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POLYGYNY IN THE WHITE-CROWNED SPARROW (*ZONOTRICHIA LEUCOPHRYS*)

LEWIS PETRINOVICH

AND

THOMAS L. PATTERSON

Blanchard (1941), in her classic monograph on the White-crowned Sparrow (*Zonotrichia leucophrys*), referred to one instance of polygyny. Earlier she described this case in more detail (Blanchard 1936: 149): "In winter both females made free of their common mate's territory, though with some tendency to localization . . . with the approach of reproduction, however, each female created for herself a subdivision of the main territory which she defended against the other female by loud singing and fighting, and in which she finally chose her nest site." She reported that these two females were completely intolerant of one another. In five years of observation she found only three cases of polygyny (DeWolfe 1968). During a long-term study of reproductive success, territoriality, and song of the White-crowned Sparrow, we observed several cases of polygyny.

METHODS

During the 1975 breeding season, (between 21 March and 14 July) we spent a total of 1500 man-hours observing 42 pairs of breeding White-crowned Sparrows. The main study area was on the east side of Twin Peaks in San Francisco, California. We also made numerous observations at the Presidio of San Francisco, about 4 km NE of Twin Peaks. Twenty-five color-banded pairs were studied in detail. Seventeen pairs of birds were studied less completely in other regions of Twin Peaks and at Baker Beach in the Presidio of San Francisco. Most of these latter birds were color-banded for identification, but not all of their nests were located throughout the entire breeding season. Territories were mapped and nests were located and monitored during the breeding season. In addition to gathering data on territorial and reproductive behavior, we observed each of the pairs from 3 to 9 continuous hours, recording all their behavior. When polygynous consorts were identified, we made more observations in order to better describe their behavior.

The study area at Twin Peaks had three separate portions: (A) 120 × 68 m, the southern-most, containing 9 territories; (D) 124 × 77 m, 75 m northward, in a draw, containing 5 territories; and (E) 120 × 100 m, 50 m north of D, containing 11 territories. Areas A and D each contained a male with two mates. No territories were located between the areas, probably because these zones were open, grassy and rock outcrops, lacking vegetation in which to nest or find shelter.

We found one male with two mates in the Presidio (P) but do not know their reproductive success because we found only three nests for these birds and the females were unbanded.

RESULTS

Of the 25 males at Twin Peaks, two (8%) had two

mates; of all 42 males studied during the season, three (7.1%) were polygynous.

Territory size. One of the functions of territoriality is to ensure an adequate food supply for breeding birds. If food supply is important in predisposing White-crowned Sparrows toward a territorial system, we would expect that the territories of the polygynous males would be larger than usual if the birds are to have normal reproductive success. The polygynous male in D indeed had the largest of all the territories (2499 m²), but that of the polygynous male in A was the smallest (451 m²). (Data on territory size for all of the territorial pairs can be found in Patterson and Petrinovich 1978). The mean area of the territories during the first nesting for 16 monogamous pairs was 1417 m², while it was 1475 m² for the two polygynous males. The habitats of the latter did not seem to be any richer in resources than the adjacent territories. The territories of polygynous males did not have more bushes in which to build nests, differ in bush-to-grass ratio, or have differential access to water; they did not appear to be exceptional in any way.

Reproductive success. The four females mated to polygynous males in A and D built an average of 3.25 nests during the season, while the 12 females of monogamous pairs built an average of 3.08 nests. The former birds laid an average of 3.38 eggs per nest (13 nests) while the latter laid an average of 2.99 eggs (81 nests). The polygynous pairs produced an average of 1.85 nestlings and 0.77 fledglings per nest, whereas the normal pairs produced an average of 1.89 nestlings and 0.87 fledglings. (We defined a fledgling as a banded nestling that left the nest between 9 and 11 days of age. The presence of a fledgling was verified by observing the parents carrying insects.) Reproductive outcomes for the entire season are summarized in Table 1. Our findings suggest that the reproductive success of the polygynous pairs was not lower than that of the normal pairs. Each polygynous male had twice the reproductive success of monogamous males, while that of the females was not lowered.

In both the A and the D polygynous families, one

TABLE 1. Reproductive outcome for all polygynous families. (FC = full crown; BC = brown crown.)

	Eggs	Nestlings	Fledglings	Eggs	Nestlings	Fledglings
	First Nesting			Second Nesting		
D _{FC}	3	2	2	4	1	1
D _{BC}	4	3	0	4	4	0
A _{FC}	3	3	3	4	4	0
A _{BC}	3	0	0	3	0	0
P	4	3	3	4	0	0
	Third Nesting			Fourth Nesting		
D _{FC}	4	2	2	4	2	0
D _{BC}	4	1	1	-	-	-
A _{FC}	2	0	0	2	2	2
A _{BC}	Nest abandoned			-	-	-
P	Nest inaccessible			-	-	-

of the females had a fully black and white crown, while the other had a brown crown, indicating that it had been born only the year before (Ralph and Pearson 1971). In both instances, the brown-crowned female's reproductive activities were at least one stage behind those of the full-crowned female. When the full-crowned female had nestlings, the brown-crowned still had eggs; when the full-crowned had fledglings, the brown-crowned had nestlings. This temporal difference was maintained throughout the breeding season for both pairs. The two full-crowned females had higher reproductive success than the brown-crowned females because they fledged nine young while the younger females fledged only one. The low reproductive success of the brown-crowned females could have been due to (1) chance factors, (2) their relative immaturity, or (3) some factor associated with being the "second" female. Ralph and Pearson (1971) found no difference in the amount of black in the crown between successful and unsuccessful breeding males or females in their total population, although they reported that, when both sexes were combined, first-year birds with more black in their crown were less successful. Whatever the reason for the lower success of the brown-crowned females, it was probably not a lack of assistance by the males in feeding the young. In all four cases in which the brown-crowned females lost the eggs or nestlings, this was due to predation. (We either observed predation or inferred it from the fact that eggs were missing or that nestlings were missing before they were old enough to fledge; also, parents were not feeding young or giving warning calls while we searched the area.) Polygyny appeared to be a good practice for males but not for any female who is able to find a monogamous mate.

Behavior. Blanchard observed utter intolerance between females mated to the same male, but we saw complete tolerance in all instances. Both females of the polygynous male were seen feeding together for several minutes at a time, and the male was seen feeding with both females at the same time. Once, we watched the two females on A jointly chase away an intruding female while the male sat by.

The two females with a common mate whom Blanchard (1936) described subdivided the territory and each defended her portion against the other by loud singing and fighting, but we observed nothing of the kind. In fact, the two females tended to nest in the same region of the territory. Distances between nests of the two females in D were as follows: first nesting, 8 m; second, 7 m; third 11 m. The nesting distances in A were: first, 7 m; second, 5 m; third, 16 m.

DISCUSSION

Since unmated males were present throughout the breeding season, and we noted two instances in which a new male appeared to replace a mated male who disappeared, there must have been a surplus of male White-crowned Sparrows in the vicinity of the breeding territories. Our supposition agrees with the finding that surplus males exist in several species (Brown 1969). However, it has seldom been shown that territorial behavior prevents females from breeding. Lack (1968) suggested that polygyny is favored when males are prevented from breeding and nesting sites are scarce. Polygyny is rare in White-crowned Sparrows, possibly because the male normally helps to feed the brood after they have fledged. This permits the female to spend more time and energy

constructing a new nest for the next brood (Blanchard 1941).

The number of available territories in our study area seems to be limited because the number and boundaries of territories have remained stable over a three-year period. If the number of territories is limited, then a surplus female might attempt to mate with a male who is already mated but who possesses an adequate breeding territory. This would be advantageous for the male because he could enhance his reproductive success if he mated with as many females as possible. That is, as long as polygyny did not jeopardize the survival of his primary brood or overload the capacity of his territory, food, nest sites, cover, and space. As Verner and Willson (1966:144) expressed it, "It seems clear that polygyny would be advantageous to a male whenever the total number of successful offspring . . . from all his females exceeds the number that would be reared from one nest if he mated monogamously." Orians (1969) suggested that females might be attracted to an already mated male even if the alternative were to accept an inferior nest site or no site at all.

Since the male takes a major role in feeding the fledglings while the female readies a nest for the next brood and lays eggs (Blanchard 1941), it would be to her advantage to drive out intruding females. It would be of interest to understand the development of the tolerance shown by the mates of the polygynous male; how did they come to tolerate one another, yet not other females?

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Department of Psychology, University of California, Riverside, California, 92502. Accepted for publication 1 July 1976.