

INTERSPECIFIC AGGRESSION FOR FOOD BY A GRANIVOROUS BIRD¹

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Field evidence for resource competition between species comes mostly from studies of the effects of competition (Schoener 1983), with little attention paid to the behavioral processes of interspecific competition (Morse 1970, Myrberg and Thresher 1974). Interspecific territoriality has been cited as evidence of interference competition in a number of studies (reviewed by Orians and Willson 1964; Murray 1971, 1981). Evidence for interspecific aggression without territoriality in birds is provided by Livezey and Humphrey (1985), Mumme and de Queiroz (1985), and Nuechterlein and Storer (1985), but none of these studies demonstrated a competitive function. Murray (1981) has suggested that some cases of interspecific aggression may result from mistaken identity. Payne and Groschopf (1984) concluded that interspecific call-site defense by two species of indigobirds, *Vidua funerea* and *V. raricola*, is a result of mistaken identity resulting in courtship disruptions rather than competition for food. Here I present data that demonstrate that male Pin-tailed Whydahs, *V. macroura*, selectively pursue and supplant granivorous species from feeding areas on their territory.

Pin-tailed Whydahs are small (about 14 g), polygynous, brood-parasitic grassland finches in which the males are strongly interspecifically territorial during the breeding season (Collias cited in Friedmann 1960, Shaw 1984, pers. observ.). Whydahs are well-known by aviculturalists, as well as field biologists, for being very pugnacious toward other species as well, chasing all manner of birds, both small and large (e.g., Harman and Vriends 1978, Shaw 1984). Whydahs feed almost exclusively on the ground by picking up fallen grass seeds (Friedmann 1960, Fry 1975), although occasionally they will pick *Paspalum scrobiculatum* seeds directly off the plant while standing on the ground (pers. observ.). For this reason they prefer disturbed grasslands with patches of bare soil where they can feed.

METHODS

Fourteen territorial male Pin-tailed Whydahs were observed for a total of 145 hr at the Kakamega National Reserve, western Kenya (0°21'N, 34°52'E), in fall 1987 and spring-summer 1988. All intra- and interspecific interactions were recorded using continuous sampling of focal males throughout the morning (usually about

07:15 to 12:00). A "chase" was recorded anytime a whydah directly approached another bird and that individual then moved off. In most cases this involved a rapid approach followed by a pursuit of the fleeing bird for up to 2 m, but occasionally it was a simple approach and supplant (see below).

Male Pin-tailed Whydahs defend territories from which they exclude all other males using ritualized displays (described by Shaw 1984), chases, and, on two occasions, actual combat. Territory boundary disputes were frequent (2.7 interactions/male/hr; unpubl. data) and these were used to determine territory borders. The feeding areas were measured by observing where the whydahs fed and then measuring the entire area that had similar characteristics. This means that the potential feeding area was measured; the actual feeding area was probably overestimated.

Birds were censused using 30-mm mesh mist nets set up in the whydah's territories. Excluding whydahs, 276 birds of 56 species were captured and classified by diet based on personal observations and Mackworth-Praed and Grant (1957, 1960). Birds were weighed to the nearest 0.5 g with Pesola scales.

RESULTS

At Kakamega, Pin-tailed Whydahs were found in disturbed grasslands dominated by the grasses *P. scrobiculatum* and *Digitaria abyssinica* and trailing forbs such as *Centella asiatica* and *Hydrocotyle mannii* (Umbelliferae). Their territories averaged 1.4 ha, but with considerable variation (SD = 1.3, $n = 14$). Males (and visiting females) fed in their territory in areas such as trails, extinct termite mounds, and cattle pastures which were all characterized by low grass and patches of bare ground. On average, only 10% (SD = 9.3, $n = 14$) of each territory was used for feeding by whydahs. Unlike the indigobirds which feed away from their call site (Payne 1973, Payne and Groschopf 1984), male Pin-tailed Whydahs fed almost exclusively on their territories and preferred perches close to feeding areas (unpubl. data).

Male whydahs were observed to chase 56 heterospecific birds of at least nine species (Table 1). When compared to the number of chases expected for the null hypothesis that they chase birds at random (Table 2), it is clear that male whydahs chase granivorous species more often than predicted ($\chi^2 = 29.8$, $df = 4$, $P < 0.0001$). This difference is not due to whydahs chasing smaller birds; birds chased by whydahs did not differ significantly in size from those caught in mist nets (Table 3, $\chi^2 = 0.82$, $df = 2$, $P > 0.5$).

Of the 56 observed chases, 51 (91%) were of birds

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TABLE 1. Birds chased by territorial male Pin-tailed Whydahs. Weights are mean weights (in grams) of all individuals of the species caught in mist nets, except for the dimorphic Marsh Widowbird, *Euplectes hartlaubi*, in which only the males are included since it was a male that was chased. The weight for the canary is an average value of the three species at Kakamega.

Species	Common name	Weight (SD, n)	Diet type	No. chased
<i>Schoenicola platyura</i>	Fan-tailed Warbler	15.8 (1.3, 4)	Insectivore	1
<i>Nectarinia bouvieri</i>	Orange-tufted Sunbird	8.5 (0.5, 12)	Nectivore	2
<i>Euplectes hartlaubi</i>	Marsh Widowbird	41.0 (2.0, 2)	Granivore	1
<i>E. macrourus</i>	Yellow-shouldered Widowbird	20.5 (2.0, 86)	Granivore	15
<i>Ploceus nigerrimus</i>	Vieillot's Black Weaver	31.3 (1.8, 6)	Omnivore	1
<i>Vidua chalybeata</i>	Village Indigobird	12.9 (0.7, 4)	Granivore	4
<i>Uraeginthus bengalus</i>	Red-cheeked Cordon-bleu	9.7 (0.6, 4)	Granivore	2
<i>Lonchura cucullata</i>	Bronze Mannikin	9.0 (0.7, 70)	Granivore	11
<i>Serinus</i> sp.	Canary	13.1 (3.6, 13)	Granivore	5
Unidentified				14
Total				56

chased from feeding on or near the ground. Of the remainder, one was a chase of a small flock of Bronze Mannikins flying past and the other four chases from a male's preferred perch. The supplanted group included one of the Village Indigobirds, *V. chalybeata*, the Vieillot's Black Weaver, *Ploceus nigerrimus*, and the two Orange-tufted Sunbirds, *Nectarinia bouvieri*; including these in the analysis biases the results conservatively.

Despite these chases, whydahs were not excluding granivorous birds from their territory. Many finches, particularly mannikins and widowbirds, frequently were seen in the whydahs' territories, often being ignored by the whydahs. Whydahs will perch near and even feed next to other granivores, sometimes within 0.5 m. The territories of some whydahs completely overlapped those of the congeneric indigobirds and of the widowbirds.

DISCUSSION

These results show that Pin-tailed Whydahs, although not interspecifically territorial, selectively chase competitor species from their territories. This interspecific aggression is therefore unlikely to result from mistaken identity (e.g., Murray 1981) and in this respect may differ from the interspecific aggression shown among their close relatives (Payne and Groschupf 1984). Despite differences in size (Table 1) and feeding style (mannikins and widowbirds typically feed on attached

seeds rather than on the ground), whydahs can limit the opportunities for feeding on fallen seeds and may affect the foraging success of competitors. Interference competition may play a role in shaping communities even when more obvious signs such as interspecific territories are absent.

Why, then, if whydahs are dominant over other granivores, are they not interspecifically territorial? The answer may lie in the large size of the whydahs' territories. To reduce the effects of competition, all that is needed is to defend a small area from individuals actually feeding on the same resource (fallen seeds). Individuals feeding in other areas and on other resources such as standing seeds can be ignored without incurring much cost in lost resources while at the same time reducing the energy spent in territory defense. The flocking tendencies of mannikins and the larger size of the widowbirds may also make it difficult to exclude them from the entire territory (e.g., Orians and Collier 1963, Murray 1981).

These data also have relevance to the social organization of Pin-tailed Whydahs. Males defend large territories on which they court females (Shaw 1984, Barnard and Markus 1989). This system has been called a dispersed or exploded lek (Payne 1984), implying that resources are not important in attracting females. The data presented here show that resources (i.e., grass seeds) in the territory are important to the males, either for the male's own consumption or to attract females (contra indigobirds; Payne 1973, Payne and Groschupf 1984): it is premature to consider this species lek-

TABLE 2. The number of birds, by trophic level, chased by male Pin-tailed Whydahs compared to the number expected based on mist-netting captures.

Diet type	No. caught	No. expected chases	No. chased
Granivores	136	21	38
Insectivores	76	12	1
Frugivores	33	5	0
Nectivores	22	3	2
Omnivores	9	1	1

TABLE 3. The number of birds, by size class, chased by male Pin-tailed Whydahs compared to the number expected from mist-netting captures. Size class limits were selected from breaks in the frequency distribution.

Size class	No. caught	No. expected	No. chased
Small (< 18 g)	161	26	25
Medium (18-34 g)	89	14	16
Large (> 34 g)	15	2	1

breeding. However, the males' failure to defend their entire territory from competing species suggests that the size of the territory may have social functions, such as attracting females or reducing interference from other males, in addition to the control of food.

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LITERATURE CITED

- BARNARD, P., AND M. B. MARKUS. 1989. Male copulation frequency and female competition for fertilizations in a promiscuous brood parasite, the Pin-tailed Whydah *Vidua macroura*. *Ibis* 131:421-425.
- FRIEDMANN, H. 1960. The parasitic weaverbirds. *U.S. Natl. Mus. Bull.* 223:1-196.
- FRY, C. H. 1975. Viduine foraging behaviour and *Lonchura* commensalism. *Bull. Nigerian Ornithol. Soc.* 11:41.
- HARMAN, I., AND M. W. VRIENDS. 1978. All about finches and related seed-eating birds. T.F.H. Publications, Neptune, NJ.
- LIVEZEY, B. C., AND P. S. HUMPHREY. 1985. Territoriality and interspecific aggression in steamer-ducks. *Condor* 87:154-157.
- MACKWORTH-PRAED, C. W., AND C.H.B. GRANT. 1957. *Birds of Eastern and North Eastern Africa*. Vol. 1. 2nd ed. Longmans, London.
- MACKWORTH-PRAED, C. W., AND C.H.B. GRANT. 1960. *Birds of Eastern and North Eastern Africa*. Vol. 2. 2nd ed. Longmans, London.
- MORSE, D. H. 1970. Ecological aspects of some mixed-species foraging flocks of birds. *Ecol. Monogr.* 40:119-168.
- MUMME, R. L., AND A. DE QUEIROZ. 1985. Individual contributions of cooperative behaviour in the acorn woodpecker: effects of reproductive status, sex, and group size. *Behaviour* 95:290-213.
- MURRAY, B. G., JR. 1971. The ecological consequences of interspecific territorial behavior in birds. *Ecology* 52:414-423.
- MURRAY, B. G., JR. 1981. The origins of adaptive interspecific territorialism. *Biol. Rev.* 56:1-22.
- MYRBERG, A. A., JR., AND R. E. THRESHER. 1974. Interspecific aggression and its relevance to the concept of territoriality in reef fishes. *Am. Zool.* 14:81-96.
- NUECHTERLEIN, G. L., AND R. W. STORER. 1985. Aggressive behavior and interspecific killing by Flying Steamer-Ducks in Argentina. *Condor* 87:87-91.
- ORIAN, G. H., AND G. COLLIER. 1963. Competition and blackbird social systems. *Evolution* 17:449-459.
- ORIAN, G. H., AND M. F. WILLSON. 1964. Interspecific territories of birds. *Ecology* 45:736-745.
- PAYNE, R. B. 1973. Behavior, mimetic songs and song dialects, and relationships of the parasitic indigobirds (*Vidua*) of Africa. *Ornithol. Monogr.* No. 11. American Ornithologists' Union, Washington, DC.
- PAYNE, R. B. 1984. Sexual selection, lek and arena behavior, and sexual size dimorphism in birds. *Ornithol. Monogr.* No. 33. American Ornithologists' Union, Washington, D.C.
- PAYNE, R. B., AND K. D. GROSCHUPF. 1984. Sexual selection and interspecific competition: a field experiment on territorial behavior of nonparental finches (*Vidua* spp.). *Auk* 101:140-145.
- SCHOENER, T. W. 1983. Field experiments on interspecific competition. *Am. Nat.* 122:240-285.
- SHAW, P. 1984. The social behaviour of the Pin-tailed Whydah *Vidua macroura* in northern Ghana. *Ibis* 126:463-473.