

ECOLOGICAL AND SOCIAL IMPLICATIONS OF SEXUAL DIMORPHISM IN FIVE MELANERPINE WOODPECKERS

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Sexual differences within species have provided material for debate on a number of issues. Recently, several reports have indicated the ecological importance of sexual dimorphism in certain species, primarily birds (c.f. Amadon 1950, 1959; Cade 1960; Ward 1965; Sibley 1957; Selander 1966) and lizards (Schoener 1967, 1968, 1970). These discussions have indicated certain relationships between sexual differences in size of trophic appendages and specialization in foraging patterns. This report considers the ecological effects of sexual dimorphism as related to foraging behavior in five species of melanerpine woodpeckers and suggests certain social implications of such differences which have thus far received little attention.

Current ecological theory assumes differences in ecological pressures on species of islands and continents partly as a result of increased interspecific competition provided by the greater number of species on continents. It is believed that those differences may be reflected in bill sizes of birds inhabiting the two types of areas. Variation, expressed as sexual dimorphism, in the bill and tongue of woodpeckers is considered to be one type of adaptation to intraspecific competition for food, particularly in environments relatively free of the restraints of strong interspecific competitors. The adaptiveness of such variation may be indicated by correlations of sexual dimorphism and separation of the sexes in foraging patterns. Such sexual specialization is considered a means of finer niche partitioning by the species.

Niches may be partitioned by sexes in a number of ways, such as by foraging in the same ways in different topographical areas or by developing sexual specialization in exploiting the same general foraging area in different manners, such as by females foraging on smaller branches or employing a particular foraging mode more frequently than males. Furthermore, the means by which niche partitioning by sexes is achieved may be partly a function of the social system of the species. In those species in which sexes interact fre-

quently, there may be a tendency to exploit the same foraging area. This tendency may then encourage greater variation in bill sizes as a means of permitting more intense social interaction. So, whereas sexual dimorphism may be a means of permitting the sexes to separate in foraging behavior, it may also be a means of facilitating social behavior by permitting sexes to forage in the same area.

The subjects of this study are three insular species of melanerpine woodpeckers occurring in the West Indies and two melanerpines of the continental United States. Following the nomenclature of Selander and Giller (1963) and Selander (1966), the insular species are the Puerto Rican Woodpecker (*Melanerpes portoricensis*), the Hispaniolan Woodpecker (*Centurus striatus*), and the Jamaican Woodpecker (*C. radiolatus*). Each of these is the sole resident representative of the melanerpine group on its respective island. Rare sightings of the Cuban Green Woodpecker (*Xyphidopicus percussus*) on Jamaica and Hispaniola have been reported and the Yellow-bellied Sapsucker (*Sphyrapicus varius*) is an uncommon winter visitor on all three islands.

The two continental forms are the Golden-fronted Woodpecker (*Centurus aurifrons*) which ranges from Honduras north to central Texas, and the Red-bellied Woodpecker (*C. carolinus*), which ranges from central Texas to the east coast of the United States.

MATERIALS AND METHODS

MORPHOLOGY

Body weight (g) was recorded in the field, and linear measurements (mm) of alcoholic specimens were made with dial calipers. Bill length was measured from the anterior margin of the nostril to the tip of the culmen. Width and depth of the bill were measured at the level of the anterior margin of the nostril; and gonys length was measured from the median raphe to the tip of the lower mandible.

Measurements of the tongue included: (a) the number of groups of barbs along the horny tip; (b) the length of the horny tip; (c) the width of the base of the horny tip; and (d) the width and depth of the basihyal, measured at a point 3 mm proximal to the base of the horny tip. The cube root of body weight was used as an index of body size.

FORAGING BEHAVIOR

Observations on the foraging behavior of *C. carolinus* in the Austin area were made in the period from 4 February to 7 September 1968, mainly along the west bank of the Colorado River near Austin, Texas. Other woodpeckers recorded foraging in these areas include *Dendrocopos villosus* (Hairy Woodpecker), *D. pubescens* (Downy Woodpecker), *Colaptes auratus* (Common Flicker), and *Sphyrapicus varius*. The vegetation was typical of river-bottom areas and was dominated by *Salix nigra* and *Populus deltoides*. *Centurus aurifrons* was not recorded in these areas but occurred within one-half mile of the western limit of Austin and was seen occasionally within other parts of the city. The ranges of these birds overlap narrowly in central Texas, and Selander and Giller (1963) report the birds hold mutually exclusive territories where they forage in common areas in Austin.

The studies of *M. portoricensis* of Puerto Rico and *C. striatus* of Hispaniola were conducted during two visits to the West Indies, the first being in the dry winter months, from 13 November 1967 to 7 January 1968. The second part of the study began 18 March and continued until 10 June 1968, the early part of the rainy season.

The Puerto Rican records were made, for the most part, in coffee plantations near Maricao. Large trees have been cultivated in these areas to provide shade for the coffee plants.

In the Dominican Republic, the winter records of *C. striatus* were made almost entirely in the hills west of the city of San Cristobal. The predominant trees of the area were several dicotyledonous species and groves of cultivated coconut trees.

In spring, the Dominican records were taken from a wider area, including the coconut and plantain farms of San Cristobal, and the arid areas near Moca, where the larger vegetation types are the timber trees *Guaicum* sp. and *Adenantha pavonina*, and the cacti *Opuntia moniliformia* and *Neoblotia paniculata*. Also included in the study was a cacao plantation area near Santiago, where large trees provide shade for the crops.

Most of the winter records in Haiti were made near Petionville, in a mountainous area outside Port-au-Prince. In spring, records were obtained from a wider area but, for the most part, were taken from areas near Petionville and in the farmland along the road from Port-au-Prince to Daumien. The major tree species in the mountain areas of Haiti are similar to those in other parts of the island. In the lowland study areas, the principal tree is the coconut (*Cocos nucifera*).

Most of the records of the Jamaican Woodpecker were gathered in a bird sanctuary near Rocklands. The area is hilly, with the heavy dicotyledonous vegetation which is typical for the area.

Foraging records were made by observing the birds in the field and recording each instance of foraging behavior by placing it into one of the three common foraging categories (probing, gleaning, or hammering) as described by Selander (1966). Rare instances of foraging in other ways were not considered. Probing is a motion in which the bill or tongue is inserted into cracks, crevices, small holes, under bark, or into fruit or epiphytes. Gleaning actions are those in which food items are picked from the surface of the trees, and hammering is the striking of a tree with the bill in order to remove bark or to excavate a hole. In a foraging context, the latter

activity is usually performed to remove buried insect larvae or to loosen bark so probing or prying can be accomplished, but the motor pattern itself may be indistinguishable from early stages of nest hole excavation.

The type of foraging mode (*sensu* Short 1970) performed does not necessarily indicate the type of food being taken. For example, ants may be taken by utilizing either gleaning or probing techniques. Also, what appears to be a food-getting motion actually may be a food-searching motion. Searching motions are especially noticeable in the Puerto Rican Woodpecker, which frequently "taps" trees as it moves over the surface of a limb in what is apparently an attempt to locate burrowed larvae by the resonance of their chambers (see Kilham 1965). Apparent search-tapping activities were excluded because of the possibility of misinterpreting the action. Other foraging patterns were also observed, such as lizard-chasing and scratching in the earth, but these occurred too infrequently for valid comparisons.

The data also include the geographic location of the record, the foraging site, the tree type (whether monocotyledonous or dicotyledonous), and the height at which the bird foraged.

RESULTS

MORPHOLOGY

In size of body parts, with relatively few exceptions, the insular species are more sexually dimorphic than those of the continent (table 1). The average size of the bill in males and females of *C. striatus* does not differ greatly from that of the continental species, but *M. portoricensis* has a smaller bill. This difference is related partly to the smaller body size of *M. portoricensis*; however, a comparison of ratios of culmen length to cube root of body weight (table 2) shows that bill size in *M. portoricensis* is disproportionately small in both sexes but especially so in the female. Also, relative to the continental species, culmen length in males of *C. striatus* is disproportionately large. This evidence indicates that selection is operating specifically on the body part and that the sexual variation is not due solely to simple allometric growth differences.

Melanerpes portoricensis and *Centurus striatus* are sexually dimorphic in all measurements except in basihyal width for the latter species (table 1). It is noteworthy that *C. aurifrons* is sexually monomorphic in all measurements (except tongue tip width), while *C. carolinus* is sexually dimorphic in several body parts including bill length. Marked sexual dimorphism in continental woodpeckers has been reported elsewhere (c.f. Ligon 1968; Short 1971) but, in the case of *C. carolinus*, probably should not be given undue importance as an ecological factor for reasons discussed beyond.

The tongue of woodpeckers is utilized directly in obtaining food and is morphologically

TABLE 1. Measurements of body parts.

	Males			Females		
	Sample size	Mean	Variance	Sample size	Mean	Variance
Bill						
Length						
<i>C. aurifrons</i>	13	24.0	1.28	13	24.2	1.27
<i>C. carolinus</i> ^b	10	24.8	1.14	16	23.2	1.49
<i>C. radiolatus</i> ^c	10	27.0	1.27	5	26.0	1.01
<i>M. portoricensis</i> ^{b,c}	21	22.3	1.94	19	18.5	1.05
<i>C. striatus</i> ^{b,c}	33	26.9	1.15	41	20.9	1.11
Width						
<i>C. aurifrons</i>	13	7.7	0.34	13	7.7	0.57
<i>C. carolinus</i>	13	7.7	0.29	13	7.6	0.44
<i>C. radiolatus</i> ^c	10	8.2	0.59	5	8.4	1.06
<i>M. portoricensis</i> ^{b,c}	13	7.5	0.36	11	6.6	0.43
<i>C. striatus</i> ^{b,c}	13	7.9	0.60	13	7.2	0.40
Depth						
<i>C. aurifrons</i>	13	7.6	0.34	13	7.3	0.20
<i>C. carolinus</i>	13	7.6	0.25	16	7.5	0.37
<i>C. radiolatus</i> ^c	10	8.7	0.51	5	8.7	0.75
<i>M. portoricensis</i> ^{b,c}	21	7.2	0.53	18	6.4	0.52
<i>C. striatus</i> ^{b,c}	34	7.8	0.73	41	6.7	0.49
Gonys						
<i>C. aurifrons</i>	13	18.7	1.58	13	19.0	1.13
<i>C. carolinus</i> ^a	11	19.2	1.18	13	17.9	1.20
<i>C. radiolatus</i> ^c	10	20.6	1.53	5	19.0	1.10
<i>M. portoricensis</i> ^{b,c}	22	17.3	1.79	19	14.4	0.99
<i>C. striatus</i> ^{b,c}	35	19.4	0.98	40	15.1	0.94
Tongue						
Tip Length						
<i>C. aurifrons</i>	9	13.6	0.82	5	12.9	0.64
<i>C. carolinus</i> ^a	9	14.8	1.23	16	13.4	1.38
<i>M. portoricensis</i> ^{b,c}	10	14.1	1.72	9	10.8	1.23
<i>C. striatus</i> ^{b,c}	14	14.8	1.07	12	9.6	0.81
Tip Width						
<i>C. aurifrons</i> ^b	7	1.7	0.10	5	1.5	0.06
<i>C. carolinus</i> ^a	13	1.6	0.13	13	1.5	0.08
<i>M. portoricensis</i> ^{b,c}	10	1.7	0.14	9	1.5	0.13
<i>C. striatus</i> ^{b,c}	14	1.6	0.18	12	1.3	0.23
Basihyal Depth						
<i>C. carolinus</i>	6	0.13	0.010	4	0.13	0.008
<i>M. portoricensis</i> ^{b,c}	6	0.11	0.008	5	0.09	0.009
<i>C. striatus</i> ^{a,c}	11	0.11	0.017	7	0.09	0.011
Basihyal Width						
<i>C. carolinus</i>	6	0.21	0.013	4	0.20	0.024
<i>M. portoricensis</i> ^{a,c}	6	0.22	0.031	5	0.17	0.030
<i>C. striatus</i> ^c	11	0.19	0.023	8	0.17	0.019

^a Significant sexual difference according to *t*-test analysis; $P < 0.05$.

^b Highly significant difference; $P < 0.01$.

^c Insular species.

specialized accordingly (see George and Berger 1966). In the species considered here, the horny tip of the tongue is flattened dorso-ventrally, with groups of barbs extending posteriorly from the lateral margins. In each group the barbs are shorter anteriorly. There are four to seven barbs in each group, except on the proximal part of the tip, where exceptionally long barbs exist singly. Numbers of barb groups range from 6 to 17, show great

overlap, and, statistically, no sexual differences could be demonstrated for any species.

The degree of sexual dimorphism in tongue width as demonstrated in differences in means is only slightly greater in *C. striatus* than in *M. portoricensis*; but, in the length of the horny tip, *C. striatus* is more dimorphic (table 1). Table 2 indicates the strong sexual differences in tongue tip length for the insular species when corrected for general size differences of

TABLE 2. Ratios of linear measurements of body parts to cube roots of body weights.

Body part	<i>Centurus aurifrons</i>		<i>Centurus carolinus</i>		<i>Centurus striatus</i> ^a		<i>Melanerpes portoricensis</i> ^a	
	Male	Female	Male	Female	Male	Female	Male	Female
Tarsus Length	5.32 ^b	5.30	5.08	5.10	5.41	5.49	5.42	5.31
Bill Length	5.60	5.79	5.80	5.61	6.26	5.18 ^c	5.51	4.92 ^c
Bill Width	1.80	1.84	1.81	1.76	1.80	1.80	1.87	1.73
Bill Depth	1.78	1.75	1.78	1.80	1.94	1.79	1.86	1.79
Gonys Length	4.36	4.53	4.50	4.33	4.57	3.86 ^c	4.34	3.81 ^c
Tongue Tip Length	3.18	3.08	3.47	3.23	3.40	2.39 ^c	3.52	2.84 ^c
Tongue Tip Width	0.39	0.35	0.38	0.37	0.36	0.33	0.42	0.39
Basihyal Width	0.04	0.04	0.04	0.04	0.04	0.04	0.06	0.04
Basihyal Depth	0.02	0.02	0.03	0.03	0.03	0.02	0.03	0.02

^a Insular species.^b mm/3√wt(g).^c Designates greatest sexual differences (♀/♂ > 70%, arbitrarily chosen).

the sexes. Tongue tip length may be ecologically important since prey-holding ability is influenced by the ratio of barb numbers to the length of the horny tip.

Sexual differences were found in the insular species in the size of the basihyal, which supports the tongue anterior to the glottis (table 1 and table 2). Relatively few sexual differences were seen in the continental species; and, in fact, the range of measurements of females of *C. carolinus* included that of the males in basihyal width. A high degree of sexual overlap in basihyal length and width occurred in both *C. carolinus* and *C. striatus*. The sexual differences shown in insular species were not surprising on the basis of the greater length of the entire tongue complex in males, as reported by Selander (1966).

When the value of the coefficient of difference (difference in means divided by the sum of the standard deviations) is 1.28, joint non-overlap of the two samples is 90% (Mayr et al.

1953:146), a value high enough to be considered by many taxonomists to indicate subspecific differences between populations represented by the samples (Davis 1965). Ecologically, degree of nonoverlap in bill length in the sexes is more significant than ratios of sexual dimorphism based on mean measurement (Selander 1966). A coefficient of difference of 1.28 is reached only in culmen length (2.65), gonys length (2.24), and tongue tip length (2.77) in *C. striatus*. *Melanerpes portoricensis* approaches this critical ratio only in culmen length (1.27).

FORAGING BEHAVIOR

Winter foraging modes. The records of foraging techniques compiled for insular forms in the winter season are shown in table 3a. Note that in every case the predominant technique employed by females was gleaning, and that females used hammering and probing techniques less frequently than did the males.

TABLE 3. Sexual differences in foraging mode.

Population	Probing		Gleaning		Hammering		$\chi^2_{(2)}$
	Males n ^a	Females n	Males n	Females n	Males n	Females n	
(a) Winter							
<i>M. portoricensis</i> ^c	34 (28)	21 (14)	33 (27)	80 (54)	54 (45)	46 (31)	20.93 ^d
<i>C. striatus</i> , Haiti ^c	98 (46)	94 (35)	87 (41)	156 (58)	26 (12)	20 (7)	18.53 ^d
<i>C. striatus</i> , D. R. ^c	28 (23)	14 (11)	49 (40)	86 (67)	46 (37)	29 (22)	18.53 ^d
<i>C. striatus</i> , Pooled ^c	126 (38)	108 (27)	136 (41)	242 (61)	72 (22)	49 (12)	29.95 ^d
(b) Spring							
<i>C. carolinus</i> ^c	48 (40)	31 (36)	47 (39)	43 (51)	24 (20)	11 (13)	3.08
<i>C. radiolatus</i> ^c	17 (16)	17 (17)	76 (72)	67 (67)	13 (12)	16 (16)	2.40
<i>M. portoricensis</i> ^c	50 (29)	27 (24)	46 (26)	49 (43)	78 (45)	38 (33)	8.63 ^c
<i>C. striatus</i> , Haiti ^c	60 (40)	72 (25)	57 (38)	162 (57)	34 (23)	50 (18)	15.24 ^d
<i>C. striatus</i> , D. R. ^c	29 (31)	38 (20)	43 (46)	119 (64)	22 (23)	30 (16)	8.21 ^d
<i>C. striatus</i> , Pooled ^c	89 (36)	110 (23)	100 (41)	281 (60)	56 (23)	80 (17)	23.43 ^d

^a Number of records in the category.^b Percent of total records for that sex.^c Significant sexual difference according to chi-square analysis; $P < 0.05$.^d Highly significant sexual difference; $P < 0.01$.^e Insular species.

TABLE 4. Overlap values for niche utilization.

Sexual Overlap in Foraging Mode (Winter)	Overlap value
<i>M. portoricensis</i> , Puerto Rico	0.729
<i>C. striatus</i> , Haiti	0.834
<i>C. striatus</i> , Dominican Republic	0.731
<i>C. striatus</i> , Pooled	0.800
Sexual Overlap in Foraging Mode (Spring)	
<i>C. carolinus</i> , Texas	0.889
<i>C. radiolatus</i> , Jamaica	0.953
<i>M. portoricensis</i> , Puerto Rico	0.834
<i>C. striatus</i> , Haiti	0.807
<i>C. striatus</i> , Dominican Republic	0.820
<i>C. striatus</i> , Pooled	0.811
Population differences in Foraging Mode Dominican Republic, Haiti	
<i>C. striatus</i> males (Spring)	0.911
<i>C. striatus</i> females (Spring)	0.933
<i>C. striatus</i> males (Winter)	0.749
<i>C. striatus</i> females (Winter)	0.760
Sexual Overlap in Foraging Height (Winter)	
<i>M. portoricensis</i> , Puerto Rico	0.855
<i>C. striatus</i> , Haiti	0.896
<i>C. striatus</i> , Dominican Republic	0.794
<i>C. striatus</i> , Pooled	0.980
Sexual Overlap in Foraging Height (Spring)	
<i>C. carolinus</i> , Texas	0.837
<i>C. radiolatus</i> , Jamaica	0.737
<i>M. portoricensis</i> , Puerto Rico	0.815
<i>C. striatus</i> , Haiti	0.820
<i>C. striatus</i> , Dominican Republic	0.875
<i>C. striatus</i> , Pooled	0.925
Population Differences in Foraging Height, Dominican Republic, Haiti	
<i>C. striatus</i> males (Spring)	0.880
<i>C. striatus</i> females (Spring)	0.787
<i>C. striatus</i> males (Winter)	0.715
<i>C. striatus</i> females (Winter)	0.935
Habitat Differences in Foraging Mode	
<i>C. striatus</i> , Dominican Republic, Monocot area	0.667
<i>C. striatus</i> , Dominican Republic, Docot area	0.841

When the differences in foraging behavior of the sexes were tested with χ^2 analysis, the results were highly significant for all populations.

The degree of overlap in niche utilization for any two groups may be quantitatively determined by application of Schoener's (1968) formula:

$$D = 1 - \frac{1}{2} \sum_{i=1}^n |P_{x,i} - P_{y,i}|$$

where $P_{x,i}$ and $P_{y,i}$ are the frequencies for sexes x and y , respectively, for the i^{th} category.

The overlap values for foraging behavior in winter are shown in table 4. The greatest over-

lap of sexes in foraging technique was seen in the Haitian population of *C. striatus*. Less overlap was found in the Dominican population and in *M. portoricensis* of Puerto Rico.

In winter, most records from Haiti were taken in a large ravine between the Villa Quisqueya and Iboe Lele hotels at Petionville. Although all the birds there exhibited adult plumage, the degree of sexual dimorphism of bill size did not appear to be as great as in other populations. The bill measurements of the one male collected were within the range of those of females for other populations. It is not known whether this condition was due to a large number of first-year birds which had not achieved their definitive bill size or if the weak dimorphism was a population characteristic. In spring, the situation in the ravine had changed. Areas that were heavily foraged in winter were neglected, and several breeding pairs with apparently "normal" bill dimorphism were nesting in and near the ravine. If the impression is valid regarding the weak dimorphism in the birds inhabiting the ravine in winter, whether due to age or population characteristics, greater foraging overlap could be expected in this group.

Spring foraging modes. The second part of the study was done in the spring, at the beginning of the rainy season, a time when the birds were breeding. Most of the study was conducted early in the breeding season to reduce the likelihood of encountering young birds which had not yet achieved their definitive bill size, a constant problem in tropical areas where populations may have extended breeding seasons. Gleaning was still the primary technique employed by females of all species (table 3b), but was reduced in importance in the Puerto Rican Woodpecker. Hammering and probing continued to be utilized to a greater degree by males than by females. Sexual differences in foraging mode were significant for the Puerto Rican and Hispaniolan populations, but not for the weakly dimorphic Texan or Jamaican populations.

Overlap values of sexes for foraging mode in the spring (table 4) were greatest in the monomorphic *C. radiolatus*. *C. carolinus* also showed a relatively high degree of overlap, while the strongly dimorphic insular species exhibited lower overlap values.

Sexual variation in foraging behavior of the Jamaican Woodpecker (*C. radiolatus*), a weakly dimorphic insular species, was studied only in the breeding season. A distinctive foraging pattern was shown in this species (table 3b). Gleaning was employed to a great

extent in both sexes, the males utilizing the technique more often than the females, a situation which occurs in no other species studied. No differences were shown and, in fact, a remarkable degree of similarity existed in the foraging patterns of the sexes.

Population differences in foraging behavior. Population differences in degree of separation of foraging mode for *C. striatus* were calculated for each sex. Males of the Haitian population were compared with males of the Dominican population for both seasons, and the same comparisons were made for females. Interestingly, in the spring breeding season, population differences were insignificant ($P > 0.05$) for both sexes (for males, $\chi^2_{(2)} = 2.14$; for females, $\chi^2_{(2)} = 2.08$). But, in the winter dry season, population differences were highly significant ($P < 0.01$) for both sexes (for males, $\chi^2_{(2)} = 34.22$; for females, $\chi^2_{(2)} = 15.50$).

There was high interpopulation overlap in foraging mode for both sexes in spring but less overlap in winter (table 4). Males of the two populations showed less seasonal overlap in foraging behavior than did females. The Haitian and Dominican populations were closely similar in their foraging patterns in a period of abundant food, but the populations separated in foraging mode when food became scarce. This finding indicates that foraging mode within a species is strongly influenced by local conditions, especially in times of low food supply.

When the separation of the sexes in foraging mode is compared, seasonal differences appear in the populations of Puerto Rico ($\chi^2_{(2)} = 182.69$), the Dominican Republic ($\chi^2_{(2)} = 774.56$), Haiti ($\chi^2_{(2)} = 69.96$), and the pooled populations of Hispaniola ($\chi^2_{(2)} = 194.58$). However, when the percentage differences between the sexes for each technique were totaled, the results showed little difference in the sexes of the Haitian population but identical degrees of difference in the Puerto Rican and Dominican species: 54% in the dry season and 36% in the wet season. The overlap values (table 4) point out seasonal differences more clearly. In every population, except the Haitian, overlap in foraging mode was greater in spring than in winter. So, whereas sexual differences are found for the two species in both seasons, greater separation was actually shown in the dry season, a period of low food abundance. The seasonal similarity in the Haitian population may be associated with a weakly dimorphic population studied in the dry season, as previously mentioned.

Habitat utilization by C. striatus. The study area near San Cristobal, Dominican Republic,

provided a situation for testing other ideas regarding habitat utilization by *C. striatus*. The area is divided into two major zones of different tree types. A coconut grove covers an area of about 5 acres and consists of about 30 trees. A wooded hillside adjoins the area, larger in total area than the grove, with the major part of the vegetation here composed of small (generally less than 7 m high) dicotyledonous trees and shrubs. The separation of foraging sites of the sexes was tested to determine the "preferred" tree type, monocot or dicot, when both were available. No difference was shown ($\chi^2_{(2)} = 0.03$). The results may be biased by the fact that, although these records were gathered in the dry winter season when little nesting and nest-hole defense would be expected, the birds were roosting in holes in the coconut trees and therefore might show a disproportionate amount of interest in the monocot area.

A second study conducted in the area involved determining the difference in frequencies of techniques (probing, gleaning, or hammering) the birds employed when foraging on the two types of trees. No difference was found ($\chi^2_{(2)} = 3.06$).

The monocot areas were considered to provide a simpler ecological situation for arboreal foragers than the dicot areas in which *C. striatus* foraged. Fewer species of trees were present in the monocot areas, and these provided relatively little diversity in their potential foraging sites. Most foraging by the woodpeckers was done on the trunks of these trees, although some food was taken from the fronds and seed clusters. The dicot trees, on the other hand, provided a three-dimensional canopy and a variety of limb sizes on which the birds might forage. To compare differences in foraging behavior on the two substrate types, foraging modes were analyzed statistically. It was found that the frequency of techniques employed in the two areas was different ($\chi^2_{(2)} = 27.40$). The overlap value for the sexes was 0.841 in the dicot area, while in the monocot area, it was 0.667. So, greater sexual divergence in technique occurred in the simpler area. The implication is that less food per unit of foraging area is found in the "simpler" area, an idea which is also suggested by the greater number of foraging records from the dicot (563) as compared to monocot areas (173). (There was no attempt to equalize the observation time in each area, but I was drawn to each study area by the calls of birds, which were clearly audible across both areas.)

Foraging height. Selander (1966) found no

TABLE 5. Foraging height.

Population	0-9 m		10-16 m		17+ m		$\chi^2_{(2)}$
	Males n ^a	Females n	Males n	Females n	Males n	Females n	
	% ^b	%	%	%	%	%	
(a) Winter							
<i>M. portoricensis</i> ^e	25 (54)	23 (40)	19 (41)	28 (49)	2 (4)	6 (11)	2.73
<i>C. striatus</i> , Haiti ^e	95 (58)	108 (48)	64 (39)	11 (50)	4 (2)	5 (2)	4.06
<i>C. striatus</i> , D. R. ^e	30 (30)	46 (44)	67 (68)	49 (47)	2 (2)	9 (9)	8.45 ^c
<i>C. striatus</i> , Pooled ^e	125 (48)	154 (47)	131 (50)	160 (49)	6 (2)	14 (4)	1.74
(b) Spring							
<i>C. carolinus</i>	49 (42)	26 (28)	60 (52)	64 (68)	7 (6)	4 (4)	5.77
<i>C. radiolatus</i> ^e	68 (65)	88 (87)	37 (35)	9 (9)	0 (0)	4 (4)	23.49 ^d
<i>M. portoricensis</i> ^e	99 (62)	50 (44)	56 (35)	55 (48)	3 (2)	9 (8)	9.82 ^d
<i>C. striatus</i> , Haiti ^e	61 (40)	89 (32)	50 (39)	157 (57)	32 (21)	29 (11)	15.71 ^d
<i>C. striatus</i> , D. R. ^e	36 (41)	102 (54)	43 (49)	76 (40)	8 (9)	12 (6)	3.67
<i>C. striatus</i> , Pooled ^e	97 (41)	191 (41)	102 (43)	233 (50)	40 (17)	41 (9)	10.43 ^d

^a Number of records in the category.

^b Percent of total records for that sex.

^c Significant sexual difference according to chi-square analysis; $P < 0.05$.

^d Highly significant sexual difference; $P < 0.01$.

^e Insular species.

significant difference in the foraging height of the sexes of *C. striatus*. But, in the current study, a different system of partitioning the strata was used, and the results are shown in table 5. In the dry season (table 5a), insignificant sexual differences in foraging height were seen for both *C. striatus* and *M. portoricensis*. When the Dominican and Haitian populations of the Hispaniolan woodpecker were analyzed separately, a significant difference was found only in the Dominican group.

In the breeding season (table 5b), significant sexual differences in foraging height were found for all insular populations except *C. striatus* of the Dominican Republic. [L. Short (pers. comm.) has corroborated the data from the Dominican Republic.] The results of a study of *C. radiolatus* of Jamaica and *C. carolinus* of Texas were included, and sexual differences were shown for the Jamaican but not the continental species.

Overlap values in foraging height (table 4) for the sexes in winter showed that the least overlap occurred in the Dominican population and the greatest overlap, in the pooled Hispaniolan populations. A comparison of the overlap values in foraging height for spring and winter showed greater overlap in winter for all populations except the Dominican. With the sexes pooled, overlap in foraging height between the Dominican and Haitian populations of *C. striatus* was greater in winter than in spring; and, interestingly, when sexes of the two populations were compared, there was greater overlap in foraging height between males in spring, but females in winter.

The degree of sexual overlap in *C. carolinus* (table 4) was very similar to that found for the

dimorphic species. Of particular interest, however, was the value obtained for *C. radiolatus*. The Jamaican Woodpecker showed very high overlap for sexes in foraging mode but, in foraging height, the value was remarkably low.

When the Haitian and Dominican samples of *C. striatus* were pooled, the overlap value for foraging height for sexes was higher than that for either population alone, a finding which is considered to be due to strong differences in the behavior of males of the two populations in winter (table 5a), and of females in spring (table 5b). These data may be interpreted as evidence that, although the degree of sexual dimorphism is similar in different populations, the method whereby the morphological adaptations are utilized may vary from one ecological situation to the next. Thus assumptions regarding the exact methods whereby sexually dimorphic species are subdividing the niche should be carefully considered.

DISCUSSION

The evidence given here indicates that variation in bill size of *C. striatus* and *M. portoricensis* has increased through polymorphism in response to intraspecific competition and the availability of relatively wider niches on these islands (see Mayr 1963; Van Valen 1965). The monomorphic *C. radiolatus* has taken a different evolutionary route and will be considered in a separate paper. [It should also be noted that *M. herminieri* (Guadeloupe Woodpecker) of Guadeloupe Island in the Lesser Antilles is sexually dimorphic in bill size (unpubl. data) and is not social (L. Short, pers. comm.).]

The morphological and ecological similarity of *Centurus aurifrons* and *C. carolinus* invites speculation as to the significance of the stronger sexual dimorphism in bill size of the latter species as sampled here. One factor that might account for the difference in dimorphism relates to the parts of the respective ranges from which the samples were collected. Specimens of *C. aurifrons* were taken well within their own range, whereas those of *C. carolinus* were collected at the extreme western boundary of their range where the species narrowly overlaps with *C. aurifrons*. Perhaps, then, *C. carolinus* was collected from areas where neither it nor *C. aurifrons* was particularly well suited. (No samples of *C. aurifrons* in the zones of overlap were taken.) If some undefined character of the habitat at the periphery of the species' range hindered the efficient exploitation of food resources, intra-specific competition for a reduced food supply might result in separation of the sexes in size of trophic appendages. Such separation might be due to specific selection for sexual dimorphism in peripheral areas, or due, at least partly, to the areas being continually more successfully invaded by individuals of particular sizes from the more central areas of the population. [*C. carolinus*, when sampled throughout its range is found to be relatively sexually monomorphic in bill length (Selander and Giller 1963).] The variation in trophic appendages in certain areas at the periphery of the range of *C. carolinus* might be permitted by low numbers of the essentially parapatric competitor, *C. aurifrons*, in these places. Interspecific competition in narrow areas of sympatry for the two species would be reduced further by the maintenance of interspecific territoriality (Selander and Giller 1963).

Whereas the above considerations indicate the need for more information regarding sub-populational differences in degree of sexual dimorphism, the sexual variation in *C. carolinus* should probably not be given undue ecological importance. In these samples taken from the periphery of the species' range, the sexes fail to show a high level of joint non-overlap (or coefficient of difference) in any parameter. Also, the sexes show a low degree of sexual dimorphism when mean measurements are considered (table 1) and in table 2 the low differences in ratios of linear measurements of body parts to cube roots of body weights for both continental species do not suggest that selection has operated specifically on trophic appendages as it apparently

has in the insular dimorphic species. Therefore, in an ecological context and on the basis of other studies, both continental species may be considered sexually monomorphic. It is apparent that population differences in levels of variation present interesting problems for further study.

It should be noted that Hutchinson (1959) described a minimal bill-size ratio of about 1.28 (taken as the ratio of larger to smaller) for sympatric species of birds. It is interesting that this "biological constant" is reached in some measurements between sexes of the Puerto Rican and the Hispaniolan Woodpeckers. The ecological significance of this difference in sexes is emphasized by Schoener's (1970) suggestion that for animals of similar morphologies and foraging patterns the ratio which would result in taking different foods is probably much lower. In general, the niche width-variation model of Van Valen (1965) is supported. The model holds that species may increase in variation (continuous or polymorphic) as a correlate of the wide niches believed to exist on islands.

SOCIAL INFLUENCES ON VARIATION

There is no way to determine precisely, or perhaps even generally, at this time, the spectrum of adaptive influences which operate in the selection for sexual differences within species. We are broadly aware of the effects of sexual selection which might increasingly drive the sexes apart in appearance and behavior. It seems, however, that even this hallowed concept is based largely on circumstantial evidence, with surprisingly little supportive data considering the enormity of its implications. Sexual differences may also arise or be reinforced (we have little information regarding the sequence of selective factors in the development of sexual differences) on an ecological basis through resource partitioning, as has been discussed here. However, it should be apparent that our investigative techniques in the search for the adaptiveness of variation at any level, continuous or polymorphic, are crude at best. Natural phenomena detectable by such means would need be rather blatant. Perhaps because of the difficulties inherent in such studies, little attention has been given to the variety of potential interplay between forces selecting for variation. I would like to suggest two ways selection working through social means might implement or reinforce ecological mechanisms to influence variation between and within sexes in woodpeckers.

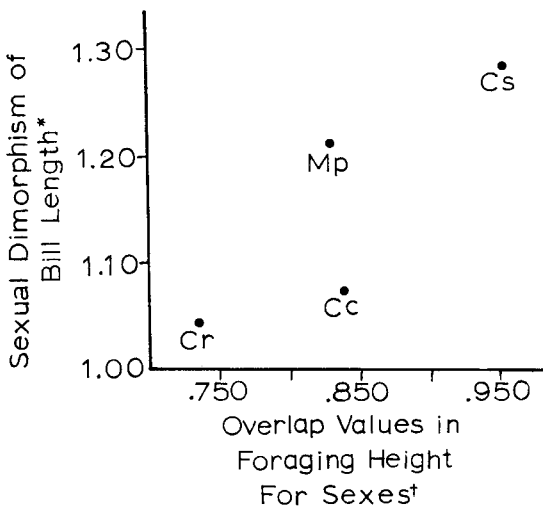


FIGURE 1. A correlation between sexual dimorphism in bill size and sexual overlap in foraging height. Cr, *Centurus radiolatus* of Jamaica; Cc, *C. carolinus* of the eastern U.S.; Mp, *Melanerpes portoricensis* of Puerto Rico; Cs, *C. striatus* of Hispaniola. *Calculated as male/female. †Populational and seasonal data pooled.

INTERSEXUAL VARIATION

Kilham (1965) suggested that in sexually dimorphic (i.e., most) species of woodpeckers the sexes may tend to take different foods, at least seasonally, and so avoid the aggression that is shown toward food competitors, thus facilitating social behavior by permitting the sexes to forage in closer proximity. Although low intersexual aggression could probably best be accounted for in other ways, such behavior might be expected in those species for which mating is an elaborate or lengthy process or for which extended maintenance of pair bonds is adaptive.

The correlations shown in figure 1 indicate a relationship between foraging proximity (in terms of foraging height) and sexual dimorphism in bill size for the species considered here. The strong correlation, especially for the insular species, indicates that sexual dimorphism in bill length may be associated with foraging association of the sexes by permitting a finer division of the niche. Such an interpretation is recommended by the previously discussed tendency of the sexes of the Hispaniolan Woodpecker to interact frequently when foraging, as females follow their mates to new foraging sites, even in the nonbreeding season. There are obvious advantages to both members of a pair being able to forage near the nest in the breeding season as a means of nest protection, energy conservation when carrying food, and coordination of nesting activities. The strong tendency of

pairs to remain in close association throughout the year cannot be accounted for on any adaptive basis at present. A certain degree of association in the nonbreeding season, however, could be expected in woodpeckers as a means of facilitating breeding activities in the spring. The high population density of the colonial-nesting Hispaniolan species might contribute to continual close sexual association by decreasing the likelihood of socially disruptive aggression arising through intra-sexual competition as a result of uncertainties regarding the mating status of individuals.

In the case of the strongly dimorphic Puerto Rican Woodpecker, pairs seem to be rather loosely bonded in the nonbreeding season. However, foraging flocks comprised of both sexes are common at this time. The foraging advantage of forming such groups when exploiting foods of certain distributions as well as the protective role of groups are discussed in Wallace (1973). It may be, then, that strong dimorphism may permit the sexes to maintain close social contact, not only as pairs when nesting but also at times when they are not tending offspring and foraging flocks are formed. Flocking might be facilitated by variation, continuous or polymorphic, in the population. The advantages of forming such groups, then, might contribute to increased sexual dimorphism in trophic appendages.

The ecological situations of the relatively monomorphic Jamaican and Red-bellied Woodpeckers obviously are not identical. However, it may be assumed that there has not been the necessity or the opportunity for the development of events leading toward close foraging association in these species. The Red-bellied Woodpecker would probably be constrained from the level of niche expansion necessary for subdivision by sex, by the presence of competing species. Thus, its relative sexual monomorphism in trophic appendages may be explained on the basis of a "narrow" niche. [For a discussion of possible social advantages of sexual differences in the selection of plants in xeric habitats by *Picoides scalaris* (Ladder-backed Woodpecker), see Short 1971.] The monomorphism of the Jamaican Woodpecker probably has occurred on another adaptive basis. In another paper I will consider the large size of the Jamaican Woodpecker as a means of niche expansion which may arise on islands through intra-specific competition as an alternative to increased sexual dimorphism. It may be, then, that where increased contact of the sexes is necessary, or permitted by the competitive

situation, sexual dimorphism in trophic appendages may be promoted as a means of reducing competition between sexes. Any changes in morphology which can be influenced by social pressures are more likely to occur in insular situations where complexities brought about by interspecific competition are minimized.

INTRASEXUAL VARIATION

A recent criticism (Soulé and Stewart 1970) of the niche width-variation model refers to several island species which do not show increased intrasexual variation over their mainland relatives. It is suggested that the increased intrasexual variation in some island species is nonadaptive, a result of directional selection decreasing canalization and that the variation will decrease as a new adaptive norm is selected for. The real usefulness of the suggestion is probably in accounting for the lack of variation in certain old, established island species rather than as a replacement for the general theory. It may be that increased variation within sexes on islands is adaptive—the result of selection—in one case and an intermediate condition leading to a new adaptive norm in another case.

It is tempting to consider strongly dimorphic sexes in insular environments as “ecological species” in that they may diverge in foraging behavior to the same degree as do sympatric species in more packed systems, and thus might be thought to occupy what would be separate niches in habitats harboring species of similar adaptive types. However, there are stronger strictures on morphological variation between sexes (particularly under insular conditions) than between species, and these may affect both qualitatively and quantitatively the ecological separation of the sexes. Clearly, intrasexual variation of trophic appendages would be expected to be low for any species sympatric with strongly competing species, as a concomitant of competitive influences which limit variation within species. However, variation within sexes might be reduced even further in trophic characters which also function in mate selection. For example, a larger bill in males might function as a sexual signal since some birds are known to be attentive to characters associated with the head in individual recognition as well as sexual recognition (c.f., Short 1971; Wallace 1973). Overlap in bill size for the sexes might then be selected against.

In addition, there may be another social influence operating to restrict intrasexual variation. The curves in figure 2a show the theoretic

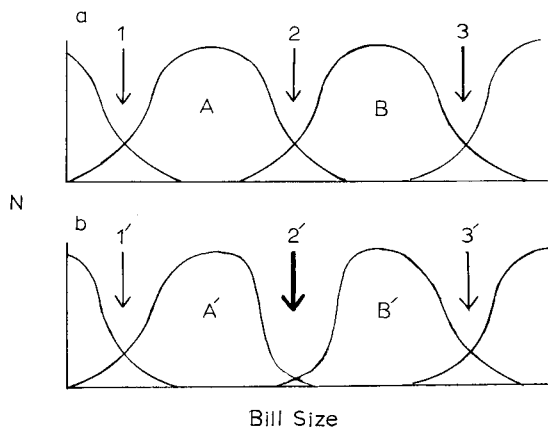


FIGURE 2. A theoretical effect of social behavior on variation. See the text for an explanation.

cal distribution of trophic appendages, such as bill size, which might be expected in sympatric species A and B. The mean and variation for each species would be largely a result of selection for a morphology appropriate to the ecological conditions. Selection against the extremes (1, 2, or 3) for any morph is determined primarily by factors relating to competition at these points. However, in figure 2b, if A' and B' are sexes of a single species, selection against the extremes would be due to foraging success at 1' and 3' but the “ecological” selection against the extremes at 2' might be reinforced by pressures for close association, as described above, and conceivably by sexual selection as well. Differential selection against one tail of each curve at 2' could result in a certain skewness of the curves thus producing a “mirror-image” effect. Such a trend is indicated in the samples considered here in that the medians for bill length fall closer together than the means in insular species but not in continental ones. So, concomitant with the increase in variation via polymorphism within a species there may be a reduction in variation for each sex due to selection operating through social pressure. Considerations of the restrictions on variation, then, must include, as well as ecological factors, social influences in senses other than that of sexual selection.

SUMMARY

The interrelationships of sexual dimorphism, differential niche utilization by the sexes, and social behavior are considered for three insular species of woodpeckers of the West Indies and two related continental species. Sexual differences in bill and tongue size are found for *Centurus striatus* of Hispaniola and *Melanerpes portoricensis* of Puerto Rico. Less

sexual differences in bill and tongue size are found in *Centurus aurifrons* and *C. carolinus* of Texas and *C. radiolatus* of Jamaica. Sexual dimorphism in bill and tongue size is positively correlated with sexual differences in employment of the various foraging modes. In *C. striatus* stronger differences appear in the dry winter season, considered to be a time of low food abundance. Less sexual differences in foraging mode are found in this species in ecologically more complex areas.

Possible social influences on variation in trophic appendages are considered. Evidence is presented which indicates that intersexual variation may be adaptive as a means of permitting specialization through differential foraging in the same part of the habitat in those species in which close association of the sexes is important in pair-maintenance or flocking. Intrasexual variation, on the other hand, may be reduced by (1) interspecific competitive influences; (2) by sexual selection; and (3) by pressures for close association while foraging, as sexual overlap in bill size is selected against, thus permitting finer partitioning of food resources through sexual specialization.

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