SEXUAL SELECTION AND INTERSPECIFIC COMPETITION: A FIELD EXPERIMENT ON TERRITORIAL BEHAVIOR OF NONPARENTAL FINCHES (*VIDUA* SPP.)

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ABSTRACT.—Singing male indigobirds (*Vidua raricola* and *V. funerea*) are interspecifically territorial in their local distributions and, as well, respond to experimental presentations of interspecific stimuli. When singing males were experimentally removed from their territories, however, they were replaced by other males of the same species. The distribution of replacements was consistent with an hypothesis of sexual selection but not with one of interspecific competition. Males matched the songs of the males they replaced, suggesting intraspecific song mimicry. *Received 12 April 1983, accepted 6 September 1983.*

SPACING behavior in birds is due both to interspecific competition and intraspecific aggression, but the relative importance of these determinants has not been tested or indeed questioned. Interspecies competition has been inferred from mutually exclusive distributions or reciprocal abundances (Terborgh 1971, Diamond 1973, Terborgh and Weske 1975, Morse 1976), broader habitat ranges where related species are absent ("competitive release") (Terborgh 1971, Diamond 1973, Cody 1974, Terborgh and Weske 1975, Morse 1976), overlap in resources (Cody 1974), and differences in morphology and ecology of coexisting species (Lack 1971). Interspecific competition has been observed more directly in interspecific territoriality (Murray 1971, Catchpole 1978) or in niche expansion or increased demographic success when an ecologically similar species is removed experimentally (Davis 1973, Dhont and Eyckerman 1980). Field experiments on competition among breeding birds are few and have not compared interspecies and intraspecies effects (Slagsvold 1978, Reed 1982, Schoener 1983). Territorial spacing behavior is well known within species and is usually explained in terms of competition for resources necessary for rearing the young (Davies 1978). Intraspecific territorial behavior can also be explained as a result of sexual selection: males hold exclusive mating areas in order to attract females and to ensure paternity, particularly where the young do not depend on the resources of the

male's territory (Hinde 1956, Davies 1978, Morse 1980, Wade and Arnold 1980).

We designed a brief field experiment to test these two interpretations of territorial spacing in two African finches, the indigobirds *Vidua raricola* and *V. funerea*. Each indigobird species lays its eggs in the nest of a foster species of firefinch (*Lagonosticta* sp.), which then rears the young in a mixed-species brood (Payne 1982). Because *Vidua* are brood parasites, there is no conspecific parental care. Males defend "call-site" territories for mating only; a female is active over a large area (2–10 km^2), including the territories of several males (Payne and Payne 1977). Males and females often feed together without apparent aggressive interactions on commons, and even near the call-sites resident males tolerate other males feeding on the ground. The territories are defended for mating, not for the resources necessary to rear a family.

By experimentally removing the singing males and by observing the species identity of the males that replaced them, we tested the relative importance of interspecific competition and intraspecific sexual selection for their local spatial organization. To compare the two hypotheses we tested the following predictions. (1) If male call-site dispersion results from interspecies competition, then the experimental replacements should be by either species according to the numbers of available males of each species. (2) If the dispersion results from
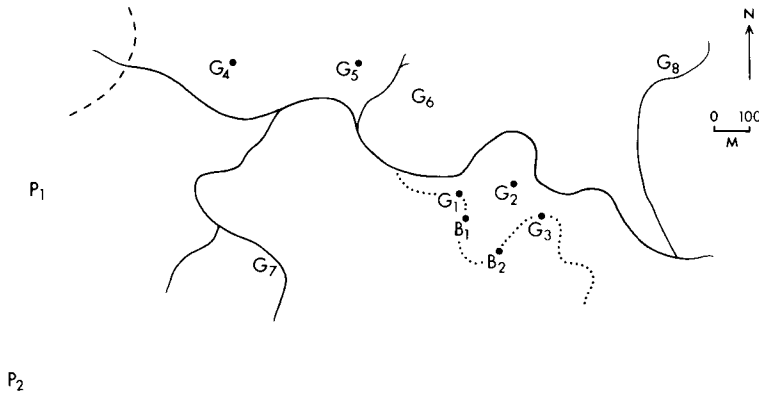
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Fig. 1.   Distribution of call-sites of singing male indigobirds at Banyo, Cameroon. B = *V. funerea*, G = *V. raricola*, P = *V. wilsoni*. Letters indicate the initial local distribution of singing males. Dots indicate the seven call-sites at which males were experimentally removed. B_1 and B_2 were sites of more than one removal. Solid lines indicate streams, the dotted line is a wooded scarp, and the dashed line is the road into Banyo.

intraspecific interactions in the context of sexual selection, then males should replace only their own species. Prediction (1) assumes that interspecific and intraspecific aggressive behaviors are equally intense, as suggested by the interspecific territorial behavior, natural replacements, and chasing observed in other species populations (Payne 1973, 1980). Prediction (2) follows from the behavior of female indigobirds, which visit the call-sites of their own species almost exclusively (Payne 1973, 1980), and recognizes that male interactions are sexual and not resource-related.

METHODS

We observed and experimentally removed singing male indigobirds from their territories in old, shrubby, cultivated fields along a stream at Banyo, Cameroon (6°45'N, 11°50'E). RBP discovered the mixed population two breeding seasons earlier in January 1979; the observations and experiments reported here were made from 5 to 12 November 1980. All indigobird call-sites within 2 km² were mapped. *Vidua raricola* and *V. funerea* were in the same habitat and appeared to be spaced as if they were a single species (Fig. 1). The distances between neighboring call-sites were not obviously greater between conspecifics than between birds of the other species. Field observations of territorial behavior similarly suggested that males did not socially differentiate among species in their spacing. Chases of intruding males were seen both within and between species and involved the singing males of either species on neighboring call-site territories and intruding nonresident males of

either species. Males of the two species are morphologically similar, and we could not identify all intruders to species, although, when they perched we distinguished *V. raricola* as green-glossed and *V. funerea* as blue-glossed. A third local indigobird species, *V. wilsoni*, was found singing only in town, not in the old cultivated fields.

For each territory of *V. raricola* and *V. funerea*, we sampled the percentage of grass cover, percentage of tree cover, height (m) of the call-site perch, and the number of firefinches of each species (*Lagonosticta* spp.). We searched for nests, and we found active nests of both *L. rara* (the foster species of *V. raricola*) and *L. rubricata* (the foster species of *V. funerea*) in the weedy fields. Active nests of *L. rufopicta* (the foster species of *V. wilsoni*) were found only in town. Standardized habitat photographs were taken at each call-site.

We permanently removed 10 males (7 *V. raricola*, 3 *V. funerea*) over a week by attracting the birds into a mist net with the recorded songs and a mounted specimen of another indigobird species, *V. chalybeata*, which occurs within 200 km but not at Banyo. All tested males rapidly attacked the playback speaker and were captured, even though the playback songs were different in detail from their own songs and the mounted specimen was visually distinct (blackish wings vs. light brown wings in the two species tested). The experimental call-site was then observed to determine the species identity of the replacing male. A male was determined to have replaced if he sang on the call-site tree within 1–2 days after the earlier male was removed. A few replacement males were removed in turn, and their replacements were identified. All original and replacement males were tape recorded using a Uher 4000-L tape recorder with a

TABLE 1. Results of removal experiments of singing male indigobirds from their call-sites.

Species removed	Species replacing	
	V. funerea	*V. raricola*
V. funerea	3	0
V. raricola	1	6

parabolic reflector. Their songs were later audiospectrographed on film with a Princeton PAR 4512 real-time spectrum analyzer; selected samples also were analyzed with a Kay Elemetrics Co. Vibralyzer 7030-A. Sample sizes of songs per bird were 3–220 ($n = 1,076$) for 15 *V. raricola* and 8–159 ($n = 562$) for 5 *V. funerea*.

RESULTS

Replacement males at the experimental call-sites were mainly within the same species (Table 1). They were considered to come from a "replacement pool" of local birds that did not have their own call-sites. All of the sites observed before the removals began remained active through the period of observation. The experiments did not exhaust the replacement pool, insofar as we observed chases among males after the removals were completed. If males of the two *Vidua* species behaved as a single species with respect to competition for territories (that is, if the estimated competition coefficient $\alpha = 1$), then the observed replacements at each species' call-sites should be proportional to the number of each kind of male in the active replacement pool (e.g. the 10 males observed to replace removed males; Table 1). If the replacement patterns were due to intraspecific responses, however, then the males should replace only their own species. The ratio of the two species in the replacement pool was used to derive the expected proportions of like-species and unlike-species replacements on the experimental call-sites. A one-tailed test is appropriate in testing the interspecific competition hypothesis, insofar as the alternative hypothesis predicts a direction. The observed values were significantly different from those expected values (Fisher's exact test, one-tailed, $P = 0.03$). The replacements might also conceivably be due to chance, and we cannot totally exclude this possibility (two-tailed $P = 2$ times the one-tailed P, marginally significant at $P = 0.06$). Given the observed intensive ag-

gressive interactions among males and other observed behavior, however, a hypothesis of chance occupancy of the call-site trees seems biologically unrealistic to us. From the results we can reject the interspecific competition hypothesis. The results are consistent with the sexual selection hypothesis.

The results were not explained by any habitat differences in the call-sites of the two indigobirds as far as we could see. The small number of call-sites used precludes statistical testing of the habitat variables, but there were no differences obvious to us in the habitats of the two species' call-sites. Both species had sites at the bushy edges of active manioc plantings, both had perch heights of 2–5 m, both had mean grass cover within 10 m of the site of 10–20%, and both had less than 10% tree cover within 20 m of the call-site. The photographs of each call-site revealed no differences in habitat. There was no tendency for each species' site to be centered on a local site of activity of its foster species of *Lagonosticta*. We regularly saw males foraging away from their call-site, and both indigobird species used the same foraging sites.

Audiospectrograms of songs showed that each species population had a repertoire of distinct song types. Each song type was characterized by an identical sequence of complex song figures or notes. We visually recognized 23 song types in *V. raricola* and 18 song types in *V. funerea*. All *V. raricola* and *V. funerea* at Banyo matched songs with other local conspecifics (Fig. 2); none matched the other local species except in a simple chatter that is common to all indigobird species (Payne 1973, 1982). Nearly all song types were shared by two or more local conspecifics. Within the sample limits of the recorded songs, it appears that all or nearly all song types were shared by all local conspecifics. In replacing a male of the same species, a male with the same complex songs as the original resident took over a site. Except for those songs that mimicked the foster species, no song types matched those of other populations of the same indigobird species recorded in Cameroon and Nigeria. Song dialect populations in indigobirds typically are no more than 10 km² (Payne and Payne 1977, Payne 1981). *Vidua raricola* and *V. funerea* resemble other species of indigobirds in having local nonmimetic song dialects (Payne 1973, 1979, 1981). All nonmimetic song types for each species are population-specific, not species-specific. The conspe-

cific call-site replacements thus were cases of apparent intraspecific song mimicry as well.

DISCUSSION

The distribution of indigobird replacements was correctly predicted from the sexual selection hypothesis. Sexual selection is also indicated by the high variance in male mating success of other species of indigobirds, effected through both competition among males and male choice by females (Payne 1983). Male indigobirds have a greater variance in mating success than such polygynists as *Agelaius phoeniceus* (Payne and Payne 1977, Wade and Arnold 1980). Matings of indigobirds were not observed at Banyo, although females visited the call-sites and males courted the females. In another indigobird species, *V. chalybeata*, it is known that one male may account for more than half of all matings in a local song population of 15–20 singing males in Zambia (Payne and Payne 1977). In that species, both males with call-sites and nonsinging males visited call-sites over a wide area. Marked individuals visited several call-sites within several square kilometers, and some birds moved more than 1 km between their old call-site and their new call-site. The area over which an individual moved also included the call-sites of another indigobird species (*V. purpurascens*), although males only infrequently landed at the call-sites of the other species (Payne 1980). Males did not restrict their movements to the area of a single call-site (Payne and Payne 1977, *contra* Payne 1973). Thus, the potential "replacement pool" involves several males for any one site, but an individual male may occupy one of several sites. In the present field test, individual males were seen visiting at least three sites in succession. The social organization of the two indigobird species at Banyo appears to be similar to that of *V. chalybeata* in Zambia.

The adaptive basis for within-species male replacement on the call-sites may be related to the local population-specific song dialects: a male that replaces an established male at a traditional call-site matches the song repertoire of the original male, and his take-over of a territory may be facilitated by the song mimicry. The replacement male may thereby deceive other males and females into identifying him as the original male, facilitating both his territorial establishment and mate attraction. Tra-
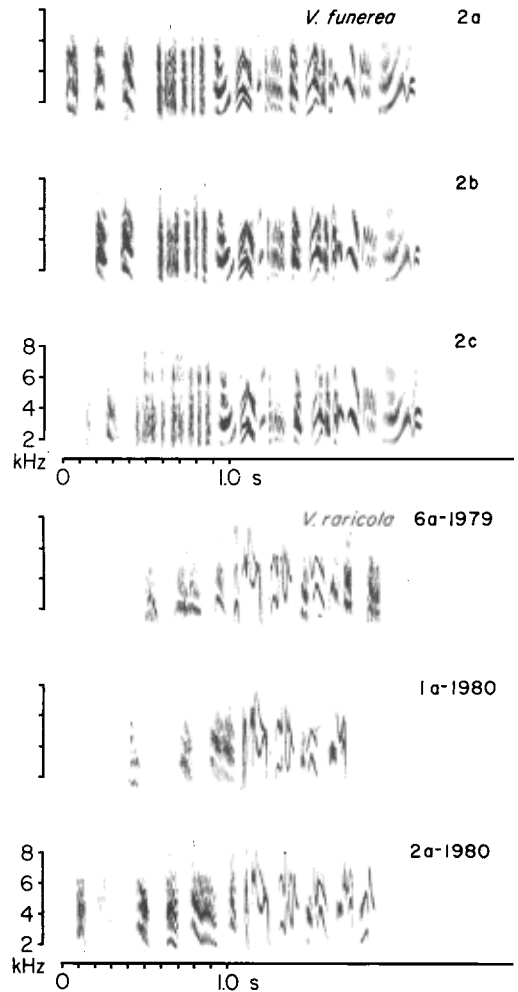

Fig. 2. Song matching within local populations of indigobirds. The top three figures indicate the similarity of one song type of *V. funerea* in the original male (2a) at call-site B₂, his first experimental replacement (2b), and his second experimental replacement (2c). The bottom three figures indicate the similarity of a song of *V. raricola* in early 1979 and the songs of two other males two breeding seasons later. The songs shown are the closest apparent structural match between the species.

ditional use of a call-site was seen at Banyo, as the one site that was active late in the season in January 1979 was used also two breeding seasons later in November 1980 by a different male *V. raricola* with the same song types. The observation that nearly all replacements sang the same song as the male they replaced is consistent with the view that the song sharing of

local indigobirds is a form of intraspecific competitive behavioral mimicry (Payne 1981).

Indigobirds are nevertheless interspecifically territorial. Both at Banyo (Fig. 1) and in other populations (Payne 1973, 1982), indigobird males appeared to be dispersed as if they were a single species, the distances between call-sites of conspecific neighbors being similar to that of allospecific neighbors. Chases were common between species as well as within species. The rapid approach and attack directed to the recorded songs of yet another indigobird species and dummy in the present experiment attest to the intensity of interspecific territoriality.

Why are indigobirds interspecifically territorial? Males court females of other species on the infrequent instances when the females visit their call-site (Payne 1973, 1980). Males without a successful call-site intrude at the successful call-sites and attempt to steal matings, usually within but sometimes between species (Payne 1973, 1980). Occasionally, hybrid offspring result (Payne 1980). With such birds as neighbors, a male that puts other males at a distance from his own call-site is less likely to suffer sexual interference, regardless of whether or not the other males are conspecific. The lack of investment in parental care in these brood parasites minimizes the costs to both sexes of the sexual adventures. We do not regard the interaction of allospecific males interfering with matings as "competition" in the usual sense of that word in population ecology (Wiens 1977, Schoener 1983). Females are not mere "resources." Insofar as males of the other species are real biological threats to a singing male, and as both indigobird species are mutually aggressive to each other, it seems unrealistic to term the active interspecific territorial exclusion as "mistaken identity" or "misdirected intraspecific territoriality," as proposed for other cases of interspecific territoriality by Murray (1971). The intense sexual selection favoring a male that holds a successful call-site indicates the potential benefits to any male of taking over such a site and mating with several females. Reproductive interference within and between species (regardless of whether or not any interspecies hybrids may be produced) and sexual selection within a species thus may determine the observed male territorial behavior between species. In the many other species of birds in which territorial behavior is more closely related to sexual activities than to defense of food resources, it may be helpful to look at territoriality, both within and between species, as the result of sexual selection rather than resource-exclusion competition.

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