nectarinia famosa*) males three times by flying directly at them and landing above or near them. She approached a Bronzy Sunbird female in the same way, but without effect. This suggested she could not dominate the female Bronzy Sunbird.

When a Golden-winged Sunbird female removed an intruder, the territory holder's resources were defended by the tolerated intruder. This is similar to resource defense achieved by territorial Pied Wagtails (*Motacilla alba*) tolerating a second conspecific (Davies and Houston 1981). The payoff was different in this case, however, because the intruder consumed rather than defended resources most of the time it was present, did not remove intruders when the territory holder was present, and was only able to remove certain of the intruders. Consequently, it was not clear that the Bronzy Sunbird territory holder derived a net economic benefit from tolerating the Golden-winged Sunbird female.

It seemed clear that Golden-winged Sunbird females were able to feed

in the territories of Bronzy Sunbird males by exploiting the responses of both Bronzy Sunbird males and females to their displays. The Golden-winged Sunbird females gained improved foraging opportunities. I cannot think of any way in which this outcome benefited Bronzy Sunbirds. The males' responses seem likely to have been selected to serve a reproductive function that inhibited aggression to facilitate mate acceptance. Tail spreading and quivering are included in the courtship repertoires of at least some species of sunbirds (Skead 1967). The females' responses seem likely to have been selected to facilitate feeding their young. The pattern of fanning the tail and drooping and quivering the wings was reported as a juvenile begging display in several species of sunbirds (Skead 1967), and the wing quivering component was observed in juvenile Bronzy Sunbirds (van Someren 1956). The Bronzy Sunbird males van Someren observed never fed either their incubating mates or their young. Even if Bronzy Sunbird males never did so, inhibition of aggression in response to an appropriate display by either their young or their mate would be selected, as would females' responses to their young. Communication within dyads (i.e., mate-to-mate or offspring-to-parent), too important to ignore, is particularly vulnerable to exploitation by a second sender (Markl 1985) such as the Golden-winged Sunbird females.

The Golden-winged Sunbirds' displays are in some ways similar to Wolf's (1975) report of "prostitution" in female hummingbirds. Wolf observed that female hummingbirds sometimes participated in courtship and copulation with conspecific territory-holding males several weeks before either reached their seasonally-limited reproductive readiness. During the courtship period, the female fed in the male's territory. Female Golden-winged Sunbirds were also allowed to forage, but the Golden-winged/Bronzy Sunbird interaction differed from the hummingbird phenomenon in interesting ways. The male hummingbirds initiated courtship displays, whereas it was the female Golden-winged Sunbirds that displayed first. (As L. Wolf [pers. comm.] has pointed out, however, the female hummingbird initiates interaction by repeatedly returning to the territory and this could even function as a display.) Moreover, the female hummingbird will repay courtship and intrusion tolerance with potentially fertile copulations in a few weeks, whereas the Golden-winged Sunbird will not. Finally, Wolf noted that the male hummingbird's behavior may contribute to his reproductive fitness immediately by inseminating an occasional precociously fertile female or developing a relationship with an individual female before the breeding season that could increase his mating success when the breeding season started. This female Golden-winged Sunbird's behavior appeared to be a clearer case of managing or manipulating behavior to the disadvantage of another animal via social signals than did "prostitution" in hummingbirds.

It is puzzling that the Bronzy Sunbird males' responses to this display were not more widely exploited. Bronzy Sunbird females, which seem certain to be more similar to a mate or offspring than Golden-winged Sunbird females, should have been able to exploit this trait in males.

Perhaps the behavior of the Bronzy Sunbird males was a simple misfiring that was not exploited often enough in nature to produce significant selection against it. But if that is true, how did selection favor the Golden-winged Sunbird females' display?

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