

# COMPARATIVE BREEDING BIOLOGY OF THE TWO BILL MORPHS OF THE BLACK-BELLIED SEEDCRACKER

THOMAS BATES SMITH

*Museum of Vertebrate Zoology and Department of Zoology, University of California,  
Berkeley, California 94720 USA*

**ABSTRACT.**—I studied comparative breeding biology of bill morphs of the African finch *Pyrenestes ostrinus* in south-central Cameroon. Bill morphs bred randomly with respect to bill size and differed in diet and feeding efficiencies on various seeds. I designed an analysis to uncover evidence for reproductive divergence between morphs which might be indicative of sympatric speciation. Bill morphs showed no differences in habitat selection for nest sites, clutch size, predation rates, reproductive behavior, and nestling mouth patterns. The distribution of nest initiation dates for large-large and small-small pairs, however, differed significantly. Additionally, the abundance of juvenile large-billed and small-billed morphs were differentially correlated with the densities of two species of sedges on which they differed in handling efficiencies. I hypothesize that reproductive divergence could occur in some geographic regions if changes in rainfall dramatically affected fruiting phenology or diversity of major seeds on which finches feed. Received 17 October 1988, accepted 9 September 1989.

SINCE the 1860s, a major controversy in evolutionary biology has been whether speciation may occur without geographic isolation (Mayr 1982). There are many proposed mechanisms of sympatric speciation (Maynard Smith 1966, Pimentel et al. 1967, Dickinson and Antonovics 1973, Bush 1975a, Rosenzweig 1978, Bengtsson 1979, Gibbons 1979, Rice 1984, Wilson and Turelli 1986, Wilson 1989). One of the earliest models was proposed by Maynard Smith (1966), who showed how a single population that utilized distinct niches could diverge reproductively into isolated subunits. Central to his model is the notion that a stable polymorphism evolves first, with reproductive isolation occurring later between morphs that reproduce separately in the two niches. Although controversial (Mayr 1963, Bush 1975a, Futuyma and Mayer 1980, Felsenstein 1981), several workers claimed to have found evidence for this mode of speciation in insects (Bush 1969, 1975a, b; Knerer and Atwood 1973; Tauber and Tauber 1977a, b, 1982, 1989).

Among vertebrates, possible examples of polymorphism-mediated sympatric speciation events are rare. Perhaps the most noted cases are the species flocks of cichlid fishes in some east African lakes (reviewed in Echelle and Kornfield 1984). Examples of species in the process of sympatric speciation are generally lacking (but see Grant and Grant 1989). Instead, most proposed examples of sympatric speciation involve post hoc analyses in which the

process of sympatric speciation is inferred from the dispersion pattern of already discrete species.

It is in this context that species that show trophic polymorphisms present a unique opportunity. If sympatric speciation occurs and niche divergence by morphs is the vehicle, then polymorphic species with differential niche utilization are strong candidates for investigation of the sympatric speciation process. Yet, despite the ubiquity of polymorphisms (Mayr 1963), there are relatively few examples of *multiple niche* polymorphisms (Hedrick et al. 1976, Mitter and Futuyma 1979, Hindar and Jonsson 1982, Smith 1987, Ehlinger and Wilson 1988).

Recently, an African estrildid finch, the Black-bellied Seedcracker (*Pyrenestes ostrinus*), was found to exhibit a non-sex-linked trophic polymorphism in bill size (Smith 1987, 1988). I showed (Smith 1987, 1988) that morphs are adapted to distinct trophic niches, and each morph differs in its diet and feeding efficiency on hard- and soft-sedge seeds (*Scleria* spp.). Despite significant differences in niche utilization, morphs mated nonassortatively with respect to bill size (Smith 1987). The possibility of differences in reproductive behavior arising as a function of dramatic differences in bill size and niche utilization remains to be examined. In particular, some theoretical models suggest reproductive divergence is more likely if the trait responsible for niche divergence varies discretely (Pimm 1979, Felsenstein 1981). Differences in habitat use or temporal patterns during

reproduction could signal a trend toward divergence and possibly an early step in a sympatric speciation. West-Eberhard (1986) proposed that discontinuous variation such as polymorphisms may be the fundamental building blocks for speciation.

My purpose is to compare and contrast the breeding biologies of two bill morphs in a single population. Specifically, I examined evidence for reproductive divergence, including those temporal and spatial factors which could be indicative of the process of sympatric speciation, such as nest-site selection, timing of nesting in relation to rainfall and food supply, as well as the influences of behavior and predation.

#### METHODS

Research was conducted over a 3-yr period (September–December 1983, January–May 1985, August 1985–November 1986) on a study area in south-central Cameroon (see Smith 1988 for details). The study area is located along the Nyong River and consists of seasonally inundated swamp forest, flood plain, and a floating grass community. To maximize information on the breeding ecology of *Pyrenestes ostrinus*, searches for nests were not restricted to the study area, but encompassed regions in a 10-km radius of the study area. This included several additional habitats such as undisturbed swamp forests (flooded and dry), primary rain forest, and disturbed or man-altered habitats (including coffee, cassava, and cacao plantations and areas in close proximity to human settlements).

The climate of this region is characterized by two distinct rainy seasons: a major rainy season from September through November and a minor season in April and May (Bates 1908; Etia 1980; Smith 1987, 1988). The most severe of the two dry seasons occurs from December to March, when there is little rainfall. Rainfall and maximum and minimum temperatures were determined daily over the course of the study (Smith 1988). I estimated seed abundance of the two most important sedge species in the seedcrackers' diet using randomly chosen quadrats, permanent plots, and quadrats sampled within sedge mats (see Smith 1988 for details).

Individual *P. ostrinus* were mist-netted on the study area, and at nest sites if parents were unidentified. I measured 12 bill and body characters, weighed each individual, and banded them using randomly chosen, unique combinations of numbered aluminum and colored plastic bands (see Smith 1988 for details). Color-banding allowed parents at nests to be identified individually with a spotting scope. Large- and small-billed morphs were identified on the basis of their lower bill width (LBW). Small-billed morphs were

defined as having LBW of  $\leq 14$  mm, large-billed morphs with LBW of  $> 14$  mm (Smith 1987). In cases where the parent was not banded and could not be netted, the bill size of the parent was estimated using binoculars or a spotting scope (Smith 1987, 1988). In trials with birds of known bill size, there was little difficulty in classifying morphs (Smith unpubl. data).

Finding *P. ostrinus* nests is difficult because seed-crackers do not defend territories (Smith 1988). With the exception of nests under construction, adults are seldom seen near the nest. Nests were found primarily by field-workers searching through the vegetation individually or in groups. Whenever possible, searches were conducted systematically: three or more workers spaced at 10-m intervals walked a transect along a compass bearing. Flooded swamp forest was searched in dugouts or inflatable boats. Villagers also helped to locate nests.

Once a nest was located, I recorded the habitat type, the species of tree or bush in which it was constructed, the height above the ground or water, the number of eggs or young, and general characteristics. I estimated nest-initiation dates based on developmental stage. Each nest was defined conservatively as either initiated during the first or second half of a month. Nests were monitored intensively, often from sunrise to sunset, to determine the bill sizes of the parents, the frequency of nest exchanges, and the behavior of parents at the nest. Observations were made either from a blind or from 20–30 m away, depending on the pair's shyness.

Statistical analysis was done using the SAS statistical programs (SAS Institute 1985) on the University of California's IBM 4341 computer. Some statistical analysis was also performed using a microcomputer and Statgraphics Statistical Package (STSC Inc. 1986).

#### RESULTS

*Nest-site selection.*—*Pyrenestes ostrinus* nested in a wide variety of habitats and was not restricted to swamp forest where foraging occurs. The 76 nesting individuals whose bill size was determined nested in six distinct habitats (Table 1). There were no significant differences in habitat choice between bill morphs nesting in plantations, near villages, and in forest ( $\chi^2 = 1.095$ ,  $P > 0.578$ ). There was, however, a nearly significant difference between morphs nesting in dry vs. swamp forests (Fisher's exact test,  $P = 0.11$ ).

To examine if nesting habitats of pairs were nonrandomly associated with certain habitats, I compared homotypic (small-small or large-large) and heterotypic (small-large) pairs between man-altered habitats (i.e. plantations and nearby villages) and habitats not altered by man.

TABLE 1. Percentages of large- and small-billed morphs that nest in various habitats.

Habitat	Small morph ( <i>n</i> = 54)	Large morph ( <i>n</i> = 22)
Plantations		
Cassava	13.0	5
Coffee	18.5	18
Cacao	11.0	9
Village	24.0	23
Swamp forest	15.0	36
Dry forest	18.5	9

No significant associations between pair type and habitat were found (Fisher's exact tests: small-small pairs vs. mixed,  $P = 0.99$ ; large-large vs. mixed,  $P = 0.37$ ; small-small vs. large-large,  $P = 0.12$ ). Comparison of homotypic pairs approached significance, which suggests that small-billed pairs may nest in man-altered habitats at a slightly higher frequency.

Average nest height of homotypic and heterotypic pairs did not differ significantly ( $F = 0.03$ ,  $df = 38$ ,  $P > 0.97$ ). Generally, most nests were constructed within a few meters of the substrate; however, the range of heights varied, with a few nests constructed as high as 9 m above the ground. There were no apparent differences among pair types in substrates chosen for nesting or nest construction.

**Breeding phenology.**—Breeding activity begins with the onset of the rainy season (Smith 1988). In 1985, nest building began toward the middle of September after rainfall had been high for nearly a month and continued through October (Fig. 1). Although there were few nests in 1985 in which the bill size of both parents were determined, there was clear overlap in nest-initiation dates of homotypic and heterotypic pairs (Fig. 1).

In 1986, most nesting was initiated during the second half of August, coinciding with the first heavy rains (Fig. 2), and peaked in September. All 10 nesting attempts between early May and the end of July, which included four pairs for which bill sizes were determined, failed to produce young. Capture data of recently fledged juveniles also suggested nesting occurred primarily from September through October. Only a single large-billed juvenile was netted during the entire month of July. The numbers of netted large- and small-billed juveniles increased in August and September, peaking in October (Fig. 3).

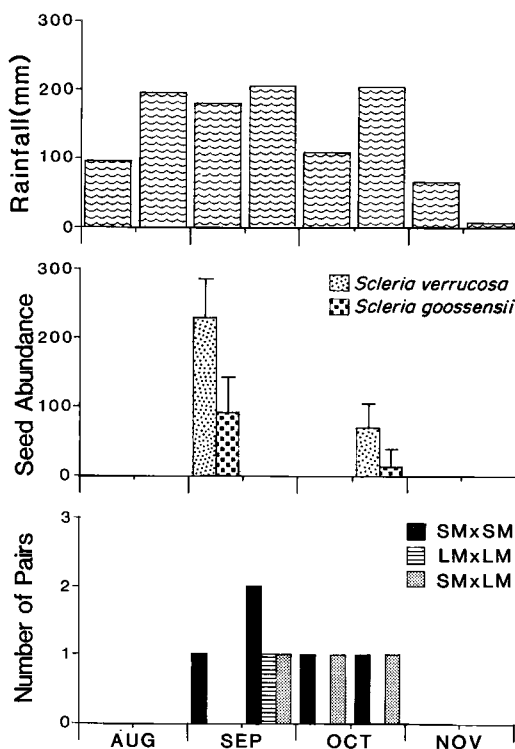


Fig. 1. Timing of nest initiation of known homotypic and heterotypic pairs in relation to rainfall and food supply during 1985. Nest initiation dates were estimated from the stage of development when the nest was found. Months were divided in halves (1-14, 15-31). Seed abundance ( $\bar{x} \pm SE$ ) was measured using random quadrats and was not sampled in August or November. SM = small morph; LM = large morph.

Although complete temporal divergence between pair types did not occur in either year, there was evidence for partial divergence. In 1986, homotypic large-billed pairs tended to initiate nesting earlier than homotypic small-billed pairs (Kolmogorov-Smirnov two-sample test,  $P < 0.001$ ; Fig. 2). The distribution of homotypic large-billed pairs was also significantly different from the distribution of heterotypic pairs ( $P < 0.001$ ). Nest initiation dates between homotypic small-billed pairs and heterotypic pairs did not differ significantly.

**Breeding in relation to food supply.**—Juvenile morph abundance estimated from mist-netting was differentially correlated with the abundances of the two major sedges, large-billed juveniles with the density of hard-seeded *Scleria*

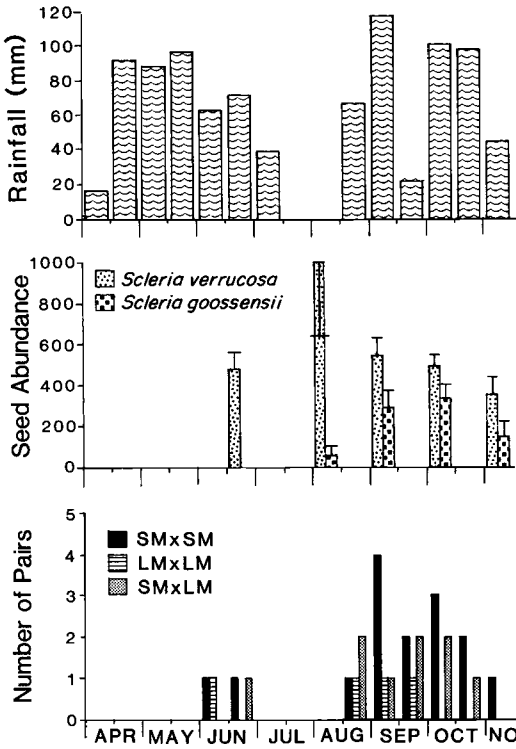


Fig. 2. Timing of nest initiation for known homo- and heterotypic pairs in relation to rainfall and food supply during 1986. Seed abundance ( $\bar{x} \pm SE$ ) was measured by sampling standing stalks within sedge mats in the forest each month (Smith 1988). SM = small-billed morph; LM = large-billed morph.

*verrucosa*, and small-billed juveniles with densities of the soft-seeded *Scleria goossensii* (Table 2). The distributions of sedge abundance in 1986 also varied (Kolmogorov-Smirnov two-sample test,  $P < 0.02$ ). The species of hard-seeded sedge was relatively more abundant earlier in the year than the species with soft seeds (Fig. 2).

**Reproductive behavior.**—Before the onset of nesting, males displayed frequently. Males display by holding a leaf, a grass panicle, or a long blade of grass in their bill tip, and they bob up and down while perched, frequently singing simultaneously. Although this behavior was not quantified, the display is similar to that found in many estrildid finches (Goodwin 1982). I observed 36 displays of which 42% involved small-billed males, 30% large-billed males, and 25% both bill types, and I found no qualitative differences in display behavior between morphs.

Males of both morphs were observed to perform displays at several locations, including near

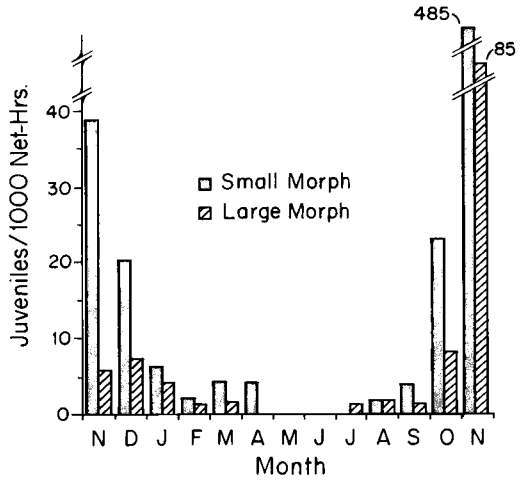


Fig. 3. Number of juveniles ( $\leq 5$  months of age) of each morph captured per 1,000 net-hours. Data are from November 1985 through November 1986 for 155 juveniles. Total net-hours for each month were, in 1985, November = 515, December = 694; in 1986, January = 475, February = 1,501, March = 1,198, April = 979, May = 904, June = 930, July = 772, August = 2,126, September = 1,589, October = 1,116, November = 67.

nests, in swamp forest on perches that varied in height above the ground, and at the roost in the evening. Displays were recorded continuously from late March through mid-November, and they peaked in April and September (Smith 1988). Displays at the roost contrasted sharply with those in the forest. Between 1700 and 1800, we frequently observed a single displaying male joined by others. These additional males did not display but would perch within 1–2 m of the displaying male. Females, although always present at the roost, were not always near the displaying males. It was not possible to determine bill sizes of all displaying birds, but it was clear that morphs did not assort positively with respect to display areas. For example, during one display by a male with an undetermined bill size, I counted six small and three large male morphs in addition to one small and one unidentified female morph, all within 2 m of the displaying male.

**Clutch size.**—Small- and large-billed females had mean clutch sizes of 3.4 and 3.9 eggs, respectively, but this difference was not significant ( $t = -1.22$ ,  $df = 15$ ,  $n = 17$ ,  $P > 0.01$ ). Larger samples will be required to assess differences in fecundity, if any.

TABLE 2. Correlation coefficients between the abundance of the two major sedges (*Scleria*) and abundance of recently fledged juvenile morphs (\* =  $P < 0.05$ ).

Species	Small morph	Large morph
<i>S. verrucosa</i>	0.4167	0.7662*
<i>S. goossensii</i>	0.6908*	0.6658

**Predation.**—Predation appears to be the major source of nest failure. I could not test for differences between morphs in fledging success because few nests were successful (only 15% of the nests fledged offspring). When nesting success was adjusted for time of development (see Mayfield 1975, Johnson 1979), the success rate was 16%. Nest failures were not significantly different between homotypic and heterotypic pairs (Fisher's exact test,  $P = 0.99$ ).

**Nestling mouth patterns.**—Juvenile estrildid finches have distinctive mouth patterns (Goodwin 1982). Similar mouth markings are believed to represent close taxonomic relationships (Delacour 1943, Steiner 1960). Nicolai (1964, 1969) claims parents may reject and not feed young with mouth markings unlike those of their species. Species-specific mouth patterns may enable parents to identify young which are not their own, thereby deterring nest parasitism (but see Immelmann et al. 1977). If nestling mouth markings differed between morphs, then differential survival of nestlings could result by parents not feeding nestlings with particular mouth patterns. However, I examined mouth markings of >50 recently fledged juveniles and found that both large and small morphs had identical mouth markings (Fig. 4).

#### DISCUSSION

There is little evidence for reproductive divergence of morphs through habitat selection. Both large and small morphs appear to utilize the same habitats for nesting. Chapin (1954), unaware that *P. ostrinus* was polymorphic for bill size, placed distinct bill forms in separate races, but he suggested the simultaneous occurrence of small- and large-billed forms was the result of recent habitat alterations caused by man. I found no significant differences in the frequency of homotypic and heterotypic pairs in various habitats, whether they were

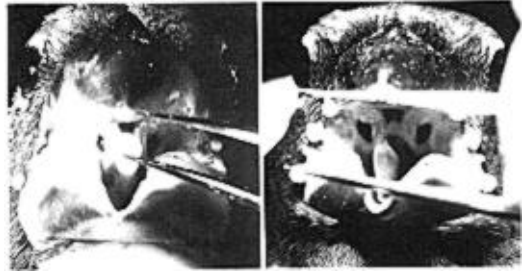


Fig. 4. Mouth markings of large (left) and small (right) morphs. Both had fledged recently, although the large morph was probably slightly older and had already lost several tubercles on the side of the gap.

man-altered or not. Nor were there differences in other structural components of the habitat, such as the heights at which pairs nested. Morphs preferred specific substrates for nesting, but these did not differ between morphs. Considering their nonterritoriality and wide foraging range even during the breeding season (Smith 1988), the high frequency of nests in plantations may be due to the large number of good nesting trees, particularly coffee trees that have crowns characterized by many small branches.

Given that bill types of male *P. ostrinus* are indistinguishable in plumage (Chapin 1954) but differ in bill size, certain differences in behavior may lead to reproductive divergence. For instance, marked differences in female choice theoretically can result in runaway selection promoting reproductive divergence and speciation (Lande 1981, Kirkpatrick 1982, Arnold 1983). In *P. ostrinus*, the sex ratio is 2:1 in favor of males (Smith 1987), which implies that half of all adult males may not obtain mates. This raises the possibility of strong female choice. In *Geospiza fortis* and *G. conirostris*, females choose mates on a variety of characteristics that include plumage coloration, courtship behavior, and bill and body size (Price 1984, Grant 1986, Grant and Grant 1987). In the 1985 and 1986 breeding seasons, *P. ostrinus* females appeared to choose mates irrespective of bill or body size (Smith 1987). Yet, female choice could potentially have an important impact on fitness. For instance, in times of food shortage a female might choose to mate preferentially with a male whose bill best matches the availability of a particular sedge. If hard seeds are more abundant than soft seeds, a small-billed female could achieve higher fit-

ness by mating with a large-billed male that was able to feed offspring processed hard seeds. Such a situation seems plausible. For instance, Price (1984) found females of *G. fortis* chose to mate with larger males after a severe drought skewed the sex ratio in favor of males.

Reproductive divergence could also occur if morphs bred at different times. Among host-specific, phytophagous, or parasitic insects, sympatric speciation is believed to occur through ecological isolation (Bush 1975b). Premating isolation results from shifts to new hosts and provides a barrier to gene flow between parental and daughter populations. This is believed to have occurred in the tephritid fly (*Rhagoletis pomonella*; Bush 1969). Temporal shifts in reproduction that arise when morphs synchronize reproduction with the most favorable seasonal conditions is also an integral part of the model of sympatric speciation in lacewings (*Chrysopa*) proposed by Tauber and Tauber (1977a, b, 1989). In southern Cameroon, there is a bimodal rainy season, and many species breed during both seasons (Bates 1908). In 1986, both large and small morphs attempted to breed in both seasons but bred successfully only during the major rainy season. Nest-initiation dates for large-large pairs, however, were significantly earlier than in small-small pairs.

Differing feeding efficiencies on the two sedges may explain the divergence in nest-initiation dates. Like many avian species, the timing of reproduction in *P. ostrinus* appears to be largely determined by the abundance of food at fledging (Lack 1968, Newton 1972). Adults feed young a mixture of foods that consists mostly of sedge seeds with some insects (Smith 1988). Small-billed morphs readily crack, and have relatively higher feeding efficiencies on, the soft sedge, but they are very poor at cracking the hard sedge. Thus survival of juvenile small morphs would be enhanced later in the main breeding season, when the density of the soft-seeded sedge is highest. This may explain the significant correlation between soft-seeded sedge abundance and numbers of recently fledged small-billed juveniles. In contrast, large morphs, although less efficient at cracking soft seeds, readily feed on hard seeds (Smith 1987). Nevertheless, handling efficiencies predict that large morph production should also coincide with abundance of soft-seeded sedge since handling times on these seeds are still less than on the hard seeds. Yet, abundance of juvenile large

morphs was correlated significantly only with the abundance of hard-seeded sedge. Thus, if morph production was maximized to coincide with maximal food availability, other factors must be operating. One factor which could result in greater reliance of large morphs on hard-seeded sedge is intraspecific competition between morphs (Smith 1988). Without additional data, however, any conclusions are speculative. In particular, the genetic and environmental mechanisms that maintain the polymorphism must be determined.

Dependence on the same foods during the breeding season contrasts sharply with diet at other times of the year. I found (Smith 1988) that, during the dry season, diet overlap between morphs fell to 12%. At this time of year, large morphs feed exclusively on the hard seeds while small morphs feed on a variety of soft seeds. This raises the possibility of reproductive isolation during extreme environmental conditions. For example, if soft-seeded sedges are absent or at low densities during the breeding season, large morphs might time breeding to coincide with the production of the hard sedge. In contrast, small morphs, unable to feed efficiently on the hard seeds, might time reproduction to coincide with other, softer foods. Under these circumstances complete reproductive divergence between morphs could occur. This appears unlikely on the study area, where the annual cycle of rainfall is predictable and the two main sedges co-occur (Smith 1988). However, in regions of Africa which experience greater variance in annual rainfall and where the dispersion of sedge species is different, reproductive divergence leading to sympatric speciation seems plausible.

#### ACKNOWLEDGMENTS

I thank the government of the Republic of Cameroon for permission to conduct the research. For assistance in the field, I thank M. Derr, M. Gellerman, H. Hill, J. Jenkins, F. Kameni, J. Mbita, J. Parrot, S. Raker, T. Sales, J. Smith, P. Springer, C. Swarth, D. Tejiogho, C. Vieth, T. Zoua, and the people of Ndibi. For identifying plant materials, I thank P. Goetghebeur and D. Thomas; and for assistance with various drafts of the manuscript, I thank H. Baker, P. Grant, J. Patton, and F. Pitelka. I am especially grateful to F. Pitelka for support and encouragement, and to my wife, Paige, who made the work feasible. Without the assistance of the staff of the Yaounde office of the United States Information Service, the British Consul, the Shaws, and G. Greer, much of the work would

have been impossible. The research was supported by grants from the National Geographic Society; National Science Foundation, dissertation improvement grant; American Ornithologist's Union, Alexander Wetmore award; National Academy of Sciences, Joseph Henry Fund; and the Museum of Vertebrate Zoology, University of California. For equipment loans, donations, and assistance, I thank Johnson Camping, Inc., The North Face, Boston Whaler, Inc., Swiss Air, and Pan American Airlines. This paper represents paper 14 of Ecology Research Associates.

## LITERATURE CITED

- ARNOLD, S. J. 1983. Sexual selection: the interface of theory and empiricism. Pp. 67-107 in *Mate choice* (P. Bateson, Ed.). Cambridge, Cambridge Univ. Press.
- BENGTSSON, B. 1979. Theoretical models of speciation. *Zool. Scr.* 8: 303-304.
- BATES, G. L. 1908. Observations regarding the breeding seasons of the birds in southern Kamerun. *Ibis* 2: 558-570.
- BUSH, G. L. 1969. Sympatric host race formation and speciation in frugivorous flies of the genus *Rhagoletis* (Diptera, Tephritidae). *Evolution* 23: 237-251.
- . 1975a. Modes of animal speciation. *Annu. Rev. Ecol. Syst.* 6: 339-364.
- . 1975b. Sympatric speciation in phytophagous parasitic insects. Pp. 187-206 in *Evolutionary strategies of parasitic insects and mites* (P. W. Price, Ed.), New York, Plenum.
- CHAPIN, J. P. 1954. The birds of the Belgian Congo. *Am. Mus. Nat. Hist.* 75: 1-846.
- DELACOUR, J. 1943. A revision of the subfamily Estrildinae of the family Ploceidae. *Zoologica* 28: 69-86.
- DICKINSON, H., & J. ANTONOVICS. 1973. Theoretical considerations of sympatric divergence. *Am. Nat.* 107: 256-274.
- ECHELLE, A. A., & E. KORNFIELD. 1984. Evolution of fish species flocks. Orono, Univ. of Maine Press.
- EHLINGER, T. S., & D. S. WILSON. 1988. Complex foraging polymorphism in bluegill sunfish. *Proc. Natl. Acad. Sci. USA* 85: 1878-1882.
- ETIA, P. M. 1980. Climate. Pp. 17-19 in *Atlas of Cameroon* (G. Laclavere, Ed.). Paris, Jeune Afrique.
- FELSENSTEIN, J. 1981. Skepticism towards Santa Rosalia, or why are there so few kinds of animals? *Evolution* 35: 124-138.
- FUTUYMA, D. J., & G. C. MAYER. 1980. Non-allopatric speciation in animals. *Syst. Zool.* 29: 254-271.
- GIBBONS, J. R. H. 1979. A model for sympatric speciation in *Megarhyssa* (Hymenoptera: Ichneumonidae): competitive speciation. *Am. Nat.* 114: 719-741.
- GOODWIN, D. 1982. *Estrildid finches of the world*. Ithaca, Cornell Univ. Press.
- GRANT, P. R. 1986. *Ecology of Darwin's finches*. Princeton, Princeton Univ. Press.
- , & B. R. GRANT. 1987. Mate choice in Darwin's finches. *J. Linnean Soc. London* 32: 247-270.
- , & ———. 1989. Sympatric speciation and Darwin's finches. Pp. 433-457 in *Speciation and its consequences* (D. Otte and J. A. Endler, Eds.). Sunderland, Massachusetts, Sinauer Assoc.
- HEDRICK, P. W., M. E. GINEVAN, & E. P. EWING. 1976. Genetic polymorphism in heterogeneous environments. *Annu. Rev. Ecol. Syst.* 7: 1-32.
- HINDAR, K., & B. JONSSON. 1982. Habitat and food segregation of dwarf and normal arctic charr (*Salvelinus alpinus*) from Vangsvatnet Lake, western Norway. *Can. J. Fish. Aquat. Sci.* 39: 1030-1045.
- IMMELMANN K., J. K. STEINBACHER, & H. E. WOLTERS. 1977. Experimentelle Untersuchungen zur Bedeutung der Rachenzeichnung junger Zebrafinnen. *Zeitschrift für Tierpsychologie* 45: 210-218.
- JOHNSON, D. H. 1979. Estimating nest success the Mayfield method and an alternative. *Auk* 96: 651-661.
- KIRKPATRICK, M. 1982. Sexual selection and the evolution of female choice. *Evolution* 36: 1-12.
- KNERER, G., & C. E. ATWOOD. 1973. Diprionid sawflies: polymorphism and speciation. *Science* 179: 1090-1099.
- LACK, D. 1968. *Ecological adaptations for breeding birds*. London, Methuen and Co., Ltd.
- LANDE, R. 1981. Models of speciation by sexual selection of polygenic traits. *Proc. Nat. Acad. Sci.* 78: 3721-3725.
- MAYFIELD, H. 1975. Suggestions for calculating nest success. *Wilson Bull.* 87: 456-466.
- MAYNARD SMITH, J. 1966. Sympatric speciation. *Am. Nat.* 100: 637-650.
- MAYR, E. 1963. *Animal species and evolution*. Cambridge, Harvard Univ. Press.
- . 1982. *The growth of biological thought*. Cambridge, Massachusetts, Harvard Univ. Press.
- MITTER, C., & D. J. FUTUYMA. 1979. Population genetic consequences of feeding habits in some forest Lepidoptera. *Genetics* 93: 1005-1021.
- NEWTON, I. 1972. *Finches*. London, William Collins and Sons.
- NICOLAI, J. 1964. Der Brutparasitismus als ethologisches Problem. Prägungsphanomene als Faktoren der Rassen- und Artbildung. *Zeitschrift für Tierpsychologie* 21: 129-204.
- . 1969. Beobachtungen an Paradieswitwen (*Steganura paradisaea* L., *Steganura obtusa* Chapin) und der Strohwitwe (*Tetraenura fisheri* Reichenow) in Ostafrika. *J. Ornithol.* 110: 421-447.
- PIMENTAL, D., G. J. C. SMITH, & J. SOANS. 1967. A population model of sympatric speciation. *Am. Nat.* 101: 493-504.
- PIMM, S. L. 1979. Sympatric speciation: a simulation model. *J. Linnean Soc. London* 11: 131-139.
- PRICE, T. D. 1984. Sexual selection on body size,

- territory and plumage variables in a population of Darwin's finches. *Evolution* 38: 327-341.
- RICE, W. R. 1984. Disruptive selection on habitat preference and the evolution of reproductive isolation: a simulation study. *Evolution* 38: 1251-1260.
- ROSENZWEIG, M. L. 1978. Competitive speciation. *J. Linnean Soc. London* 10: 275-289.
- SAS INSTITUTE. 1985. SAS user's guide: statistics. Cary, North Carolina, SAS Institute.
- SMITH, T. B. 1987. Bill size polymorphism and intraspecific niche utilization in an African finch. *Nature* 329: 717-719.
- . 1988. Evolutionary ecology of African Seed-crackers (Estrildidae: *Pyrenestes*). Ph.D. dissertation, Berkeley, Univ. California.
- STEINER, H. 1960. Klassifikation der Prachtfinken, Spermestidae, auf Grund der Rachenzeichnungen ihrer Nestlinge. *J. Ornithol.* 101: 421-447.
- STSC INC. 1986. Statgraphics statistical graphics system. Rockville, Maryland.
- TAUBER, C. A., & M. J. TAUBER. 1977a. Sympatric speciation based on allelic changes at three loci: evidence from natural populations in two habitats. *Science* 197: 1298-1299.
- , & ———. 1977b. A genetic model for sympatric speciation through habitat diversification and seasonal isolation. *Nature* 268: 702-705.
- , & ———. 1982. Maynard Smith's model and corroborating evidence: no reason for misinterpretation. *Ann. Entomol. Soc. Am.* 75: 5-6.
- , & ———. 1989. Sympatric speciation in insects: perception and perspective. Pp. 307-344 in *Speciation and its consequences* (D. Otte and J. A. Endler, Eds.). Sunderland, Massachusetts, Sinauer Assoc.
- WEST-EBERHARD, M. J. 1986. Alternative adaptations, speciation, and phylogeny (a review). *Proc. Natl. Acad. Sci. USA* 83: 1388-1392.
- WILSON, D. S. 1989. The diversification of single gene pools by density- and frequency-dependent selection. Pp. 366-385 in *Speciation and its consequences* (D. Otte and J. A. Endler, Eds.). Sunderland, Massachusetts, Sinauer Assoc.
- , & M. TURELLI. 1986. Stable underdominance and the evolutionary invasion of empty niches. *Am. Nat.* 127: 835-850.