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## SEXUAL DIMORPHISM AND DIFFERENTIAL NICHE UTILIZATION IN BIRDS

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Adaptive radiation has been defined as the evolutionary divergence of members of a phyletic line into different niches or adaptive zones (Mayr, 1963:633). Although it has been customary to think of adaptive radiation solely in terms of species or races, a growing body of evidence indicates that some degree of radiation occurs also within populations, as individuals come to occupy different subniches or adaptive subzones, subdividing and, perhaps, expanding the total niche or zone utilized by the population. Probably all species show some degree of ecological variation, either polymorphic or continuous. But this phenomenon is being studied in only a few groups of organisms, notably in *Drosophila*, in which chromosomal polymorphism has been interpreted as a means of adaptation of populations to heterogeneous environments (Dobzhansky, 1961, 1963, 1965). Theoretical bases for research on ecological variation in animal populations have been provided by Ludwig (1950), Levene (1953), da Cunha and Dobzhansky (1954), Dempster (1955), Li (1955), Carson (1959), and Levins (1962, 1963).

In birds, as in other vertebrates, the sexes usually differ in size if not also in proportions of body parts, including those used in feeding (Amadon, 1959); and, especially where the degree of sexual dimorphism, which is a form of polymorphism (Ford, 1961:12), is marked, it seems probable that the morphological divergence has ecological significance in adapting the sexes to different subniches. However, there is only an occasional reference in the literature to sexual dimorphism in relation to niche utilization (e.g., Pitelka, 1950; Rand, 1952), and, in general, the whole problem of ecological variation in populations has been neglected by vertebrate ecologists.

The primary purpose of this report is to present evidence of an adaptive function of sexual dimorphism in size in woodpeckers by relating degrees of morphological dimorphism and sexual divergence in foraging behavior in two melanerpine species, the strongly dimorphic Hispaniolan Woodpecker (*Centurus striatus*) of Haiti and the Dominican Republic and the moderately dimorphic Golden-fronted Woodpecker (*Centurus aurifrons*) of continental North and Central America. In addition, the paper surveys other evidence that sexual dimorphism in birds is related to differential niche utilization. Finally, some evolutionary aspects of sexual dimorphism and ecological variation are considered.

### SEXUAL DIMORPHISM AND NICHE UTILIZATION IN *CENTURUS* WOODPECKERS

#### GENERAL BACKGROUND

In a systematic review of *Centurus* (Selander and Giller, 1963), it was noted that certain woodpeckers endemic to the West Indies show greater degrees of sexual dimorphism in bill dimensions than do continental species of the same or related genera (fig. 1). In most woodpeckers sexual dimorphism in bill length (full culmen) does not exceed 10 per cent; but in *Centurus striatus*, a species endemic to Hispaniola, the

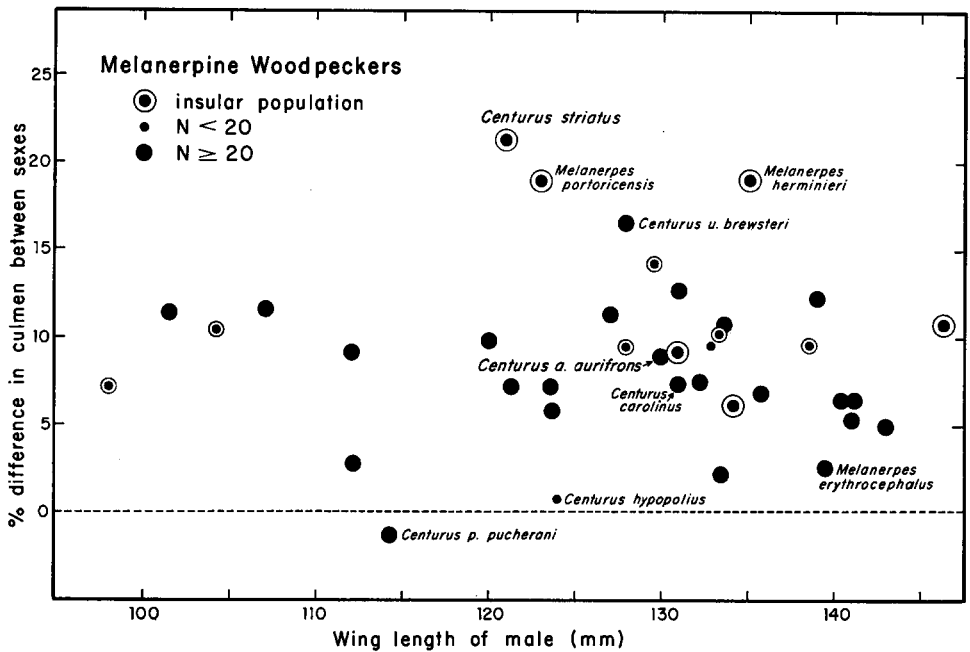


Figure 1. Variation in degree of sexual dimorphism in bill length (culmen) in melanerpine woodpeckers. Note lack of relationship between degree of dimorphism and body size (as indicated by wing length of male).

bill of the female is, on the average, 21.3 per cent shorter and 12.1 per cent shallower than that of the male, although the sexual difference is only 6.4 per cent in cube root of body weight, 9.6 per cent in tarsus length, and 4.4 per cent in wing length (table 1). In size *C. striatus* is the most dimorphic woodpecker occurring in North and Central America and the West Indies. But relatively great sexual dimorphism in bill dimensions, particularly in length, is also found in *Melanerpes portoricensis* of Puerto Rico (18.9 per cent difference in bill length), *Melanerpes herminieri* of Guadeloupe Island, Lesser Antilles (19.0 per cent), and *Xiphidiopicus percussus* of Cuba (15.2 per

TABLE 1  
SEXUAL DIMORPHISM IN SIZE IN *Centurus*  
(Expressed as percentage difference in mean measurements of sexes)

Item	<i>Centurus aurifrons</i>	<i>Centurus striatus</i>
Wing	2.2	4.4
Tail	3.3	4.3
Bill length	9.1	21.3
Bill depth	8.2	12.1
Tarsus	2.5	9.6
Weight	10.5	18.1
Cube root of weight	3.6	6.4
Mean <sup>1</sup>	4.81	9.68

<sup>1</sup> Linear dimensions and cube root of weight.

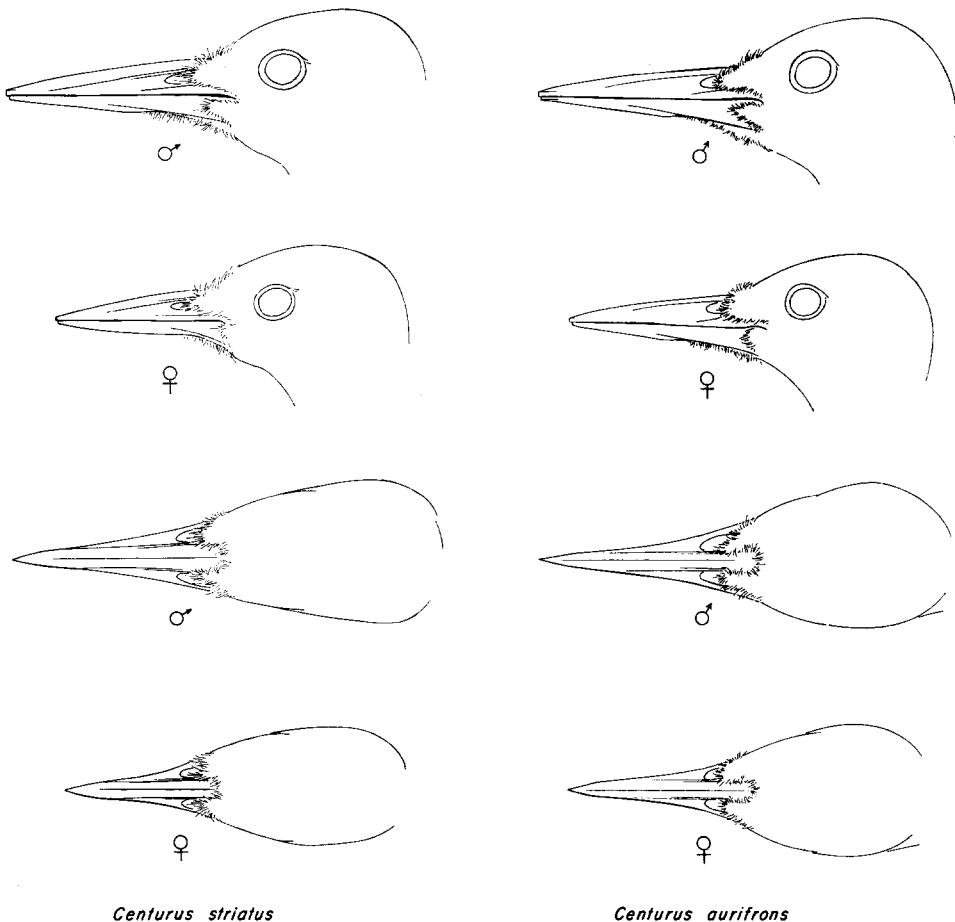


Figure 2. Lateral and dorsal views of heads of two species of *Centurus* woodpeckers, showing marked sexual dimorphism in bill size in the insular species *C. striatus* and moderate dimorphism in the continental species *C. aurifrons*.

cent). Additionally, populations of two other woodpeckers, *Centurus uropygialis* and *Dendrocopos scalaris*, occurring in the insularlike environment at the southern end of the peninsula of Baja California, apparently are more dimorphic in bill dimensions than are mainland continental populations of these species.

In bill length of adult specimens of *C. striatus* (figs. 2 and 3), there is no observed overlap between the sexes, the largest female being smaller than the smallest male. This contrasts with the situation in continental species of woodpeckers, of which *C. aurifrons* is a typical representative, in which there is extensive or, occasionally, complete sexual overlap in bill length. The percentage difference is 9.1 for the population of *C. aurifrons* studied in Texas, with a coefficient of difference (C.D.) of 0.96, indicating approximately 83 per cent joint nonoverlap between the sexes (see Mayr *et al.*, 1953:146). Because the increased dimorphism in bill dimensions in *C. striatus* is not accompanied by decreased variability within either sex, the greater dimorphism results

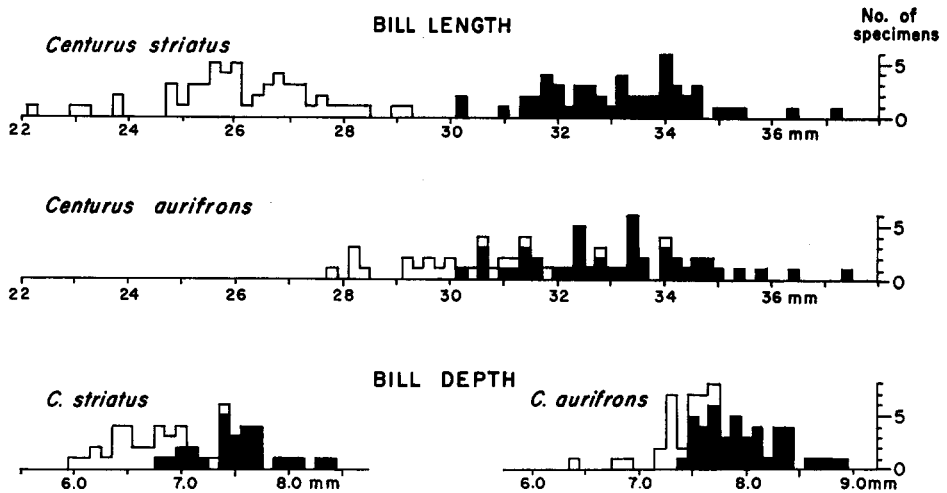


Figure 3. Individual and sexual variation in bill length and bill depth in two species of *Centurus*. Solid histograms, males; open histograms, females.

in an increase of approximately one-third in the total span of bill lengths represented in the adult segment of the population (fig. 3).

In developing a hypothesis to explain interspecific variation in the degree of sexual dimorphism in size in woodpeckers, Donald R. Giller and I (1963) were impressed with the fact that, among species of North and Central America and the West Indies, the greatest dimorphism is shown by three insular forms, *Centurus striatus*, *Melanerpes portoricensis*, and *Melanerpes herminieri*, each of which is the only resident species of woodpecker on its respective island. Because islands inhabited by these species are ecologically diversified and, therefore, seemingly provide habitats and niches for several woodpeckers, we suggested that freedom from competition with species of similar adaptive type had permitted the insular forms to achieve a wider and more thorough exploitation of available food resources through evolutionary divergence of the sexes in foraging behavior, which was accompanied by increased sexual dimorphism in size, particularly in bill dimensions. But without information on the foraging behavior of the insular woodpeckers, this hypothesis could not be tested. Field studies have now been made, and the data demonstrate a relationship between sexual dimorphism in size and differential foraging behavior.

#### SYSTEMATIC RELATIONSHIPS

The Hispaniolan Woodpecker is generally regarded as an aberrant species of *Centurus* (Bond, 1961, 1963), although Wetmore and Swales (1931) and Selander and Giller (1963) have supported W. DeW. Miller's suggestion (1915) that, pending study of generic limits in the melanerpe complex, it should be assigned to a monotypic genus, *Chryserpes*. As a result of my recent study of the behavior and ecology of this woodpecker, I now believe that it should be classified as a *Centurus*.

*C. aurifrons* is a polytypic species showing exceptional geographic variation in morphological characters and in habitat distribution within its large range, which extends from Texas to Nicaragua. The particular population studied in south-central Texas belongs to the subspecies *C. a. aurifrons*, and measurements used in this study

TABLE 2  
MEASUREMENTS OF *Centurus striatus*

Item	Males			Females		
	Number of specimens	Mean $\pm$ S. E.	Range	Number of specimens	Mean $\pm$ S. E.	Range
Wing	14	121.3 $\pm$ 1.6	113-128	23	116.0 $\pm$ 0.9	109-127
Tail	11	82.1 $\pm$ 1.8	73- 91	8	78.6	72- 85
Bill length	53	33.23 $\pm$ 0.20	30.2-37.3	54	26.16 $\pm$ 0.19	22.3-29.3
Bill depth	28	7.52 $\pm$ 0.07	6.8- 8.4	26	6.61 $\pm$ 0.11	6.0- 7.4
Tarsus	12	23.47 $\pm$ 0.27	22.6-26.2	6	21.23	20.2-22.9
Weight <sup>1</sup>	6	86.3	83- 92	6	70.7	69- 75

<sup>1</sup> Specimens of adults collected on 27 May 1963, 5 miles N San Cristóbal, Dominican Republic.

were obtained from specimens collected there and in adjacent parts of northeastern México (sample area 3 of Selander and Giller, 1963:223, fig. 2). In size, degree of sexual dimorphism, foraging habits, and general behavior, birds of this race are similar to the Red-bellied Woodpecker (*Centurus carolinus*) of the eastern United States (Selander and Giller, 1959).

#### MORPHOLOGICAL COMPARISON

Linear measurements are given in millimeters and weights are expressed in grams. Wing length is the chord of the unflattened wing; bill length is the chord of the culmen from the base to the tip; and bill depth is the vertical chord at the anterior edge of the nostril. All measurements were taken from adult specimens.

*C. aurifrons* and *C. striatus* are similar in size and in general body form. Measurements of the species are presented in tables 2 and 3 and compared in table 4. In the male of *C. striatus*, which in body size (as reflected by body weight) is little if any larger than the male of *C. aurifrons*, and also in the female of *C. striatus*, the wing is disproportionately shorter than in *C. aurifrons*. This difference may be related to the fact that *C. striatus* occupies habitats in which there is closer spacing of vegetation, with the result that this species flies shorter distances. (See discussions of the relationship of density of vegetation and wing length by Miller, 1931; Pitelka, 1951; Hamilton, 1961; and Selander, 1964.) In both sexes of *C. striatus*, but especially in the female, the tail is disproportionately longer in relation to body size than in *C. aurifrons*. The functional significance of this difference was not apparent from my observations in the field, but presumably it is related to species differences in perching or in locomotion. Ernst Mayr (personal communication), noting that tropical trees, on the whole, have smoother bark than do temperate-zone trees, suggests that the variation in relative tail length in *Centurus* species may be related to differences in texture of the trunks and limbs on which the woodpeckers forage.

Males of the two species do not differ significantly in bill length, but the bill of the female of *C. striatus* is 13.1 per cent shorter than that of the female of *C. aurifrons*. Similarly, the percentage difference in bill depth is greater in females than in males.

In tarsal length, which provides a crude index to body size, the male of *C. striatus* slightly exceeds the male of *C. aurifrons*, whereas the tarsus of the female of *C. striatus* is 4.4 per cent shorter than that of the female of *C. aurifrons*. The two males are similar in weight, but the female of *C. striatus* weighs 7.5 per cent less than the female of *C. aurifrons*.

TABLE 3  
MEASUREMENTS OF *Centurus aurifrons*<sup>1</sup>

Item	Males			Females		
	Number of specimens	Mean $\pm$ S. E.	Range	Number of specimens	Mean $\pm$ S. E.	Range
Wing	46	130.5 $\pm$ 0.4	124-136	21	127.7 $\pm$ 0.6	124-133
Tail	43	78.7 $\pm$ 0.3	75- 83	19	76.2 $\pm$ 0.6	72- 81
Bill length	46	33.15 $\pm$ 0.24	30.2-37.5	23	30.09 $\pm$ 0.33	27.9-34.0
Bill depth	44	7.97 $\pm$ 0.06	7.4- 8.9	20	7.31 $\pm$ 0.22	6.4- 7.7
Tarsus	45	22.77 $\pm$ 0.10	21.3-24.3	22	22.20 $\pm$ 0.17	20.3-23.3
Weight <sup>2</sup>	29	85.4 $\pm$ 1.3	73- 99	14	76.4 $\pm$ 1.7	66- 90

<sup>1</sup> Specimens of *Centurus a. aurifrons* from southern Texas, Tamaulipas, and Nuevo León; sample area number 3 of Selander and Giller (1963).

<sup>2</sup> Specimens from San Luis Potosi; see Selander and Giller (1963: table 1; sample areas 10 and 11).

In sum, males of the two species are more similar in size and in body proportions than are females. In all linear dimensions and in weight, *C. striatus* exhibits a greater degree of sexual dimorphism. The greatest sexual difference (21.3 per cent) is in bill length in *C. striatus*; in both species, as in woodpeckers in general (Selander and Giller, 1963), the degree of dimorphism is greater in bill dimensions than in wing length or in dimensions of other body parts.

It is significant that sexual dimorphism in bill structure involves differences in the proportion of length to depth as well as in absolute size (table 5). Bill length/bill depth ratios for the two sexes are similar in *C. aurifrons* but differ in *C. striatus*. The bill of the male of *C. striatus* is disproportionately shallow, and that of the female is disproportionately deep, in relation to length. Ratios of bill length to cube root of weight and of bill length to tarsal length are similar in males of the two species, but they differ in females, those of *C. striatus* being smaller. If *C. striatus* evolved from an ancestor with body proportions similar to those of the present-day Texas population of *C. aurifrons*, the increased sexual dimorphism must have been achieved largely by reduction in size of the female; however, the body proportions of the form ancestral to *C. striatus* are unknown. If one calculates average bill length/tarsus ratios for all races of *C. aurifrons*, several of which have relatively smaller bills than do birds of the Texas population studied, the ratios are 1.36 for males and 1.28 for females (Selander and Giller, 1963). Thus comparison of *C. striatus* with the species *C.*

TABLE 4  
COMPARISON OF SIZE IN TWO SPECIES OF *Centurus* (Per cent deviation of mean measurements of *Centurus striatus* from those of *Centurus aurifrons*)

Item	Per cent deviation	
	Males	Females
Wing	-7.0	-9.2
Tail	+4.3	+3.3
Bill length	+0.2	-13.1
Bill depth	-5.7	-9.7
Tarsus	+3.1	-4.4
Weight	+1.0	-7.5
Cube root of weight	+0.3	-2.5

TABLE 5  
RELATIVE LENGTH OF BILL IN *Centurus*

Ratio <sup>1</sup>	Sex	<i>Centurus aurifrons</i>	<i>Centurus striatus</i>
Bill length/cube root of weight	M	7.53	7.52
	F	7.09	6.33
Bill length/tarsus	M	1.46	1.42
	F	1.36	1.23
Bill length/bill depth	M	4.16	4.42
	F	4.12	3.96

<sup>1</sup> Calculated from mean measurements (tables 2 and 3).

*aurifrons* as a whole reveals that the male of the former species has a disproportionately longer and the female has a disproportionately shorter bill. Comparisons of bill length/tarsus ratios for the strongly dimorphic insular species *Melanerpes portoricensis* and *M. herminieri* with those of their continental congeners *M. erythrocephalus* and *M. formicivorus* show a similar pattern, suggesting that the increased sexual dimorphism in bill size in the insular forms has been achieved by two-way displacement of the sexes.

*Structure of the tongue.* Because the highly specialized tongue of woodpeckers is closely adapted to characteristic foraging methods in different species (Lucas, 1895; Leiber, 1907; Gardner, 1925), a comparison of its size and structure in the sexes of the two *Centurus* woodpeckers seemed especially desirable. Some features of the tongue are illustrated in figures 4 and 5, and measurements are presented in table 6. Not unexpectedly, the degree of sexual dimorphism in the tongue is greater in *C. striatus* than in *C. aurifrons*; and it is noteworthy that, in *C. striatus*, dimorphism

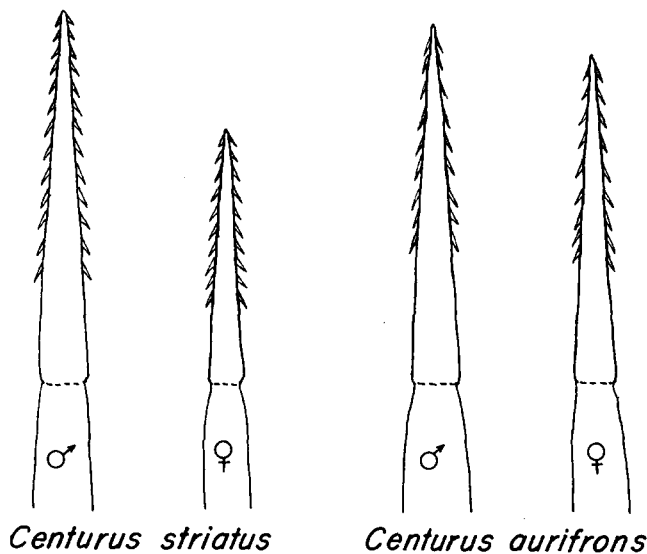


Figure 4. Sexual dimorphism in horny tip of tongue in two species of *Centurus*. All four tongues drawn to same scale.

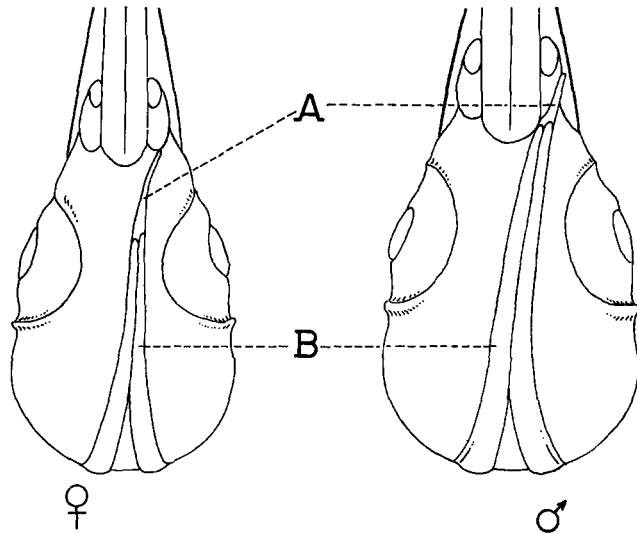


Figure 5. Sexual dimorphism in structure of tongue in *Centurus striatus*. Skulls in dorsal view. A. Connective tissue representing forward continuation of sheath enclosing epibranchials. B. Epibranchials enclosed in geniohyoid muscles.

in tongue size exceeds that of bill size. In *C. striatus* important sexual differences in the tongue are as follows: the horny tip enclosing the fused ceratohyals is disproportionately smaller in females, especially in length (34.5 per cent sexual difference). There are, on the average, three fewer groups of posteriorly directed barbs on the lateral margin of the horny tip in females. The soft part of the tongue posterior to the horny tip is disproportionately narrow, and the dorsal patch of small spines on the soft part of the tongue is disproportionately short in females.

In melanerpine woodpeckers the epibranchial horns of the hyoid apparatus, which are enclosed in the tubelike geniohyoid muscles, curve up over the occipital region of the skull and extend forward dorsally on the skull toward the right nostril (fig. 5). As the tongue is extruded, the epibranchials and the attached geniohyoid muscles slide posteriorly and ventrally over the surface of the skull in a sheath of connective tissue. When the tongue is retracted to its normal resting position within the bill, the epibranchials in the male of *C. striatus* extend forward to the posterior rim of the right nostril, from which point a band of connective tissue runs forward to attach on the lateral margin of the nostril. In the female the epibranchials of the hyoid are relatively thin, and they terminate between the orbits, about 7 mm short of the posterior margin of the right nostril (fig. 5); from the ends of these elements a thin extension of the sheath material continues forward to the base of the right nostril.

In *C. aurifrons* there is relatively little sexual difference in size of the tongue (table 6) or in diameter and forward extension of the epibranchials, and there is extensive overlap between the sexes in all features. In longer-billed specimens, whether male or female, the epibranchials extend forward to the posterior rim of the right nostril, as in the male of *C. striatus*; but in shorter-billed specimens of either sex they terminate a few millimeters posterior to the nostril. However, in none of the female specimens of *C. aurifrons* examined are the epibranchials as short and thin as in the female of *C. striatus*.



TABLE 6  
MEASUREMENTS OF TONGUE IN *Centurus*

<i>Centurus striatus</i> <sup>1</sup>					
Item	3 Males		3 Females		Percentage difference between sexes
	Mean	Range	Mean	Range	
Length of horny tip (mm)	15.57	15.4-15.7	10.20	10.2-10.4	34.5
Width of horny tip (mm)	1.80	1.6- 1.9	1.30	1.3- 1.3	27.8
Number of groups of spines on horny tip	12.7	12 -13	9.7	9 -10	23.6
Width of soft tongue (mm) <sup>3</sup>	2.90	2.7- 3.1	2.27	2.2- 2.4	21.7
Length of spine area on soft tongue (mm) <sup>3</sup>	14.37	13.3-15.3	11.73	10.2-14.1	18.4
Mean					25.20
<i>Centurus aurifrons</i> <sup>2</sup>					
Item	5 Males		4 Females		Percentage difference between sexes
	Mean	Range	Mean	Range	
Length of horny tip (mm)	14.96	14.6-16.1	13.55	12.2-15.0	9.4
Width of horny tip (mm)	1.74	1.6- 1.9	1.65	1.6- 1.7	5.2
Number of groups of spines on horny tip	9.4	8 -11	9.2	9 -10	2.1
Width of soft tongue (mm) <sup>3</sup>	3.34	3.2- 3.4	3.18	3.0- 3.3	4.8
Length of spine area on soft tongue (mm) <sup>3</sup>	12.58	10.8-15.1	12.37	11.2-13.0	1.7
Mean					4.64

<sup>1</sup> Specimens from 5 miles N San Cristóbal, Dominican Republic, May 1963.

<sup>2</sup> Specimens from Bexar and Atascosa counties, Texas, July and August 1963.

<sup>3</sup> Variation in these dimensions due in part to individual differences in degree of retraction of tongue.

#### HABITATS OF *CENTURUS* WOODPECKERS

Before examining the data on foraging, it will be helpful to consider the habitats of the two species in which the field studies were made.

*Centurus striatus*. This species is abundant in Hispaniola in all types of woodland and forest from mangrove swamps on the coast, inland through thorn scrub and other dry forest types, sparsely wooded hillsides, coffee plantations, and moist broad-leaved forest to the pinelands of the interior hills and mountains; it reportedly shows no "preference" for any one habitat type (Wetmore and Swales, 1931:291; Wetmore and Lincoln, 1933:44). Like many insular birds (Lack and Southern, 1949; Amadon, 1950; Miller, 1955; Crowell, 1961, 1962), *C. striatus* is more eurytopic than its continental congeners. Within its extensive geographic range in North and Central America, *C. aurifrons* is found in a variety of habitats equivalent to that occupied by *C. striatus*, but any one race or local population is relatively stenotopic (Selander and Giller, 1963:238).

The study area near San Cristóbal, Dominican Republic (see below), is in a forested region that has been cleared for farming and for pasture land for dairy cattle. According to the classification proposed by Holdridge (1945), the forest is representative of the dry division of the dry forest type. Important timber trees include *Swietenia mahagoni*, *Guaiacum officinale*, *Cordia alliodora*, *Krugiodendrum ferrea*, *Colubrina ferruginea*, *Petitia domingensis*, *Phyllostylon brasiliensis*, and *Acacia scleroxyla*. Large fig trees are found along streams, and a strangler fig is common in some parts of the study area. Exotic elements include mango trees and numerous royal and coconut palms. As noted by Wetmore and Swales (1931:292), the royal palm is the favorite nesting tree for the woodpecker in the lowlands of Hispaniola.

From observations in the study area, I estimated that the population density of *C. striatus* was four to five times greater than that maintained in continental areas by any species of woodpecker with which I have had field experience. I believe that the population density of this one insular species probably exceeds the combined densities of all species of woodpeckers occurring in any area in continental North and Central America. Among other birds present in the study area, only the Palm Chat (*Dulus dominicus*) was more abundant.

Unlike the continental species of *Centurus* and most other woodpeckers, pairs of *C. striatus* do not hold large territories in which to forage and nest. Instead, the species nests colonially, with each pair defending a small territory in the immediate vicinity of its nest hole, and members of a nesting colony forage over an extensive area surrounding the communal nest tree (Selander, MS).

*Centurus aurifrons*. The ecological distribution of this species has been discussed by Selander and Giller (1959, 1963) and will not be considered in detail here. The nominate race studied in south-central Texas occurs primarily in xeric Sonoran zone associations, including mesquite woodland, mixed oak-juniper-mesquite woodland, and riparian stands of willow, cottonwood, and cypress. In towns and in farm country it forages and nests in elms, live and deciduous oaks, pecans, junipers, chinaberries, and other trees, but it tends to frequent stands of vegetation in which mesquite and juniper are common elements.

In the study area in Eastwood Cemetery, Austin (see below), the habitat of *C. aurifrons* is structurally equivalent to a woodland and consists largely of native trees, including oaks, mesquite, hackberry, and juniper; additionally, there are a few cultivated magnolia trees and scattered patches of ornamental shrubs. In the study area near Cotulla, *C. aurifrons* inhabits a more xeric woodland of mesquite and oak in which there is little or no understory of shrubs. Both floristically and structurally, habitats of *C. aurifrons* in Texas are less complex than those occupied by *C. striatus* in the study area near San Cristóbal.

#### COMPARATIVE FORAGING BEHAVIOR

Foraging behavior and other aspects of the natural history of the Hispaniolan Woodpecker were studied at the Hacienda La Fundación, near San Cristóbal, Dominican Republic, from 22 May through 28 May 1963. During this period 197 observations of foraging technique and position were obtained. To compensate for difficulties in detecting birds in dense vegetation and at high levels in trees, special attention was given to these areas. The number of successive foraging stations recorded for an individual bird was limited to three, and usually only a single foraging location was recorded for an individual. Records of birds in juvenal plumage were not included in the data presented in this paper, but a small percentage of the records may pertain to first-year birds that had recently completed the postjuvenal molt.

Using field techniques similar to those employed in studying the Hispaniolan Woodpecker, 104 records of foraging by *C. aurifrons* were obtained in south-central Texas from 2 to 27 July 1963. The total includes 78 records made in Eastwood Cemetery, Austin, Travis County, between 6 and 27 July, and 26 records obtained near Cotulla, La Salle County, on 2 July 1963. Of the 104 records, 76 pertain to adults and 28 to fledged immature birds that were independent of their parents but were recognized by their juvenal head pattern.

FORAGING BEHAVIOR OF *CENTURUS STRIATUS*

*Description and definitions.* Records of feeding activities were grouped in three major categories according to the foraging technique employed (table 7); these are (1) probing, (2) pecking and otherwise excavating, and (3) searching and gleaning. A fourth category includes records of birds feeding on the fruit fronds of palms.

In probing, a bird inserted the bill, the tongue, or both into crevices or the soft flesh of fruit. In all probes by males, I noted that the bill itself was inserted, but on one occasion, when a female probed in an epiphyte, only the tongue was sent into the plant.

In probing into large fruits such as those of the mango and strangler fig, the woodpeckers generally hung from the fruits by their feet; and occasionally the "probes" were so forceful that they might have been classified as pecks. Once when a male probed into fig fruits, I was able to see that the bird extracted seeds; but in other cases, particularly when the fruit was the mango, it seemed likely that the birds were eating fruit pulp or insects within the fruit.

Cavities in which the woodpeckers probed included knot holes, cracks in bark, weathered holes previously excavated by the woodpeckers themselves, holes in ends of dead stumps, and cracks between trunks and frond bases of palm trees. In gleaning (see below) a bird frequently poked the tip of the bill or tongue into small cracks in bark. But the term "probing" was reserved for activities in which most of the length of the bill or tongue was inserted into fruit or into cracks or crevices measuring at least 0.5 inch in diameter. When foraging involved both probing and gleaning, or some other combination of techniques, the records were assigned to the dominant technique employed.

Pecking refers to the act of sharply striking an object with the bill. Usually it is a repetitious activity, with several blows being delivered in rapid succession. In addition to pecking, the woodpeckers sometimes excavated in wood by prying off flakes, especially in areas where the bark was rotted.

The pecking blows of *C. striatus* were generally lighter than those of *C. aurifrons*, and those of females of *C. striatus* seemed especially weak and were often barely audible at a distance of 20 feet. In three records of pecking (all pertaining to females), the birds hung upside down while working over rotted bark on the undersides of limbs.

In searching and gleaning, the birds moved slowly along limbs and trunks, actively scanning the bark and clumps of leaves and occasionally picking up insects or other small food items with the bill or tongue. The general pattern was as follows: a bird "hitched" along a limb at a rate of approximately three inches per second and made a food-taking motion every five seconds. Periodically the bird stopped for a few seconds to glean in a small area, taking several items of food before moving on. Unfortunately I was unable to identify food items taken by birds employing the searching and gleaning technique, but undoubtedly most of them were small insects.

In recording the activities of birds employing the searching and gleaning technique, care was taken to exclude cases in which birds were simply resting on a limb or trunk. I also found it necessary to exclude from this category several records in which males were searching not for food items on bark or leaves but for crevices in which to probe.

*Comparison of the sexes.* Foraging records for *C. striatus*, classified according to technique and location, are presented in table 7. The data demonstrate significant sexual differences ( $P < 0.001$ ) in foraging behavior that are in directions expected on

TABLE 7  
RECORDS OF FORAGING OF *Centurus striatus*

Technique and location	Males			Females		
	No. of records	Per cent of total	Per cent for technique	No. of records	Per cent of total	Per cent for technique
<b>Probing</b>						
Large epiphytes <sup>1</sup>	9	9.8	28	2	1.9	22
Large fruit <sup>2</sup>	8	8.7	25	1	1.0	11
Crevice and holes	15	16.3	47	6	5.7	67
Subtotals	32	34.8	100	9	8.6	100
<b>Pecking and excavating</b>						
Rotted bark	6	6.5	20	8	7.6	31
Large seed pods <sup>3</sup>	1	1.1	3	1	1.0	4
Small <sup>4</sup> branches and twigs	5	5.4	17	5	4.8	19
Medium <sup>5</sup> branches	6	6.5	20	8	7.6	31
Large <sup>6</sup> branches and trunks	12	13.0	40	4	3.8	15
Subtotals	30	32.5	100	26	24.8	100
<b>Searching and gleaning</b>						
Large fruit	0	0.0	0	1	1.0	2
Leaves and clusters of small fruit	5	5.4	22	6	5.7	10
Small <sup>4</sup> branches and twigs	1	1.1	4	11	10.5	18
Medium <sup>5</sup> branches	7	7.6	30	16	15.2	26
Large <sup>6</sup> branches and trunks	10	10.9	44	27	25.7	44
Subtotals	23	25.0	100	61	58.1	100
<b>Eating insects and/or fruit in royal palm fruit fronds</b>						
	7	7.6		9	8.6	
Totals	92	100.0		105	100.0	

<sup>1</sup> Bromeliads and other epiphytes forming masses > 3" in diameter.

<sup>2</sup> Presumably taking seeds but some insects perhaps also obtained.

<sup>3</sup> Removing seeds of open pods, presumably to uncover insects.

<sup>4</sup> < 2" in diameter.

<sup>5</sup> 2-4" in diameter.

<sup>6</sup> > 4" in diameter; includes trunks of palm trees.

$\chi^2$  for distribution of total records of foraging by the three techniques = 29.82;  $P < 0.001$ .

the basis of sexual differences in the feeding apparatus, the bill and tongue. It is noteworthy that despite their considerable anatomical differences males and females employ the same repertoire of foraging techniques. Hence the sexual difference in foraging is quantitative rather than qualitative.

Compared with the female, the male was more often seen probing, a not-unexpected finding considering the greater length of the bill and tongue in the male, which doubtless facilitates the capture of insects deep within crevices and the extraction of seeds and insects in large fruits. Note that 34.8 per cent of the records of male foraging activity but only 8.6 per cent of female records fall in the probing category. When the sexes are compared with respect to percentages of total probing records at various positions, the observed differences are not statistically significant ( $P > 0.5$ ).

The sexes differ only slightly in observed frequency of pecking (table 7), with the males being more often recorded pecking (32.5 per cent) than were the females (24.8 per cent). Although observed sexual differences in positions at which pecking occurred (table 7) are not statistically significant ( $P = 0.15$  for the three positions, small, medium, and large branches), the data suggest the possibility that females

TABLE 8  
HEIGHT OF FORAGING IN *Centurus striatus*

Feet above ground	Number of records in indicated range	
	Males	Females
0-20	8	14
21-40	13	13
41-60	14	15
61-90	9	11
Total records	44	53
Average height in feet	46	42

tend to do relatively more of their pecking on rotted bark and on small and medium-sized branches than do males, while the pecking activity of males is more confined to large branches and trunks.

Limited data on the frequency of pecking on live versus dead branches suggest a further sexual difference, although, again, the observed difference does not reach a conventional level of statistical significance. Males were more frequently recorded pecking on live than on dead branches (14 of 23 records on live branches), while the converse was true for females (7 of 17 records on live branches).

In pecking, as in probing, the observed sexual differences are in a direction that was predictable on the basis of structural differences in the bill. The larger and stronger bill of the male undoubtedly is better suited for excavating, especially in the thicker bark of large branches and trunks and in the harder wood of live limbs.

A sexual difference in foraging behavior is shown in the distribution of records in the searching and gleaning category, to which 25.0 per cent of male and 58.1 per cent of female records were assigned (table 7). A comparison of the sexes with respect to percentage distribution of total searching and gleaning records at various locations reveals no statistically significant difference, although the data suggest the possibility that gleaning by males is more frequently focused on leaves and small clusters of fruit, whereas a greater percentage of the gleaning activities of females occurs on small branches and twigs. Because the bills of both sexes are well-adapted for picking insects from surfaces, the similarity in distribution of gleaning activities at various locations is perhaps not surprising.

Males and females visited the fruit fronds of royal palms with approximately equal frequency. These fronds are an important source of food, providing not only the palm fruits themselves, which are eaten by adults and also fed to nestlings (Selandier, MS), but also insects, which the birds pick from the clusters of fruit. When visiting fruit fronds, the birds usually searched for insects for a short period and apparently took fruits as a second choice only after failing to find insects. The fruits of the royal palm were also heavily exploited by Palm Chats in the study area.

For 97 of the 197 foraging records obtained for *C. striatus*, the height above ground was estimated, and the data (table 8) show an absence of stratal segregation of the sexes in foraging.

For 55 of the male records of foraging and 60 of the female records, the time spent in each activity was recorded to the nearest second with a stop watch (table 9). Because the number of records is small and the duration varies from a few to as many as 570 seconds (for a female excavating in rotted bark), there undoubtedly is a large sampling error involved. However, the data show a sexual difference paralleling that

TABLE 9  
TIME DEVOTED BY *Centurus striatus* TO VARIOUS FORAGING TECHNIQUES

Technique and location	Males			Females		
	No. of records	Time in seconds	Per cent	No. of records	Time in seconds	Per cent
<b>Probing</b>						
Large epiphytes <sup>1</sup>	8	672	18	1	29	0.6
Large fruit <sup>2</sup>	2	125	3	0	0	0
Crevices and holes	8	475	13	0	0	0
Subtotals	18	1272	34	1	29	0.6
<b>Pecking and excavating</b>						
Rotted bark	5	168	5	7	1558	35
Large seed pods <sup>3</sup>	1	30	1	1	145	3
Small <sup>4</sup> branches and twigs	1	40	1	2	123	3
Medium <sup>5</sup> branches	6	350	10	5	445	10
Large <sup>6</sup> branches and trunks	6	590	16	4	215	5
Subtotals	19	1178	33	19	2486	56
<b>Searching and gleaning</b>						
Large fruit	0	0	0	0	0	0
Leaves and clusters of small fruit	5	505	14	4	130	3
Small <sup>4</sup> branches and twigs	1	50	1	2	50	1
Medium <sup>5</sup> branches	4	345	10	12	668	15
Large <sup>6</sup> branches and trunks	5	145	4	20	930	21
Subtotals	15	1045	29	38	1778	40
<b>Eating insects and/or fruit in royal palm fruit fronds</b>						
fruit fronds	3	150	4	2	135	3
Totals	55	3645	100	60	4428	100

1, 2, 3, 4, 5, 6 See footnotes Table 7.

demonstrated by the distribution of foraging records (table 7); in addition, for the male, the percentages of total time spent in probing, pecking, and searching and gleaning correspond closely with the percentages of total records for these activities. For the female, however, the percentages are somewhat different, in part because of the inclusion of seven very long bouts of pecking on rotted bark, which amounted to 35 per cent of the total time recorded. Nonetheless, the data on foraging time support the previous conclusion that females expend less of their foraging effort in probing and more in searching and gleaning than do males.

There is no reason to assume that a more meaningful comparison of foraging activity necessarily is provided by data on percentage time spent foraging than by numbers of records. The most ecologically significant data would be the percentages of the total energy obtained in food using each technique at various positions, which could be approximated by determining the weights of all food items taken. However, we might expect a reasonably close correlation between the amount of time expended in any type of foraging activity at any position and the amount of food obtained. And since the number of records of any one type of activity will be directly proportional to the time spent by the birds in that activity, numbers of foraging records are believed to serve as a reliable index to relative amounts of energy obtained by various foraging techniques at various positions.

TABLE 10  
RECORDS OF FORAGING OF *Centurus aurifrons*

Technique and location	Males			Females		
	No. of records	Per cent of total	Per cent for technique	No. of records	Per cent of total	Per cent for technique
Probing						
Crevices and holes	11	17.2		4	10.0	
Pecking and excavating						
Rotted bark	2	3.1	11	1	2.5	9
Small <sup>1</sup> branches and twigs	1	1.6	6	1	2.5	9
Medium <sup>2</sup> branches	7	10.9	39	6	15.0	55
Large <sup>3</sup> branches and trunks	8	12.5	44	3	7.5	27
Subtotals	18	28.1	100	11	27.1	100
Searching and gleaning						
Leaves	3	4.7	9	2	5.0	10
Small <sup>1</sup> branches and twigs	3	4.7	9	2	5.0	10
Medium <sup>2</sup> branches	8	12.5	25	8	20.0	40
Large <sup>3</sup> branches and trunks	18	28.1	57	8	20.0	40
Subtotals	32	50.0	100	20	50.0	100
Flycatching	2	3.1		3	7.5	
Feeding on ground <sup>4</sup>	0	0.0		1	2.5	
Eating fruit	1	1.6		1	2.5	
Totals	64	100.0		40	100.0	

<sup>1</sup> < 2" in diameter.

<sup>2</sup> 2-4" in diameter.

<sup>3</sup> > 4" in diameter.

<sup>4</sup> Technique of foraging not determined.

$\chi^2$  for distribution of records in categories of probing, pecking, and searching and gleaning = 0.74; P = 0.7.

#### FORAGING BEHAVIOR OF *CENTURUS AURIFRONS*

*Comparison of the sexes.* Records of foraging behavior in adult and independent juvenal individuals of *C. aurifrons* are presented in table 10. Immature birds apparently glean more frequently than do adults, and the addition of records of immatures to those of adults increased the proportion of gleaning records for both sexes by 5 per cent, at the same time reducing by a comparable amount the percentage of records in the pecking category.

A comparison of the foraging behavior of the sexes of *C. aurifrons* reveals a close similarity, unlike the situation in *C. striatus*. Neither the distribution of records nor the relative number of records of each activity at various locations shows a statistically significant sexual difference. However, because the small observed difference for the two sexes of *C. aurifrons* is in the same direction evident in the more extensive data available for *C. striatus*, there is reason to believe that a real but small difference could be demonstrated in a larger sample. Note that males probed more frequently than did females, although the difference in the percentages was less (7.2) than in the case of *C. striatus* (26.2). Also, the distribution of pecking records suggests a slight sexual difference, with males pecking relatively less frequently than females on small and medium-sized branches and more frequently on large branches and trunks.

## COMPARISON OF THE SPECIES

Several differences are apparent in the foraging behavior of the sexes in the two species of *Centurus*. The male of *C. striatus* probed twice as frequently as did the male of *C. aurifrons* and searched and gleaned less often. Females of the two species probed with approximately equal frequency, but the female of *C. aurifrons* pecked more often and gleaned less frequently than did the female of *C. striatus*.

It is of interest that *C. striatus* was not observed flycatching or foraging on the ground, whereas these activities were noted in *C. aurifrons*. Otherwise the repertoires of foraging techniques of the two species are similar. The extent to which the observed species differences in foraging reflect differences in distribution of food in the habitats of the study areas remains to be determined.

It would be interesting to determine the relative contributions of genetics and of prior experience to the observed differences in foraging behavior of the sexes in *Centurus* woodpeckers. In discussing the basis of interspecific variation in foraging behavior in birds, Hinde (1958, 1959, 1961) has emphasized the importance of learning, and his discussion may be applied equally well to intraspecific variation. The observed differences in the sexes need not depend on different genetically determined motor patterns of foraging, since each sex will learn to use those techniques that are most efficient in food-getting, given the structure of the feeding apparatus. Thus, the sexual differences in structure of the bill and tongue could alone account for the differences in foraging behavior.

## DISCUSSION OF FORAGING IN WOODPECKERS

In *Centurus* woodpeckers the data demonstrate a relationship between the degree of sexual difference in foraging behavior and the degree of sexual dimorphism in the feeding apparatus. This suggests the possibility that much if not all sexual dimorphism in the bill and in other structures used in foraging by birds is related to differential niche utilization. I hasten to note that I am not contending that *all* sexual dimorphism in feeding structures has arisen specifically and solely through selection for niche divergence; rather, I wish only to emphasize the possibility that any degree of sexual difference in size or structure of the feeding apparatus will result in some degree of differential niche utilization by the sexes as far as food is concerned. Whether this is the secondary result of morphological dimorphism caused by sexual selection (Selander, 1965a) or is selected per se must be determined by investigations of the behavior and ecology of individual species.

Since this was written, significant sexual differences in feeding behavior of the Hairy Woodpecker (*Dendrocopos villosus*) have been described by Kilham (1965). Males feed predominantly by excavating, while females more frequently utilize superficial types of feeding, including pecking, poking, and scaling. The sexes also tend to forage on different species of trees. As noted by Selander (1965b), *Dendrocopos villosus* is an unusually dimorphic species. Sexual difference in length of the culmen is 11.0 per cent, and joint nonoverlap in bill length between the sexes is 92 per cent for *D. v. villosus* and 95 per cent for *D. v. leucothorectis*.

It might be argued that sexual variation in bill size and proportions in woodpeckers is primarily related to differences in the roles of the sexes in excavation of nesting and roosting cavities, and that differential foraging behavior is merely a secondary effect imposed by the morphological dimorphism. However, field studies of *Centurus* (Selander, MS) show no species differences in the roles of the sexes in cavity construction; in both species the female takes an active part in the excavation of cavities.



More importantly, the observed sexual dimorphism in tongue size and structure can, in my opinion, be explained only in terms of differential adaptation for foraging.

It would be instructive to determine if the evolution of increased sexual dimorphism in *C. striatus* has resulted in expansion of the total feeding niche of the species or has simply involved subdivision of the niche of a less dimorphic ancestral form. Data required for an objective comparison of the "size" of the feeding niches of woodpeckers are not presently available; but, because the total span of bill and tongue sizes is greater in populations of *C. striatus* than in those of *C. aurifrons* and other less dimorphic species, it seems probable that *C. striatus* takes a greater variety of kinds or sizes of food and, in this sense, exploits a relatively larger feeding niche.

Whether or not *C. striatus* and other strongly dimorphic woodpeckers utilize expanded niches, I believe that the increased sexual difference in foraging behavior is related to a reduction in intensity of interspecific competition resulting from the absence or rarity on the islands of other woodpeckers and birds of similar adaptive type, as originally suggested by Selander and Giller (1963:263). Similarly, it seems probable that freedom from competition with other species has permitted the marked expansion of the ecological distribution of *C. striatus*, as compared with its continental congeners. In the following discussion I shall use the term "ecological sphere" (Miller, 1955; Dixon, 1961) in reference to aspects of the habitat distribution and niche of a population.

On Hispaniola, on Puerto Rico, and on Guadeloupe Island there is seemingly sufficient diversity of habitats to support several species of woodpeckers, as in continental areas. Yet on Hispaniola *C. striatus* is the only resident species of typical woodpecker. The Yellow-bellied Sapsucker (*Sphyrapicus varius*) is an uncommon winter visitant, but it feeds in a manner different from that of *Centurus*; and the resident endemic piculet *Nesocittes*, which is uncommon, is nuthatchlike in foraging behavior. Also absent from Hispaniola are species of the families Dendrocolaptidae, Sittidae, and Paridae, all of which employ foraging techniques similar to those used by woodpeckers. In Puerto Rico the strongly dimorphic *Melanerpes portoricensis* is the only resident species of the family Picidae, and the Yellow-bellied Sapsucker occurs only as a rare winter visitant. On Guadeloupe Island the resident *Melanerpes herminieri* is the only woodpecker recorded.

Evidence supporting the present thesis is provided by an examination of sexual dimorphism in size in the woodpeckers of Cuba, where there are five resident species, of which the West Indian Red-bellied Woodpecker (*Centurus superciliosus*) is the commonest (Bond, 1961). Only the endemic Cuban Green Woodpecker (*Xiphidiopicus percussus*) is unusually dimorphic in bill length, and it may be significant that the degree of sexual dimorphism (15.2 per cent) is less than that in the endemic woodpeckers of Hispaniola, Puerto Rico, and Guadeloupe Island.

An obvious exception to the trend for increased sexual dimorphism in insular woodpeckers is provided by the endemic Jamaican Woodpecker (*Centurus radiolatus*). Although *C. radiolatus* is the only resident woodpecker on Jamaica, it is no more dimorphic (bill-length dimorphism, 6.2 per cent) than its continental congeners (Selander and Giller, 1963: table 6, p. 262).

Current ecological theory holds that insular faunas are impoverished because not all species of adjacent continental faunas reach the islands and only some of these find habitats or niche requirements in sufficient quantity to permit long-term maintenance of populations, with the result that the rare species are subject to periodic extinction (Serventy, 1951; Preston, 1962; Mayr, 1963; MacArthur and Wilson,

1963; Hamilton and Rubinoff, 1963; Hamilton *et al.*, 1964). Consequently there is a chronic vacancy of ecological spheres that permits adaptive radiation of species that are able to establish and maintain populations. The successful species are able to exploit the vacant habitats and niches as well as their own preferred ones (Crowell, 1963). Where there is opportunity for speciation through geographic isolation, as in archipelagos, new species can arise to exploit the unoccupied niches and habitats (Lack, 1947; Amadon, 1950). But even where there is no opportunity for geographic speciation, as on single, isolated oceanic islands, some degree of adaptive radiation may be achieved by a single species population through an expansion of its ecological range and, as I am contending, an increase in individual or sexual variation in niche utilization.

Lack (1947:113) and others have suggested that the presence on an island of one species of a given adaptive type may block the colonization or evolution of another species of similar type. For example, Lack notes (1947:113) that "had a small American woodpecker been established in the Galapagos, it is most unlikely that the woodpecker-finch *Camarhynchus pallidus* could have evolved. . . . In the same way, had there been a mainland warbler on the islands, it is doubtful whether the warbler-finch *Certhidea* could ever have appeared." I believe that Lack's suggestions are valid, although they are disputed by Bowman (1961:291), and I would further suggest that the tendency of species to expand their ecological spheres is a significant factor diminishing the opportunity for establishment of new colonists or the evolution of new species on islands. Possibly this postulated effect of expanded ecological spheres is involved in the occurrence of only a single species of woodpecker on isolated mountain forests in African savannas (Moreau, 1948), where the habitats appear to be favorable for occupancy by several species specializing for different niches.

It may be instructive to compare the degree of sexual difference in foraging behavior of *C. striatus* with degrees of interspecific difference in foraging among congeneric species of passerine birds in continental areas. Brewer (1963:28) has calculated an index to the degree of distinctness in foraging behavior of various pairs of congeneric species by summing the differences between the percentages of records of feeding by each species in various foraging positions or locations. The lowest index (reflecting the greatest degree of similarity in foraging behavior) was 25.7 per cent, a value obtained for *Parus atricapillus* and *P. carolinensis*, which are allopatric semi-species. The largest index value, 121.9 per cent, was calculated for two allopatric populations of *Parus atricapillus* occupying drastically different habitat types. For various species pairs of *Parus* and *Dendroica* occurring sympatrically and foraging in the same habitats, index values of from 46.4 to 99.9 per cent were calculated by Brewer (1963). For example, from data supplied by MacArthur (1958), an index of 48.4 per cent was obtained for the Blackburnian Warbler (*Dendroica fusca*) and the Cape May Warbler (*D. tigrina*). Comparison of the sexes of *C. striatus* with respect to foraging positions (nine categories) yields an index of 49.8 per cent. Thus, the difference in foraging positions in the sexes of *C. striatus* is as great as that found in many of the sympatric species pairs that have been studied in continental North America.

Seasonal variation in degree of sexual divergence in niche utilization in *Centurus* woodpeckers and in other birds remains to be studied. My investigations of *Centurus* were made in a period in which young were fledging from the nests and food was probably at maximum abundance. A similar study conducted at another time of the year when there are lesser total supplies or varieties of food types available might

reveal a different degree of divergence in the foraging behavior of the sexes. In several British titmice of the genus *Parus*, interspecific overlap in food is minimal during the winter, when food is relatively scarce (Hartley, 1953; Gibb, 1954). But working with *Parus wollweberi* and *P. bicolor atricristatus* in Tamaulipas, México, Dixon (1961) found a greater difference in foraging positions of the species in April, at the beginning of the breeding season, than in the nonbreeding season in December.

Whether studies of *C. striatus* in other seasons reveal lesser or greater degrees of sexual difference in foraging behavior, one important conclusion emerges from the ecological data available for this insular form. Through increased divergence in the foraging behavior of the sexes, which is associated with increased sexual dimorphism in the feeding apparatus, and through an expanded range of habitat distribution, this single species manages to exploit its insular environment to a degree which in continental North America is achieved only by the combined efforts of several species of woodpeckers or other birds of similar adaptive type. This is true whether exploitation is measured in terms of population densities of the species or of the total extent of their ecological spheres.

The problem of the relationship between coloniality and ecological polymorphism in woodpeckers is difficult to pursue at present owing to a paucity of information on their social organization, dispersion, and ecological variation. For the strongly dimorphic insular woodpeckers of the Antilles other than Hispaniola there are no reports of colonial nesting. And a statement by Danforth (1936:119) that *M. portoricensis* is "somewhat aggressive and therefore always lives in pairs" suggests that this species is not colonial in nesting; but whether pairs defend feeding territories, as do most continental species, is unknown. Even for some continental forms, such as the Acorn Woodpecker (*Melanerpes formicivorus*), the situation is complex. This species shows a colonial tendency, but the degree of coloniality apparently varies regionally and temporally with the availability of food (Bent, 1939:220).

In birds colonial nesting and common exploitation of foraging areas by colony members has developed in situations in which either the temporal or the spatial distribution of food, or both, is such that there is no advantage in pairs holding feeding territories. Swallows and swifts feeding on aerial insects, many sea birds exploiting schools of fish, and many social icterids and weaver finches furnish examples. In the evolution of coloniality in *C. striatus*, it is possible that the ancestral form which first became established on the island was exploiting food resources which were so abundant or distributed in such a way that there was no advantage to pairs defending feeding territories. Perhaps population densities were relatively low before the bird became well adapted to the environment, and food was not controlling population numbers. Under these conditions there would be selection for coloniality, the advantage being increased social facilitation (Crook, 1961; Hinde, 1961) and, perhaps, increased protection against predators (see discussion by Dixon, 1963) and ease of finding mates. Colonial nesting was established. As the species became better adapted to the insular environment, population density increased. And since nesting sites were abundant, they did not limit population density; the population continued to increase in size and eventually came up against control by the food supply. Here one course of adaptive adjustment would be the establishment of feeding territories by pairs; but another adaptive course, which would be taken if food supplies were temporally or spatially variable, is divergence in foraging behavior of the sexes, which has the effect of diminishing intraspecific competition. This is the course apparently

TABLE 11  
METHODS OF REDUCING INTERSEXUAL COMPETITION FOR FOOD

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1. Differential Niche Utilization within a Common Home Range or Territory
    - A. Sexes employ similar foraging techniques in same areas and strata but take foods of different average sizes
    - B. Sexes employ different foraging techniques in same areas or strata
    - C. Sexes forage in different areas or strata
  2. Allopatry of the Sexes (except for breeding)
    - A. Macrogeographic allopatry
      1. Sexes exploit similar habitat types and niches
      2. Sexes exploit different habitat types and niches
    - B. Microgeographic allopatry
      1. Sexes occupy adjacent areas of similar habitat
      2. Sexes occupy different but adjacent habitats
  3. Increased Territory Size
- 

taken by *C. striatus*, and the sexual divergence in niche utilization presumably was possible because of the absence of species of similar adaptive type on the island.

#### METHODS OF REDUCING INTERSEXUAL COMPETITION FOR FOOD

A general consideration of the subject of intersexual competition for food suggests that differential foraging behavior is but one of several methods by which a reduction in degree of sexual overlap in exploitation of food resources may be effected. A tentative classification of methods is presented in table 11, which is adapted in part from material presented by Rand (1952). It will be obvious, I trust, that the methods in categories 1 and 2 grade into one another and that a species need not employ one method to the exclusion of others. The reader should also note that, by substituting "establishment of interspecific territoriality" for category 3 and replacing "species" for "sexes," this classification could serve equally well as a list of possible methods of reducing interspecific competition.

#### DIFFERENTIAL NICHE UTILIZATION WITHIN A COMMON HOME RANGE OR TERRITORY

The Black-faced Dioch (*Quelea quelea*) of Africa, which forages in large compact flocks, is a species in which the sexes apparently utilize the same foraging techniques in the same areas and strata but, at least in certain seasons, take food of different sizes (category 1A in table 11). In an intensive study of the feeding ecology of *Quelea quelea* in Nigeria, Ward (1965:197) noted no obvious sexual difference in food taken in the dry season. But he found a significant difference in the early-rains period, "the males with their stouter bills taking a higher proportion of the larger types of seed [mainly wild sorghum and wild rice] than do the females." At the beginning of the early-rains period in July, the dry-season food supply of seeds is lost owing to the simultaneous germination of seeds over large areas. Thus the early-rains period (July) is one of food shortage, reflected in a rapid decrease in body weight (Ward, 1965, fig. 8, p. 189). Judging from the fact that females lose weight at about double the rate of males, it appears that the females are at a greater disadvantage.

TABLE 12  
SEXUAL DIMORPHISM IN SIZE IN *Neomorpha acutirostris*<sup>1</sup>

	Mean measurements (mm)		Percentage difference between sexes <sup>2</sup>
	14 males	8 females	
Wing	200.8	190.4	5.2
Tail	195.0	185.0	5.1
Bill length (chord)	57.38	90.75	36.8
Bill length (arc)	58.3	95.5	39.0
Bill depth	14.43	11.46	20.6
Tarsus	79.55	74.04	6.9

<sup>1</sup> Adult specimens in the American Museum of Natural History.

<sup>2</sup> Calculated by taking smaller mean as percentage of larger mean and subtracting from 100 per cent.

The Hispaniolan Woodpecker, already discussed in this paper, serves as an example of differential niche utilization in which the sexes employ different foraging techniques within a common home range (category 1B in table 11). An even more striking example is provided by another insular form, the extinct Huia (*Neomorpha acutirostris*) of North Island, New Zealand. The sexes were similar in body size and in color and pattern of the plumage, but the bill of the male was short, thick, and relatively straight, while that of the female was long, slender, and strongly decurved (table 12 and fig. 6). According to observers (Potts, 1885:476; Buller, 1888), the Huia was largely insectivorous, feeding chiefly on wood-boring insects which the sexes obtained in different ways. The male reportedly used its heavy, straight bill to dig into rotted wood for boring grubs and other insect types, while the female probed into existing crevices and crannies.

Several other examples of marked sexual dimorphism in bill size in insular species have been reported by Amadon (1950, 1953). Among the Hawaiian honeycreepers (Drepaniidae), the two large species *Vestiaria coccinea* and *Pseudonestor xanthophrys* and the smallest species of the family, *Hemignathus (obscurus?) procerus*, are unusually dimorphic (table 13). Baldwin (1953) studied the natural history of *Vestiaria coccinea* on Hawaii but did not consider possible sexual differences in foraging, and little is known of the foraging behavior of the other species (Amadon 1950:202).

The giant sunbird *Cyanomitra thomensis* of São Tomé Island in the Gulf of Guinea differs from its congeners in being much larger in body size, in having a disproportionately longer bill, and in showing increased sexual dimorphism in size (table 13). The feeding habits of *C. thomensis* are distinctive; typical sunbirds feed exclusively on nectar and small insects obtained from flowers, but *C. thomensis* forages in this fashion and also probes into crevices in the bark of trees in the manner of creepers of the family Certhiidae (Amadon, 1953).

In the Trembler (*Cinlocerthia ruficauda*), a genus and species of the Mimidae endemic to the Lesser Antilles, the bill of the male of the race on Dominica Island is 15.1 per cent shorter than that of the female, yet the tarsus in the male is 1.4 per cent longer and the wing 4.1 per cent longer than in the female (Ridgway, 1907:273). Moreover, the degree of dimorphism in bill length varies from island to island, being, for example, only 3.6 per cent on Guadeloupe Island. This interesting situation, in which it is probable that bill dimorphism is related to differential foraging, is being studied by Robert W. Storer (personal communication).

A few cases in which the sexes are known or presumed to forage in different spatial

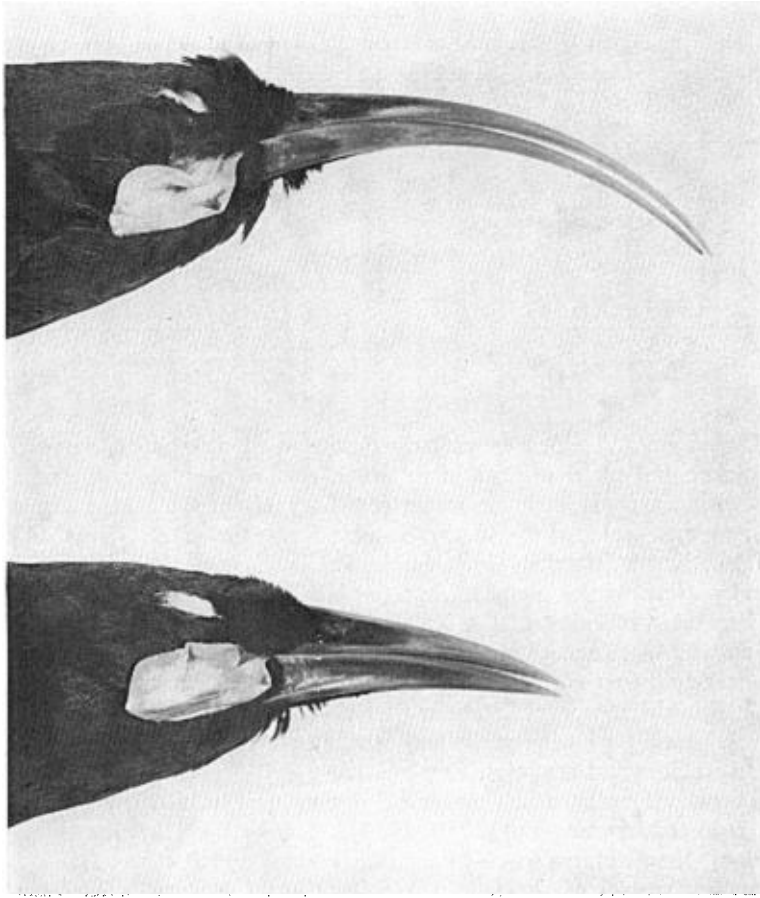


Figure 6. Sexual dimorphism in bill size and structure in the Huia (*Neomorpha acutirostris*) of New Zealand. Female above, male below. Specimens in lateral view.

areas or vertical strata within a common home range or territory have come to my attention. In the Brown-headed Nuthatch (*Sitta pusilla*), but not in the closely allied Pigmy Nuthatch (*Sitta pygmaea*), Norris (1958:253) found a strong tendency for males to forage lower on tree trunks than did their mates. In view of this behavioral difference in the species, it is significant that the faintly dimorphic trend in morphology shown by these nuthatches is more regular in *S. pusilla* than in *S. pygmaea*. Measurements of bill length (table 13) indicate that *S. pusilla* is slightly more dimorphic than *S. pygmaea*, although there is overlap among populations of the two species in percentage sexual difference in bill length. In a series of 21 cranial and postcranial skeletal dimensions measured by Norris, females of *S. pusilla* were exceeded by males in all but one, the length of the tibiotarsus. Regarding the adaptive significance of this exception, Norris (1958:175) suggests that "this irregularity in an otherwise uniform pattern of sexual variation in skeletons of . . . [*pusilla*] may well be functionally related to a slightly differing forage niche. It would seem that females with relatively longer tibiotarsi might be less well adapted to trunk foraging than are males." This example is significant in demonstrating that the sexes may differ in

TABLE 13  
SEXUAL DIMORPHISM IN SIZE IN SOME SPECIES OF BIRDS

Form	Number of specimens <sup>2</sup>	Region	Percentage sexual difference <sup>1</sup>		Reference
			Wing	Bill length	
<i>Vestiaria coccinea</i>	8-4	Hawaii	10.0	15.5	Amadon (1950: 184)
<i>Pseudonestor xanthophrys</i>	5-4	Maui	9.2	22.5	Amadon (1950: 182)
<i>Hemignathus procerus</i>	11-8	Kauai	4.8	22.3	Amadon (1950: 181)
<i>Cyanomitra thomensis</i>	?	São Tomé	1.7	27.5	Amadon (1953: 447)
<i>Cinclocerthia r. ruficauda</i>	4-4	Dominica	4.1	*15.1	Ridgway (1907: 273)
<i>Quiscalus mexicanus prosopidicola</i>	30-30	Texas	22.2 <sup>3</sup>	20.7	Selander (1958: 372)
<i>Quiscalus major major</i>	20-20	Louisiana	22.1	18.8	Selander (1958: 372)
<i>Euphagus cyanocephalus</i>	10-10	W U.S.	8.5 <sup>4</sup>	11.1	Selander (1958: 372)
<i>Sitta pusilla pusilla</i>	6 samples <sup>5</sup>	SE U.S.	2.5	2.7	Norris (1958: 154-155)
<i>Sitta pygmaea melanotis</i>	6 samples <sup>6</sup>	W U.S.	0.8	0.7	Norris (1958: 132-134)
<i>Sitta p. pygmaea</i>	31-20	Calif.	0.7	2.0	Norris (1958: 124)
<i>Sitta p. leuconucha</i>	54-32	Baja Calif.	1.8	1.9	Norris (1958: 142)
<i>Limnodromus scolopaceus</i>	87-85	Calif.	*3.6	*14.0	Pitelka (1950: 17)
<i>Limnodromus griseus</i>	87-116	Calif.	*1.9	*8.4	Pitelka (1950: 17)
<i>Pelecanus erythrorhynchus</i>	9-10	N Amer.	8.2	16.0	Palmer (1962: 266)
<i>Pelecanus o. carolinensis</i>	28-23	E U.S.	4.8	7.7	Wetmore (1945: 579)
<i>Pelecanus o. occidentalis</i>	16-14	West Indies	3.3	9.4	Wetmore (1945: 578)
<i>Pelecanus o. californicus</i>	34-23	Calif.-Mex.	5.8	10.1	Wetmore (1945: 581)
<i>Aechmophorus occidentalis</i>	4-5	Canada	7.1	14.8	Palmer (1962: 95)
<i>Podiceps grisegena holböllii</i>	20-14	U.S.-Siberia	3.2	7.0	Palmer (1962: 65)
<i>Podiceps auritus cornutus</i>	23-22	N Amer.	4.1	4.6	Palmer (1962: 73)
<i>Podiceps caspicus californicus</i>	16-8	W U.S.	4.4	10.6	Palmer (1962: 81)

<sup>1</sup> Male the larger sex (= 100%) unless otherwise indicated by an \*.

<sup>2</sup> Males—females.

<sup>3</sup> Sexual difference in tail length = 29.1 per cent.

<sup>4</sup> Sexual difference in tail length = 10.0 per cent.

<sup>5</sup> Sample sizes range from 28-16 to 71-46.

<sup>6</sup> Sample sizes range from 28-16 to 47-28.

niche utilization even though the species exhibits no marked increase in degree of sexual dimorphism over other, less ecologically variable species.

In Darwin's finches (Geospizinae) of the Galápagos Islands, females average slightly smaller than males in bill length and in other linear dimensions in all but one species, the Warbler-Finch (*Certhidea olivacea*), in which the bill of the female is slightly longer than that of the male, although in wing length (and, hence, presumably in body size) the female is the smaller sex (Swarth, 1931; Lack, 1945). Commenting on this fact, Lack (1945:80) noted that "in this species the female has different habits from the male, foraging nearer the ground. Whether or not, however, the bill difference is correlated with feeding habits is unknown." It is unfortunate that Lack provided no detailed information on foraging differences and that other workers (Gifford, 1919; Bowman, 1961) have not commented on this matter.

Harrison and Buchan (1934:144) reported that the members of a pair of the St. Kilda race of the wren *Troglodytes troglodytes* had separate feeding "territories." Since there was no defense of area, Armstrong (1953:135) has rightly criticized use of the term "territory," and he notes that "no other observer has found evidence of foraging areas peculiar to one or the other of the pair." In spite of the lack of area defense, pair members of this species may in fact tend to exploit different parts of the

territory for food, as observations by Armstrong himself (1953, 1955) suggest, for he reports that male and female pair members forage independently and that the male "seldom forages near the female."

According to Miller (1941), the Bewick Wren (*Thryomanes bewickii*) exhibits behavior comparable to that of Darwin's Warbler-Finch:

I frequently saw mated birds foraging in early spring, the male up in trees, while the female kept a foot or two off the ground. The female followed the course set by the male and was even fed by him. This separation of forage locations for mated birds occurs in early spring when wrens first mate. After nestbuilding foraging occurs separately or together. If together, there is no separation of the foraging locations. Both wrens forage on all levels. It is possible that the separate foraging location procedure may have developed because of the smaller amount of food present in the territory early in the season. Later in the spring there is plenty of food and no need for the sexes to forage in separate locations.

Even if further study should show that aggressiveness of the male or the female prevents close contact of the sexes in the period before nest-building, and that habituation and other behavioral adjustments alter the relationship of pair members later in the season, this would not invalidate the explanation proposed by Miller, which attaches adaptive value to differential niche utilization in time of food scarcity. Aggressive behavioral interactions early in the season could be viewed as a mechanism by which differential foraging is achieved.

Pair members of the Indigo Bunting (*Passerina cyanea*) on breeding territories show marked stratal separation in foraging (W. L. Thompson, personal communication), which, however, may be more directly related to problems of efficient use of foraging time than to reduction of intersexual competition for resources in short supply. The male, which sings from tree-top positions, often forages high in trees near his singing perches and rarely descends to the ground, whereas the female, which alone is involved in duties at the nest placed one to four feet above the ground (Simmons, 1925:225), commonly forages on the ground and is seldom seen feeding at heights above 10 feet.

Pitelka (1950) was among the first to recognize an adaptive ecological basis for sexual dimorphism in size in birds. Working with the dowitchers (*Limnodromus*), he showed that, in the Short-billed Dowitcher (*L. griseus*), the bill of the male averages 8.4 per cent shorter than that of the female, while, in the Long-billed Dowitcher (*L. scolopaceus*), the bill of the male is fully 14.0 per cent shorter than that of the female (table 13). *Limnodromus scolopaceus* is the larger species and is also the more dimorphic in weight.

To explain the species differences in body proportions and in degree of sexual dimorphism in the dowitchers, Pitelka (1950:57) has proposed that the "increased length of bill and tarsus and decreased length of wing permit *scolopaceus* to feed in water of greater average depth than *griseus*, and thus to increase the breadth of its total forage zone along the periphery of a shallow pond. This advantage . . . is augmented by the greater . . . sexual dimorphism in *scolopaceus*." Dowitchers feed by wading and probing for invertebrates and seeds, often immersing the head partly or entirely. *Limnodromus scolopaceus* frequents chiefly freshwater areas, and its longer bill and tarsi presumably represent adaptations whereby the area of a water-covered pond margin that can be explored effectively for food is increased. In its freshwater habitats *L. scolopaceus* feeds without the benefit of the tidal fluctuations that increase the foraging area for *L. griseus*, which usually feeds in shallow water at the margin of the receding tide or in tide pools and, occasionally, on recently exposed mudflats.



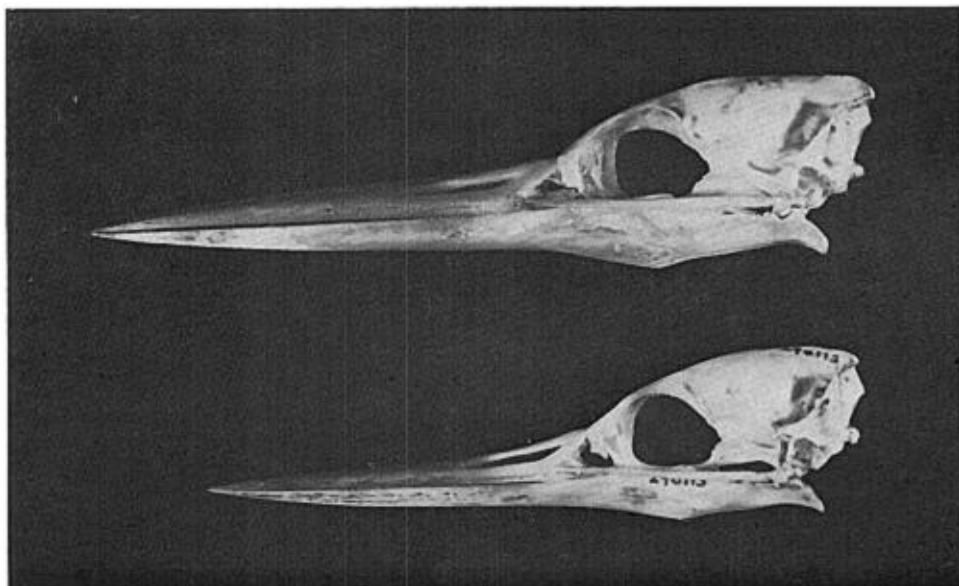


Figure 7. Sexual dimorphism in skulls of the Western Grebe (*Aechmophorus occidentalis*). Male above, female below. Skulls in lateral view.

The sexes of certain hummingbirds differ in bill structure, as previously noted by Darwin (1871). For example, in the large species *Rhamphodon naevis* of Brazil, the bill of the male is hooked and serrated near the tip, but that of the female is neither hooked nor serrated, and the mandible curves upward near the tip, leaving an open space between it and the maxilla (Elliot, 1878:4). In the allied form *Androdon aequatorialis* of Ecuador, both male and female have a hooked and serrated bill. The functional significance of this dimorphism remains to be determined.

Dean Amadon (personal communication) has called my attention to variation in degree of sexual dimorphism in size in pelicans. In the two North American species, the White Pelican (*Pelecanus erythrorhynchus*) and the Brown Pelican (*P. occidentalis*), the percentage sexual dimorphism in bill length is about twice that of wing or tarsus length (table 13). Sexual dimorphism in bill length is 16.0 per cent in *P. erythrorhynchus* but ranges from 7.7 to 10.1 per cent in races of *P. occidentalis*. It may be significant that *P. occidentalis* appears to have a more restricted diet, feeding largely on a few species of marine fishes, which it takes by diving (Palmer, 1962). The other species frequents freshwater areas in the breeding season and perhaps takes a greater variety of food types, for it is known to eat fishes, amphibians, and crayfish, which it obtains by plunging the head under water to scoop up food in the gular pouch. Possibly both the selective pressures and the opportunities for niche divergence of the sexes are greater for *P. erythrorhynchus*.

Rand (1952) has called attention to the unusual degree of sexual dimorphism in bill size and shape shown by the Western Grebe (*Aechmophorus occidentalis*). The bill of the female is smaller than that of the male and has a distinctive upward curvature (fig. 7). Measurements of bill length given by Palmer (1962:95) indicate non-overlap between the sexes, with the bill of the female being 14.8 per cent shorter than that of the male (table 13). In a sample of 89 males and 30 females, Nero (*in Pal-*

mer, 1962:95) found no sexual overlap in "head length" as measured from the back of the head to the anterior border of the nostril; males ranged from 67 to 75 mm, females from 59 to 65 mm. Despite the marked dimorphism in cranial structure, the species is not unusually dimorphic in wing length (table 13).

Students of the food habits of the Western Grebe (Wetmore, 1924; Munro, 1941; Lawrence, 1950) apparently have not considered the possibility of sexual differences. The diet of this species reportedly includes a greater number of fishes than does that of any other grebe; and, according to Storer (1960a:705), this species is unique among grebes in that it spears fishes with the bill.

Of possible significance in relation to the marked sexual dimorphism in the Western Grebe is the fact that this species is the most gregarious grebe, nesting colonially, often by the hundreds of pairs (Nero *et al.*, 1958). Feeding by colony members occurs in a common area outside the small nesting territories, where, according to Lawrence (1950), the birds scatter, with at least 200 feet of open water between individuals. In the nonbreeding season the species migrates and winters in large flocks. Where large numbers of individuals exploit a common area for food, selection for polymorphism in feeding techniques may be greater than where pairs feed within territories that are not visited by other members of the species. It is interesting that, in the genus *Podiceps*, the species *P. grisegena* and *P. auritus*, which are solitary nesters and feed to a large extent if not completely within territories held by pairs, are less dimorphic in bill length than is the colonially nesting, gregarious *P. caspicus* (table 13).

Among the Falconiformes there is great variation in degree of sexual dimorphism in size. Females are on the average larger than males, a characteristic which, as Amadon (1959) has noted, is associated with a predatory way of life. "Reversed" sexual size dimorphism has also developed independently in a number of other groups of predatory birds, including the frigate-birds (Fregatidae), jaegers and skuas (Stercorariidae), and owls (Strigiformes). Moreover, in the Falconiformes, sexual dimorphism is much less in forms having vulturine or scavenging habits, such as the New World vultures (Cathartidae), than in the predators, such as the falcons (Falconidae). As noted by Stresemann (*vide* Amadon, 1959:535), dimorphism is greatest in two bird-catching groups, the accipiters and the falcons (table 14). Note that in the accipiters there is an inverse relation between body size (as indicated by wing length) and degree of sexual dimorphism in bill size. This is not the case in *Falco*, for the smallest species, *F. sparverius*, is only slightly dimorphic, while the larger species are strongly dimorphic.

Most theories advanced to explain size dimorphism in the Falconiformes fall into two groups: those which interpret dimorphism as an adaptation for differential feeding behavior by the sexes (Brüll, 1937; Hagen, 1942; Dementiev, 1951; Storer, 1952, 1960b) and those which explain the larger size of the female as an adaptation for insuring behavioral dominance of the female over the male to protect her from harm during the mating season and, possibly, to enable her to prevent the male from attacking the young in the nest (Hagen, 1942; Amadon, 1959). (In the Goshawk, *Accipiter gentilis*, Schnell (1958:283) reports that the female "expels" the male from the nest area through use of a "dismissal call"; and Schnell postulates that the female's hostility causes the male to increase his foraging rate so that the food demands of the young can be met.) Actually the two theories are not mutually exclusive; as noted by Cade (1960:246), the chief problem is to determine whether the size differential has been selected mainly in relation to niche utilization or in relation to

TABLE 14  
SEXUAL DIMORPHISM IN SIZE IN SOME NORTH AMERICAN FALCONIFORM BIRDS  
(Calculated from data in Friedmann, 1950)

Form	Number of specimens <sup>2</sup>	Wing length of females <sup>3</sup> (mm)	Percentage difference between sexes <sup>1</sup>		
			Wing	Bill	Tarsus
<i>Accipiter striatus striatus</i>	5-6	182	18.3	20.8	10.9
<i>Accipiter s. velox</i>	51-40	200	14.6	18.9	9.1
<i>Accipiter cooperii</i>	34-27	260	11.1	14.7	9.8
<i>Accipiter gentilis atricapillus</i>	27-22	334	2.5	7.2	7.0
<i>Falco sparverius sparverius</i>	64-68	195	6.1	4.0	0.5
<i>Falco columbarius columbarius</i>	28-32	208	9.1	12.0	5.2
<i>Falco albicularis albicularis</i>	11-18	220	14.0	12.9	7.9
<i>Falco tinnunculus tinnunculus</i>	7-5	252	3.4	13.7	5.3
<i>Falco femoralis femoralis</i>	11-7	271	11.0	14.0	6.8
<i>Falco mexicanus</i>	17-18	343	12.7	15.3	7.9
<i>Falco peregrinus anatum</i>	20-22	356	11.8	16.2	6.8
<i>Falco rusticolus obsoletus</i>	42-59	403	9.5	10.2	4.0

<sup>1</sup> Female larger than male in all species.

<sup>2</sup> Males—females.

<sup>3</sup> Provides an indication of body size.

behavioral dominance of the female. Unlike Cade (1960), I believe the basic adaptive function of the dimorphism is related to differential niche utilization. The fact that the dimorphism is "reversed" is, however, explicable in terms of an advantage in female dominance in the breeding season.

For the Falconiformes there is good evidence of differential niche utilization by the sexes in several strongly dimorphic forms. Commenting on the prey of falcons, Cade (1960:243) notes that

males tend to take somewhat different species of prey than do females. Male peregrines [*Falco peregrinus*], for example, catch small birds most frequently (passerines and shore birds in the 30- to 150-gram categories) but also prey on birds up to the size of teal and ptarmigan (400- to 600-gram categories). Females are more prone to take larger passerines, shore birds, and small waterfowl (in the 200- to 600-gram categories), but also prey on waterfowl up to 1,500 grams. On the other hand, male and female kestrels [*Falco sparverius*], which show less dimorphism in size than peregrines do, take the same kinds of prey in about the same proportions (Cade, unpublished).

For the Goshawk convincing evidence of differential niche utilization by the sexes is provided by Höglund's study (1964) in Sweden, in which prey species were identified from the stomach contents of 45 males and 63 females (table 15). The average weight of birds and mammals eaten by the male is smaller than that of those eaten by the female. Additionally, as Höglund (1964:316) has shown, the weights of birds preyed upon by the female average 79 per cent the weight of the female, and the weights of mammals taken by the female average 42 per cent the weight of the female. Corresponding figures for the male are 67 per cent for birds and 22 per cent for mammals. Hence the male takes relatively smaller prey items than does the female. Finally the data show that the female preys to a greater extent on mammals than does the male. Proportions of mammals in the stomachs of the Goshawks examined by Höglund were 43 per cent for females but only 24 per cent for males. In view of the marked sexual differences demonstrated for the Goshawk, it would be interesting to see comparable data for other members of the genus *Accipiter*, particularly the smaller but more strongly dimorphic Sharp-shinned Hawk (*Accipiter striatus*).

TABLE 15  
SEXUAL DIFFERENCES IN FOOD ITEMS TAKEN BY GOSHAWKS IN SWEDEN  
(Data from Höglund, 1964; table 13, p. 316)

Sex of Goshawk	Birds		Mammals	
	Number taken	Mean weight (g)	Number taken	Mean weight (g)
Female	42	960	32	515
Male	41	550	13	185

#### ALLOPATRY OF THE SEXES

Turning now to the second major category of methods of reducing intersexual competition for food (table 11), an example of macrogeographic allopatry is provided by Pitelka's study (1959) of the Pectoral Sandpiper (*Erolia melanotos*) in northern Alaska, where adult males move south from the breeding grounds soon after egg-laying is finished and females depart shortly after their young hatch. Because the adult segment of the population has withdrawn from the breeding grounds before the young make their heaviest demands on the food supply, food available to the young presumably is augmented, thereby increasing their survival. In a similar example, the Oldsquaw Duck (*Clangula hyemalis*) is cited by Rand (1952) as a species in which males desert the breeding grounds before the young are hatched.

In the Yellow-bellied Sapsucker (*Sphyrapicus varius*), as in many migratory birds (Nice, 1933; Morley, 1943; Lack, 1944), the sexes winter in different areas (Howell, 1953). The fact that males tend to winter farther north than do females probably is explicable in terms of a selective advantage of early arrival of males on the breeding grounds in the spring in order to establish territories, but it may be worthwhile to consider the hypothesis that there is an advantage in differential winter ranges of the sexes in connection with a reduction in intersexual competition. Male birds wintering in the northern part of the winter range simultaneously avoid intersexual competition and insure for themselves an advantage in intrasexual competition for breeding territories.

Ptarmigan (*Lagopus*) show a strong tendency for spatial and habitat segregation of the sexes in the nonbreeding season (Anon., 1924; Weeden, 1964). In Alaska and apparently in other parts of their respective ranges, males of the Rock Ptarmigan (*L. mutus*) and the Willow Ptarmigan (*L. lagopus*) remain through the winter above timberline on or near the breeding grounds, while females leave the breeding areas in the autumn and move down to winter in shrubby openings in the boreal forest, in some recorded instances traveling 20 or more miles to reach suitable areas of this habitat. Speculating on the adaptive significance of this example of macrogeographic allopatry, in which males and females exploit different habitat types in the winter, Weeden (1964) offers several suggestions, the most plausible of which is that "movement of part of the autumn population may be necessary because of food shortage in winter in [the] breeding habitats."

In species in which the sexes are macrogeographically allopatric on the wintering grounds, they necessarily are subject to different selective pressures during part of the year. It is probable that this promotes sexual dimorphism in the feeding apparatus and in other characters, and it is likely that in some cases the dimorphism in structure and behavior that is selected on the wintering grounds secondarily results in some degree of differential niche utilization when the sexes are together on the breed-

ing grounds. In some species sexual dimorphism in bill structure may be adaptively related to differential niche utilization during only part of the year, being selectively neutral, if not maladaptive, at other times.

An example of microgeographic allopatry in which males and females occupy adjacent areas of similar habitat is provided by the Mockingbird (*Mimus polyglottos*), where individuals of either sex hold solitary feeding territories during the nonbreeding season (Laskey, 1935:373; Michener and Michener, 1935). Similar behavior is displayed by the Loggerhead Shrike (*Lanius ludovicianus*) (Miller 1931:148), the Red-headed Woodpecker (Kilham, 1959), and numerous other species. In all cases the territorial bird insures for itself an adequate food supply during the critical winter months. Not infrequently winter territories are defended against intrusions of other species (Kilham, 1959; and personal observations on *Mimus polyglottos*).

The Great-tailed and Boat-tailed grackles (*Quiscalus mexicanus* and *Q. major*) provide examples of microgeographic allopatry in which the sexes exploit different habitats. In the nonbreeding season these strongly dimorphic species forage in unisexual flocks which tend to frequent different types of habitats within the same general area (McIlhenny, 1937; Selander and Giller, 1961; Selander and Nicholson, 1962; Tomkins, 1963). For example, in Texas male flocks of *Q. mexicanus* tend to forage in city parks and about cattle pens and barns, while female flocks are visiting agricultural fields (Selander, 1965a). Comparable behavior is exhibited by the Red-winged Blackbird (*Agelaius phoeniceus*) and, to a lesser extent, by the less dimorphic Brown-headed Cowbird (*Molothrus ater*). Judging from the behavior of these icterids, it seems probable that the degree to which unisexual flocking and differential foraging is shown in a species is directly related to the degree of sexual dimorphism in the feeding apparatus.

The grackles *Q. mexicanus* and *Q. major* also provide examples of differential foraging by the sexes. However, the sexual variation in behavior presumably is not selected per se but is a consequence of morphological dimorphism maintained by intense sexual selection (see Discussion, below). Females sometimes forage for fish or refuse by hovering over water and dipping down to pick items from the surface with the bill; and, occasionally, they plunge below the surface of the water (Griscom, 1932:400; Sprunt, 1958:369; personal observation). Because of their larger body size (table 13) and disproportionately longer tails (Selander, 1958:372), males apparently cannot forage in this way. But, in the related Brewer Blackbird (*Euphagus cyanocephalus*), in which the sexes are only moderately dimorphic (table 13), both males and females forage in this manner (Richardson, 1947).

#### DISCUSSION AND CONCLUSIONS

The foregoing survey provides evidence supporting the view that sexual size dimorphism in birds is often associated with differential niche utilization. Additional studies of sexual differences in feeding behavior are needed, but there can be no doubt that adaptive radiation in the form of divergence of the sexes in foraging is a common phenomenon.

Sexual dimorphism in size is almost universal among birds, and the degree of dimorphism is variable from species to species, even within genera. As with other adaptive characters, there is variation in degree of dimorphism at the population level within species. Examples are provided by the melanerpine woodpeckers (fig. 1), by the accipiters and falcons (table 14), and by other groups treated in this paper. I have previously reviewed variation of this type in wrens of the genus *Campylorhyn-*

*chus* (Selander, 1964), and additional examples are cited by Rensch (1950), Selander (1958), Amadon (1959), and Selander and Giller (1963). It is significant from the standpoint of adaptation in relation to niche utilization that many groups of birds tend to be more dimorphic sexually in bill dimensions than in dimensions of other body parts such as the wing, tail, or tarsus.

#### BODY SIZE AND SEXUAL DIMORPHISM

Rensch (1950, 1960) discusses a "rule" relating body size and degree of sexual dimorphism in size in birds and other animals. He notes (1960:157) that "in species of birds in which the male is larger than the female, the relative sexual difference [in size] increases with body size. If, by way of exception, the females are larger than the males, as among many species of birds of prey, the opposite correlation applies, *i.e.*, the greater sexual difference is found in the smaller species." Actually, the correlations are weak and the exceptions so numerous as to raise questions concerning the validity of the "rule."

A trend toward greater degrees of sexual dimorphism in species of larger body size is best shown by groups of birds (*e.g.*, the Tetraonidae and Icteridae) in which polygamous and promiscuous mating systems are represented. For reasons not readily apparent, there is a tendency in some families of birds for polygamous and promiscuous species to be larger than the monogamous forms (Amadon, 1959). Hence much of the increased sexual dimorphism in size and in other secondary sexual characters in the larger species is attributable to the increased strength of sexual selection that is characteristic of nonmonogamous mating systems (Darwin, 1871; Fisher, 1929; Huxley, 1938; Crook, 1964; Selander, 1965a). In avian families in which the species are strictly monogamous, and in which the strength of sexual selection presumably is relatively uniform among the species, there is little evidence supporting Rensch's "rule." For example, in the North American Picidae, the largest species, the Ivory-billed Woodpecker (*Campephilus principalis*), is not more dimorphic than the smallest species, the Downy Woodpecker (*Dendrocopos pubescens*). Again, among the Corvidae, the Common Raven (*Corvus corax*), which is the largest species of passerine bird, is not more dimorphic than the smaller species of the family.

Examining sexual dimorphism in size in the North American Falconiformes, I fail to find support for Rensch's claim that greater sexual dimorphism is characteristic of the smaller species. This relationship holds for *Accipiter*, as shown in table 14, but not for *Falco*, *Buteo*, or other genera.

Recent work by Schoener (1965) on factors influencing differences in niche relationships of sympatric species of birds suggests lines of investigation that might profitably be explored in relation to ecological dimorphism. Among sympatric congeners Schoener finds the least difference in bill size in species feeding on relatively abundant food, presumably because they are able to partition food by foraging in different microhabitats and by using different feeding techniques within a major habitat, as do certain warblers (MacArthur, 1958) and titmice (Betts, 1955). But species exploiting less abundant food more frequently partition it by size, possibly since in any one narrow range of microhabitats food is not sufficiently abundant to support a population. It is notable that families in which there is relatively great divergence in bill size among sympatric species also show relatively large degrees of sexual dimorphism in the bill; these include the Picidae, Nectarinidae, Scolopacidae, Rallidae, Psittacidae, and Sittidae.

An interspecific size effect is also demonstrated by Schoener (1965). Generally

the degree of difference in bill size among sympatric species is greater in larger species, presumably because they feed on larger, less abundant "packets" of food and therefore require relatively large foraging areas, which decreases the likelihood that niche separation can be achieved by habitat segregation and increases the probability that interspecific competition will be alleviated by partitioning of food by size. Similarly it may be possible to show that intersexual competition is more often alleviated in larger species by partitioning of food by size, thus providing a partial explanation for Rensch's "rule."

#### TERRITORIES, NICHE DIVERGENCE, AND INTERSEXUAL COMPETITION FOR FOOD

Present evidence suggests that marked sexual dimorphism in the feeding apparatus occurs more frequently in insular birds than would be expected on the basis of chance alone. It may therefore be worthwhile to compare insular and continental environments with respect to factors affecting sexual dimorphism in the feeding apparatus. To facilitate discussion, I have prepared a diagram (fig. 8) illustrating adaptive adjustments available to species facing the problem of alleviating intersexual competition for food.

Consider first a hypothetical situation involving a continental species in which pairs hold feeding and nesting territories throughout the year (A in fig. 8). We will assume that the species is sexually monomorphic in bill size and shows no sexual divergence in niche utilization, and that food is sufficiently abundant that both male and female, although they forage in similar fashion and take the same types of food, are able to obtain adequate food within their territory. Now let us assume that the total amount of food in the niche being exploited by the territorial pair becomes diminished. This could result from several causes, including a climatic change or the invasion of the area by another species of similar adaptive type that takes some food items also eaten by pair A. Whatever the cause, the effect is that pair A no longer is able to find sufficient food within its territory, and selection pressures arising from increased intersexual competition operate to produce an adaptive response. One possible course of adaptation is illustrated in C of figure 8, in which the sexes diverge in bill structure and in niche utilization, thereby decreasing sexual overlap in exploitation of food. This response is achieved without increase in territory size, and it may in fact permit some reduction in territory size.

Whether the adaptive course shown in C of figure 8 is open to a species will depend on the complex interaction of several factors. For example, there must be sufficient environmental heterogeneity to provide subniches for the sexes. Thus opportunity for divergence will depend upon the composition and structure of the biotic community of which the pair is a part and will be influenced by the presence or absence of other species exploiting "adjacent" niches. In rich continental faunas it seems probable that the niche of a species is to some degree "contained" by the presence of other species with similar if not partially overlapping niches. For this reason the extent of sexual divergence in niche utilization that a species may achieve will vary regionally but will generally be limited in continental areas owing to the relative richness of the faunas. On islands, the opportunity for sexual divergence may be greater because of reduced numbers of competing species and the resultant vacancy of niches. It is also possible that on islands, and especially on smaller ones, divergence of the sexes is more frequently selected because of lesser abundances of food items of any one small range of size or type. In any event, it is on islands that we most frequently find distinct differential niche utilization

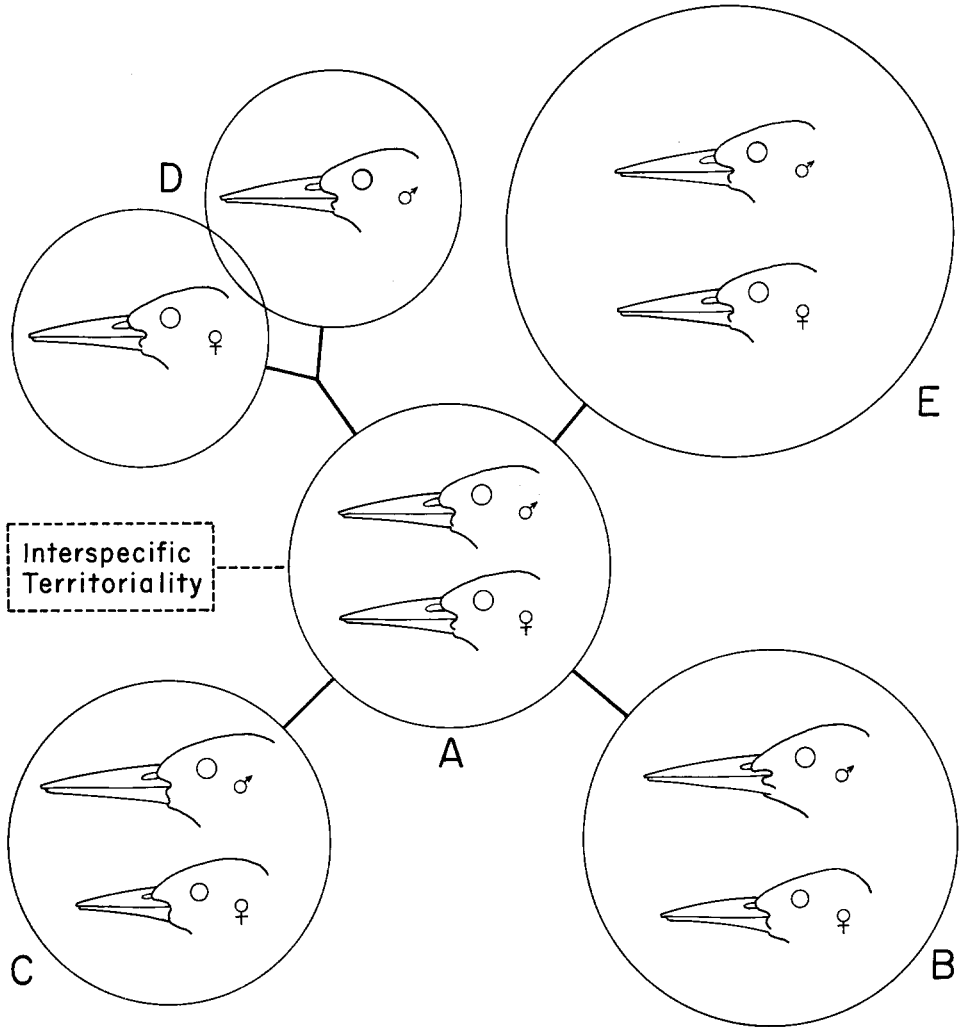


Figure 8. Adaptive adjustments alleviating intersexual competition in territorial birds. See text for explanation.

employed in the reduction of intersexual competition. Also, in insular situations there is greater opportunity for evolutionary divergence of the sexes because isolated populations are freed from the necessity of compromising between adapting to local conditions and remaining co-adapted with a gene pool shared with other populations of the species (Mayr, 1963:545). Moreover, insular forms may experience genetic revolutions and pass through periods of genetic lability which facilitate shifts in niche (Mayr, 1954, 1963). In short, many of the factors promoting adaptive radiation at the species level similarly influence radiation at the level of the population.

Returning now to pair A (fig. 8), it is obvious that an alternative to divergence in niche utilization (C) would be to increase the size of the territory, thereby aug-



menting the total amount of available food. This course of adaptation is shown in E of figure 8, in which the pair has remained morphologically and ecologically monomorphic but now exploits a larger feeding area. But owing to budgetary requirements of time and energy for reproduction and other activities, there is an upper limit to the size of the territory that a pair can effectively maintain. (This will be influenced by the population density of the species as it affects interpair competition for space, and by other factors.) Presumably for this reason many continental species apparently alleviate intersexual competition by employing a combination of the two adjustments I have discussed. This is shown in B of figure 8, in which the pair has moderately increased the degrees of morphological and ecological dimorphism and has also slightly increased the size of the territory. The particular combinations of these two adaptive adjustments may be expected to vary from species to species and from population to population within a species. Possibly a frequent use of increased territory size to reduce intersexual competition underlies the fact that continental species rarely show extremes of sexual dimorphism in the feeding apparatus.

Two other possible courses of adjustment are shown in figure 8. In D, intersexual competition is lessened by the pair members holding completely or partially separate feeding territories, an adjustment that permits survival of the pair members in critical periods of food shortage. Because reproduction will generally demand co-occupancy by pair members of a common territory in the breeding season, use of this adjustment is limited. Finally figure 8 illustrates an adaptive course involving interspecific territoriality, or the exclusion of individuals of other species competing for food (Simmons, 1951; Selander and Giller, 1959; Orians and Willson, 1964). This course, which increases the amount of food available for the pair holding the territory, may be taken by species which also employ other methods of reducing intersexual competition. The extent to which interspecific territoriality is employed is determined by many of the same factors that affect intraspecific territoriality, including the amount of time and energy available for this activity.

#### SEXUAL SELECTION, DIMORPHISM, AND NICHE UTILIZATION

Under strong sexual selection in polygamous and promiscuous mating systems there often is definite increase in body size in males owing to the advantage of large size in epigamic display and in intermale dominance relations at the "lek" or at colonial breeding sites. In some species the advantage of large size in the males may be so great that they are in a sense "pushed" by sexual selection into "inferior" subniches, with the result that mortality rates are higher in males than in females. Yet imperfection in adaptation of the male as far as niche relationships are concerned will persist because of the contribution of large size to overall Darwinian fitness (Selander, 1965a). Since in many promiscuous species the males need not be closely associated with the females for much of the year, they are able to occupy areas in which they can specialize in their own subniche; and, as previously mentioned, adaptation to different subniches by males and females of strongly dimorphic, nonmonogamous species may be facilitated by unisexual winter flocking and the use of different feeding areas.

#### FREQUENCY OF ECOLOGICAL POLYMORPHISM

Mayr (1963) has recently asked why ecological polymorphism is not more common than it is. Actually, polymorphism may be more common than it appears, especially when we consider that it may operate on a behavioral level without obvious correlates in morphology. But there is value in exploring the selective basis for poly-

morphism. Levins (1962, 1963), who provides insight into the problem of combinations of environmental conditions that promote or retard the evolution of ecological polymorphism, suggests that polymorphism is favored only when the differences between niche (or subniche) optima are large in comparison with individual homeostasis and under conditions in which the environment is heterogeneous in space but not in time.

In concluding this discussion, much of which is speculative, I wish again to emphasize the similarities between adaptive radiation as manifested in a group of species and within a species population. These extend not only to the evolutionary results of radiation but also to factors (including competition, isolation, and environmental heterogeneity) that promote or restrict radiation. As an aspect of ecological polymorphism, sexual dimorphism has important adaptive significance.

#### SUMMARY

The concept of adaptive radiation may be extended to the intrapopulation level, where it is expressed as polymorphic or continuous ecological variation. Under certain conditions, conspecific individuals come to occupy different subniches or adaptive subzones, subdividing and, perhaps, expanding the total niche or zone utilized by the population. In birds morphological and ecological polymorphism frequently is expressed in sexual dimorphism in size and structure of the feeding apparatus and in differential foraging behavior and niche utilization by the sexes. Sexual divergence is believed to have adaptive value in alleviating intersexual competition for food.

Among woodpeckers of the West Indies and of North and Central America, the greatest degrees of sexual dimorphism in bill size are found in insular species inhabiting Hispaniola, Puerto Rico, and Guadeloupe Island. Field studies have demonstrated a relationship between degrees of sexual dimorphism and sexual divergence in foraging behavior in two melanerpine woodpeckers, the strongly dimorphic Hispaniolan Woodpecker (*Centurus striatus*) and the moderately dimorphic, continental Golden-fronted Woodpecker (*Centurus aurifrons*). In the insular species *C. striatus*, in which there is a 21.3 per cent sexual difference in bill length, both sexes employ the same repertoire of foraging techniques, but males probe more often than females and females glean more frequently than males. The data on foraging behavior also suggest sexual differences in the locations of foraging. Sexual differences in foraging behavior are in directions that are expected on the basis of sexual dimorphism in the bill and tongue. In the continental species *C. aurifrons*, in which the sexual difference in bill length is only 9.1 per cent, there were no statistically significant sexual differences in foraging, although the data suggest slight sexual variation paralleling that seen in *C. striatus*.

It is likely that divergence of the sexes of *C. striatus* into different subniches has involved an expansion of the total feeding niche of the species. The divergence is believed to be related to reduced interspecific competition resulting from the absence or rarity on the island of other woodpeckers and birds of similar adaptive type. Presumably owing in part to differential niche utilization by the sexes, this insular woodpecker is able to maintain population densities much greater than those maintained by continental woodpeckers. Freedom from interspecific competition has also permitted marked expansion of the range of ecological distribution of *C. striatus* as compared with its continental congeners. The single species *C. striatus* manages to exploit its insular environment to a degree which in continental North America is achieved only by the combined efforts of several species of woodpeckers or other birds

of similar adaptive type. Evidence of sexual variation in foraging is available for several other birds, including the Huia, dowitchers, nuthatches, and grackles.

Differential foraging behavior by pair members within a common territory or home range is only one of several methods of reducing intersexual competition for food. Others include macrogeographic or microgeographic allopatry of the sexes, increase in size of territory or home range, and interspecific territoriality. Continental species of birds which form pairs holding feeding and nesting territories commonly alleviate intersexual competition by a combination of moderate ecological sexual dimorphism and moderate expansion of territory size. In insular situations extreme niche divergence of the sexes is more often possible because of a chronic vacancy of niches.

In species with polygamous and promiscuous mating systems, imperfections in adaptation of the male in regard to niche utilization may persist because of the great contribution of large body and bill size to the overall fitness of the male.

Many of the factors promoting or restricting adaptive radiation are similar at the species and intrapopulation levels. As an aspect of ecological polymorphism, sexual dimorphism has important adaptive significance.

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