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APPENDIX. Prey species delivered to Thick-billed Murre chicks at Coburg Island and Cape Hay.

Prey species	Coburg	Cape Hay
FISH		
Arctic cod, *Boreogadus saida* (Lepechin) 1774	+	+
Arctic staghorn sculpin, *Gymnocanthus tricuspis* (Reinhardt) 1841	+	
Twohorn sculpin, *Icelus bicornis* (Reinhardt) 1841	+	
Arctic sculpin, *Myoxocephalus scorpioides* (Fabricius)	+	
Nybelin's sculpin, *Triglops nybelini* Jensen 1944		+
Sand lance, *Ammodytes* spp.[a]		+
Polar eelpout, *Lycodes truneri* Bean 1978	+	
INVERTEBRATES		
Parathemisto libellula (Lichtenstein)	+	+
Parapasiphae sulcatifrons Smith		+
Gammarus wilkitzi Birula	+	
Harmothoe spp.[a]	+	

[a] All specimens were picked up from murre breeding ledges, except *Ammodytes* spp. and *Harmothoe* spp., which were visual identifications only of prey fed to chicks. All others or very similar species were seen fed to chicks by adults.

The fifth annual meeting of the **Colonial Waterbird Group** will be held **22–25 October 1981.** A symposium on the factors affecting reproductive success in colonial birds is planned. Those interested in contributing to the symposium should submit an abstract by **1 August 1981;** abstracts for contributed papers must be received by **1 September 1981.** For information on either, contact **J. Burger, Department of Biology, Livingston College, Rutgers University, New Brunswick, New Jersey 08903.** For information on registration, contact **Brian Chapman, Department of Biology, Corpus Christi State University, Corpus Christi, Texas 78412.**

A **Conference-Workshop on Southeastern Coastal and Estuarine Birds** will be held at the field laboratory of the Belle W. Baruch Institute for Marine Biology and Coastal Research of the University of South Carolina, near Georgetown, South Carolina, **11–13 September 1981.** Those working on coastal or estuarine species in the southeast are invited to present the results of their research; presentations by graduate students are especially welcome. A limited number of graduate student awards, covering room and registration fees, are available. Contact **Keith L. Bildstein, Program Chairman, Department of Biology, Winthrop College, Rock Hill, South Carolina 29733** for information on the program or student awards; contact **Bobbie Christy, Local Chairman, Baruch Field Laboratory, P.O. Box 1630, Georgetown, South Carolina 29440** for information on registration and housing (this information will be mailed to AOU, COS, and WOS members in the southeast automatically).

NEST-SITE HABITAT SELECTED BY WOODLAND HAWKS IN THE CENTRAL APPALACHIANS

KIMBERLY TITUS AND JAMES A. MOSHER
Appalachian Environmental Laboratory, University of Maryland,
Center for Environmental and Estuarine Studies,
Frostburg State College Campus-Gunter Hall, Frostburg, Maryland 21532 USA

ABSTRACT.—We quantitatively describe the nest-site habitat selected by Broad-winged Hawks (*Buteo platypterus*), Red-shouldered Hawks (*B. lineatus*), Red-tailed Hawks (*B. jamaicensis*), and Cooper's Hawks (*Accipiter cooperii*), emphasizing differences among species and between each species and the surrounding forest habitat. We subjected 53 nest sites and 100 randomly selected sites to an intensive habitat analysis based upon the James and Shugart (1970) techniques. White oak (*Quercus alba*) was the most common nest tree. Distance to water, percentage nest height, distance to the nearest forest opening, basal area, and dbh of the nest tree were important discriminating variables between the hawk species. Compared with the random sample of the available forest area, Broad-winged Hawks nested closer to water and to forest openings. Red-shouldered Hawks consistently nested near water and in large trees in stands of mature forests. Red-tailed Hawks nested higher in trees than did the other species, on or near the top of ridges, and far from water and forest openings. Cooper's Hawks nested proportionally higher in trees than did Broad-winged and Red-shouldered hawks and were associated with mature forest with a well-developed understory and ground cover layer. A discriminant function analysis revealed that each species appears to select rather specific nesting areas, as characterized by the proximity of the site to various physiographic features and the structure of the nest tree. *Received 21 April 1980, accepted 23 September 1980.*

FEW studies of raptors have attempted to describe nest-site habitat use in forested areas quantitatively (Dietzen 1978, Hennessy 1978, Howell et al. 1978, Keran 1978, Bednarz 1979). Most habitat descriptions for raptors have been qualitative, with little comparison of sympatric species. In this study we examined the habitat characteristics associated with the nest sites of four sympatric falconiformes, Broad-winged Hawks (*Buteo platypterus*), Red-shouldered Hawks (*B. lineatus*), Red-tailed Hawks (*B. jamaicensis*), and Cooper's Hawks (*Accipiter cooperii*).

Our objectives were to (1) describe habitat characteristics at the nest sites of each species quantitatively, (2) compare differences in nest sites among the species, and (3) compare nest-site habitat for each species with available nesting habitat.

METHODS

Study areas.—The study areas, located in Garrett and Allegany counties of western Maryland, are characterized by a series of long ridges oriented northeast to southwest. The ridgetops generally have stony shallow soils and steep slopes (Stone and Matthews 1977). The valley floors are relatively narrow and typically contain small streams. Forests cover 74% of Allegany County and 69% of Garrett County, and the state forests that contain the study areas are almost completely forested, being broken only by secondary roads, trails, and small clearings.

The study areas lie within the Appalachian Province (Miller 1967), where two physiographically distinct districts are represented. One of the study areas, Green Ridge State Forest, encompassing about 14,000 ha, lies within the ridge and valley district. Elevation varies from about 200 to 600 m. The general forest cover type is oak [mainly type 52; white oak (*Quercus alba*), red oak (*Q. rubra*), hickory (*Carya* spp.), Society of American Foresters 1954]. The understory is dominated by flowering dogwood (*Cornus florida*) and saplings of the dominant trees. The second study area, Savage River State Forest, encompasses about 21,000 ha and lies on the Appalachian Plateau between 500 and 1,000 m elevation, averaging about 400 m higher than the ridge and valley study site. The vegetation is more typical of a northern hardwood forest. The most common tree species are red oak, sugar maple (*Acer saccharum*), shagbark hickory (*Carya ovata*), pignut hickory (*C. glabra*), black birch (*Betula lenta*), and white pine (*Pinus strobus*). Cool moist areas contain some stands of hemlock (*Tsuga canadensis*) and yellow birch (*Betula lutea*). Shrub species include rhododendron (*Rhododendron maximum*), mountain laurel (*Kalmia latifolia*), and flowering dogwood.

Nesting habitat description.—We conducted a systematic search of the study areas in 1978 and 1979 prior to leaf-out. Old nests were rechecked for signs of activity. These methods were adequate in locating active Red-tailed and Red-shouldered hawk nests, and rechecking after leaf-out revealed active nests of the Cooper's and Broad-winged hawks. Some nests were found while traveling to and from the study areas, and interested individuals reported other nest locations. All sites were plotted on USGS 7.5-min topographic maps and on County Soil Conservation Service maps that had been updated for recent land-use changes. The method by which a nest was found was recorded to see if any habitat variables were biased by certain methods of finding nests. For the purposes of this study, a nest site was defined as the nest tree and a 0.04-ha circular plot (11.3-m radius) centered on the nest tree.

At the end of the nesting season the vegetation at 24 Broad-winged Hawk, 10 Red-shouldered Hawk, 13 Red-tailed Hawk, and 6 Cooper's Hawk nest sites was sampled by a modification of the James and Shugart (1970) technique. Within the nest site, all woody plants over 1.75 m tall were tallied according to species, diameter at breast height (dbh), and whether their predominant foliage was part of the overstory or understory. Separate size categories were later created for understory plants and overstory trees.

Table 1 lists the 29 quantitative habitat variables that were either measured directly or created by aggregation. Height measurements were made using a Haga altimeter. Most nest heights were measured directly with a tape. A comparison of tape-measured nest heights with Haga altimeter estimates of the same nest revealed that the altimeter was accurate to within about 1 m ($\bar{x}$ = 0.7 ± 0.6m, n = 17).

If the plot fell at the edge of a field or other forest opening, no corrections were made, this opening being considered as part of the plot. As an example, the percentage canopy cover in that direction would be low, thereby lowering the total percentage canopy cover.

Directional exposure or aspect was quantified by the method of Mosher and White (1976). Plots with less than 5% slope were considered to be exposed in all directions. In the case of plots in a small riparian hollow or gorge with steep banks, the exposed area was considered to be bidirectional (i.e. both up and downstream).

Random sampling of forested areas was conducted throughout the two-county area. The purpose of the random sampling was to estimate available nesting habitat. The random sampling was stratified on USGS quadrangles with approximately two random plots sampled for each nest occurring in the quadrangle for a total of 100. A random numbers table was used to select two sets of three-digit numbers corresponding to vertical and horizontal scales. The random point was then plotted with the aid of a grid overlaid on the quadrangle. Once the approximate site was located in the woods, a stick was tossed, and the tree nearest to this stick was made the center point of the random sample. A tree was used as the center of the random sample plot in order to remain consistent with a nest-site sample plot. Except for the nest-tree-specific variables, the sampling was the same as that at a nest site.

The criterion for accepting a random plot was that the plot be within a forested area with a canopy height greater than or equal to 10 m. This excluded some habitat in which woodland hawks do not nest, such as fields or roads, but included some forested areas where nesting is unlikely, such as pole-stage thickets, timber-stand-improvement areas, and pine plantations. This scheme generally allowed the sampling of the total forest area without preselecting "representative" or "typical" areas (Green 1979).

The adequacy of the sample size of the random samples was checked by plotting the variance versus sample size for the habitat variables. The variances stabilized after 50–60 samples. Also, minimum sample sizes were calculated for each of the habitat variables using the criteria of remaining within 20% of the mean for 80% of the samples. These criteria were met by 19 of 25 variables with sample sizes less than 100.

Statistical methods.—Parametric statistics were used throughout the analysis. Results and explanations concerning data screening procedures and nonparametric results are reported in Titus (1980). Univariate ANOVA's were conducted on the five groups (four raptor species and the random samples) for each of 29 independent variables. A Cochran's Q-test (Sokal and Rholf 1969) was applied to the quantified directional exposure data.

Stepwise discriminant function analysis (Cooley and Lohnes 1971) was used to describe differences in habitat structure between the four raptor species and the random samples. Twenty-nine habitat variables were available for inclusion into the discriminant analysis. Many of these were highly correlated, indicating that they measure similar features of the habitat. Many features of the environment show varying

TABLE 1. Description of quantitative habitat variables used in analysis of raptor nest-site habitat (1 = recorded with a Haga type altimeter; 2 = based on a total of 40 ocular tube readings, 10 along each of the four transects used in SHRUBDEN). An overstory tree was a stem whose major foliage component was contained in the forest canopy layer; understory was defined as a stem whose major foliage component was below the canopy, regardless of size or height.

Mnemonic	Description
1. PERSLOP	Percentage slope of plot (1)
2. CANHT	Average canopy height of the plot in meters; the mean of five measurements taken to the top of the canopy (1)
3. ALTITUDE	Altitude of plot in meters; taken from USGS 7.5-min quadrangles
4. WATER	Distance to water in meters; when less than about 100 m, measured directly in the field; otherwise measured from 7.5-min quadrangles and/or county Soil Conservation Service maps
5. DISFOROP	Distance to the nearest forest opening in meters; measured to the nearest break in the forest continuity, such as created by a trail, road, field, etc.
6. SOIL	Soil-woods suitability; woodland classes placed into units according to their suitability for productivity of trees; class 1 indicates high productivity, and class 6 indicates low productivity; standardized by the Soil Conservation Service, USDA (Stone and Matthews 1977)
7. SITINDX	Site Index; based on SOIL and the tree species present in the plot (Stone and Matthews 1977)
8. CANEVER	Percentage evergreen canopy cover (2)
9. CANTOT	Percentage total canopy cover (2)
10. UNDEVER	Percentage evergreen understory cover (2)
11. UNDTOT	Percentage total understory cover (2)
12. GRNDEVER	Percentage evergreen ground cover (2)
13. GRNDTOT	Percentage total ground cover (2)
14. SHRUBDEN	Shrub density (James and Shugart 1970)
15. SHRUBIND	Shrub index; measured along the same transects as SHRUBDEN, except all woody stems 1–6 cm diameter and 0.25–1.75 m in height are measured; includes SHRUBDEN plus shrubs that do not intersect outstretched arms (James 1978)
16. NOSPTREE	Number of species of overstory trees in the plot
17. NOSPSHRB	Number of species of shrubs and saplings in the plot
18. NOTREES	Number of overstory trees in the plot
19. UND14	Number of understory stems 1–4 cm diameter in the plot
20. UND58	Number of understory stems 5–8 cm diameter in the plot
21. UNDGT9	Number of understory stems >9 cm diameter in the plot
22. DBHLT25	Number of overstory trees < 25 cm dbh in the plot
23. DBH2650	Number of overstory trees 26–50 cm dbh in the plot
24. DBHGT50	Number of overstory trees > 50 cm dbh in the plot
25. BASAL	Basal area in m^2/ha for overstory trees
26. DBH	Diameter breast height of the nest tree
27. NESTHT	Height of the nest in meters (1)
28. PNSTHT	Percentage nest height; calculated as: (NESTHT/HTNSTTRE) (100) = PNSTHT
29. HTNSTTRE	Height of nest tree in meters (1)

degrees of correlation, and discriminant analysis assumes independence of variables (Green 1979). To avoid potential problems in the analysis, only one of a pair of highly correlated variables ($r > 0.7$) was included in the analysis (cf. Noon in press). The variable chosen was that which was most readily interpretable in an ecological sense.

Further reduction of the number of independent variables was necessary to avoid "overfitting" small

TABLE 2. Sample means, standard deviations, and ranges of habitat variables for four hawk species' nest sites and random samples. Only variables that were used in analyses are listed.

Variable	Broad-winged Hawk (24)	Red-shouldered Hawk (10)	Red-tailed Hawk (13)	Cooper's Hawk (6)	Random samples (100)
PERSLOP	22.4 ± 10.1 (9–47)	12.1 ± 12.8 (0–44)	41.6 ± 20.5 (5–86)	16.8 ± 6.3 (8–25)	22.1 ± 15.1 (3–80)
WATER	86 ± 60 (9–211)	26 ± 24 (7–72)	288 ± 188 (28–520)	193 ± 150 (17–407)	335 ± 248 (35–1,050)
DISFOROP	63 ± 61 (3–292)	180 ± 141 (6–480)	233 ± 200 (20–550)	129 ± 124 (16–350)	229 ± 194 (8–1,110)
SITINDX	72.5 ± 8.3 (50–85)	76.0 ± 10.5 (50–85)	67.5 ± 10.1 (50–80)	74.2 ± 6.6 (65–80)	63.5 ± 11.8 (40–90)
CANTOT	75 ± 11 (40–88)	74 ± 8 (58–83)	71 ± 12 (43–85)	76 ± 13 (53–85)	76 ± 8 (43–90)
UNDTOT	59 ± 12 (30–88)	69 ± 15 (40–90)	59 ± 15 (33–80)	57 ± 7 (48–65)	54 ± 14 (18–80)
GRNDTOT	44 ± 17 (13–73)	50 ± 23 (13–78)	46 ± 20 (18–98)	58 ± 14 (43–78)	41 ± 18 (10–85)
SHRUBDEN	31.8 ± 19.2 (6–74)	42.4 ± 45.6 (3–157)	37.8 ± 20.6 (6–84)	25.2 ± 16.4 (11–54)	23.2 ± 11.0 (3–64)
UNDGT9	6.6 ± 3.5 (0–13)	11.3 ± 10.6 (3–40)	5.7 ± 3.4 (0–13)	9.2 ± 4.9 (3–15)	5.6 ± 3.4 (0–14)
DBHLT25	6.4 ± 5.4 (0–21)	3.6 ± 3.6 (0–13)	5.7 ± 5.1 (0–16)	6.3 ± 6.8 (0–19)	14.6 ± 11.8 (0–50)
DBH2650	5.9 ± 2.9 (2–15)	5.1 ± 2.1 (3–9)	3.4 ± 2.0 (0–7)	5.5 ± 3.3 (2–9)	4.8 ± 2.8 (0–12)
DBHGT50	0.3 ± 0.7 (0–3)	1.0 ± 0.8 (0–2)	1.0 ± 0.9 (0–3)	1.0 ± 1.5 (0–3)	0.2 ± 0.6 (0–3)
BASAL	19.0 ± 5.7 (9.4–36.8)	26.8 ± 4.6 (15.7–31.8)	20.3 ± 5.1 (13.2–30.5)	24.3 ± 5.0 (16.4–32.0)	20.3 ± 5.6 (3.9–34.3)
DBH	38.0 ± 9.5 (25.0–62.0)	61.5 ± 20.5 (41.0–104.0)	51.8 ± 17.3 (31.0–94.0)	44.5 ± 13.6 (31.0–68.0)	
PNSTHT	59.3 ± 8.2 (41.9–73.4)	53.2 ± 10.1 (36.2–67.7)	78.5 ± 5.4 (70.4–87.5)	67.5 ± 7.7 (53.5–73.4)	
NESTHT	13.7 ± 3.0 (9.5–20.6)	13.4 ± 3.0 (8.5–20.3)	17.6 ± 3.2 (12.9–23.3)	15.4 ± 4.1 (9.2–21.3)	

sample sizes and to achieve the least complex model that would adequately discriminate between the groups (see Green 1979). Reduction of variables beyond those eliminated by high correlation was achieved through five sets of ANOVA's on the data set, including variables in the discriminant analysis that were significant at $\alpha = 0.1$.

All statistical procedures were conducted on the Statistical Package for the Social Sciences (SPSS) (Nie et al. 1975, Nie and Hull 1977). For the discriminant analyses, all default criteria were used; the stepwise selection criterion used was Rao's *V* (Klecka 1975). Cohen's kappa statistic (K_w) was calculated from the results of the classification tables based on the discriminant analysis (Cohen 1960, Wiedemann and Fenster 1978). This statistic allows one to assess how well the discriminant analysis improves prediction above chance.

Unless otherwise noted, all tests were considered significant with $\alpha = 0.05$.

RESULTS

DESCRIPTION OF NESTING HABITAT

Sample means for the quantitative habitat variables used in the discriminant analyses are listed in Table 2. No nests were found in areas with canopy heights below 15 m. Canopy height was negatively correlated with the total number of

TABLE 3. Results of one-way ANOVA's (F values) testing for significant differences of habitat variables according to five groupings (*$P \leq 0.05$; **$P \leq 0.01$; ***$P \leq 0.001$; # = variables unique to nest site). Only significant variables included.

Variable	Four hawk species	Broad-wing vs. random	Red-shoulder vs. random	Red-tail vs. random	Cooper's vs. random
PERSLOP	10.48***	0.01	4.10*	17.36***	0.73
CANHT	1.19	4.97*	2.37	0.01	1.95
WATER	13.12***	23.89***	15.48***	0.44	1.94
DISFOROP	5.38**	17.03***	0.60	0.01	1.55
SOIL	1.24	9.35**	9.71**	1.17	3.86
SITINDX	1.72	12.36***	10.32**	1.25	4.75*
UNDTOT	1.56	3.66	11.18**	2.03	0.33
GRNDTOT	0.91	0.44	1.72	0.76	4.81*
SHRUBDEN	0.71	8.52**	11.74***	15.97***	0.17
SHRUBIND	0.58	3.86	8.74**	8.67**	0.81
NOSPTREE	0.08	2.80	1.06	0.64	0.44
NOTREES	1.20	10.59**	9.19**	11.06**	2.77
UNDGT9	2.35	1.25	13.91***	0.00	5.31*
DBHLT25	0.72	10.96**	8.56**	7.20**	2.88
DBH2650	2.65	2.77	0.11	3.04	0.34
DBHGT50	3.13*	0.02	15.44**	18.15***	7.99**
BASAL	5.90**	1.05	12.32***	0.00	2.84
DBH#	6.92***				
NESTHT#	5.14***				
PNSTHT#	23.61***				

overstory trees and the number of overstory trees less than 25 cm dbh and positively correlated with basal area. These four variables were all related to forest-stand structure. No nests were found in stands with an overstory tree density greater than 650 trees/ha, and most sites occurred in stands that were much less dense ($\bar{x} = 278$ trees/ha). Areas with a high number of trees and a low canopy height were younger forests, as represented by many of the random samples.

Broad-winged, Red-shouldered, and Cooper's hawks were all found nesting in areas with a higher Site Index than the mean for the random samples (Table 3). Red-tailed Hawk nest sites were on steeper slopes than those of any of the four other groups. All Red-shouldered and Broad-winged hawk nest sites were near water (72 m and 211 m, respectively). Distance to the nearest forest opening was significant only for the Broad-winged Hawk (Table 3), the nest sites of which were closer to forest openings than those of any of the other species or than the random samples. Results of the Cochran's Q-test for directional exposure revealed that Red-tailed Hawk nest locations most frequently occurred on east-facing slopes ($P < 0.05$), while the sites of the three other hawk species and the random samples were randomly oriented.

We recorded 36 species of overstory trees on the study areas, but only 15 tree species were used as nest trees (Table 4). White oak was used as a nest tree in 20 of 53 instances. Four Red-tailed Hawk nests were in pines (*Pinus* spp.) that were isolated within a deciduous stand.

Table 2 lists the means for three of the four variables specific to the nest tree, and Table 3 provides the results of the ANOVA's on these variables. Based on Duncan's multiple range test (DMRT), the Red-tailed Hawk nested higher off the ground than the other three species ($P < 0.05$). The mean percentage nest heights were all significantly different between these species (DMRT), with the Red-shouldered Hawk nesting relatively low and the Broad-winged, Cooper's, and Red-tailed hawks nesting successively higher.

TABLE 4. Nest tree species used by raptors in the central Appalachians (BWH = Broad-winged Hawk; CH = Cooper's Hawk; RSH = Red-shouldered Hawk; RTH = Red-tailed Hawk).

Species	BWH (24)	CH (6)	RSH (10)	RTH (13)	TOTAL (53)
White oak (*Quercus alba*)	12	1	6	1	20
Red oak (*Q. rubra*)	4	1	2	2	9
Scarlet oak (*Q. coccinea*)	2	2		1	5
Chestnut oak (*Q. prinus*)	1			1	2
Sugar maple (*Acer saccharum*)	2			1	3
Red maple (*A. rubrum*)		1			1
Black locust (*Robinia pseudo-acacia*)	1			1	2
Black cherry (*Prunus serotina*)	1				1
Pignut hickory (*Carya glabra*)				2	2
Black birch (*Betula lenta*)	1				1
Short-leaf pine (*Pinus echinata*)				3	3
Pitch pine (*P. rigida*)				1	1
Tulip (*Liriodendron tulipifera*)			1		1
American beech (*Fagus grandifolia*)			1		1
Hackberry (*Celtis occidentalis*)		1			1

DISCRIMINANT FUNCTION ANALYSIS

We conducted a stepwise discriminant function analysis on the four species' nest sites (Table 5). Based on Tatsuoka's ω^2 multi, 91% of the total variability contained in the three discriminant functions was the result of group differences; this percentage may be used ". . .as a measure of the total discriminatory power residing in the discriminant function or, equivalently, in the predictory battery as a whole" (Tatsuoka 1970). The first discriminant function shows heavy weighting on distance to water and percentage nest height. Distance to the nearest forest opening shows moderate weighting. Discriminant function II has heavy weighting on basal area, dbh of the nest tree, and distance to the nearest forest opening. Along discriminant function I, Broad-winged and Red-shouldered hawks show nearly complete overlap (Fig. 1). The Red-tailed Hawk shows little or no overlap with the other three species. The only separation along discriminant function II is between the Broad-winged and Red-shouldered hawks (Fig. 1). Overall, Cooper's Hawk nest sites are intermediate between the other species.

TABLE 5. Summary of stepwise discriminant function analysis on four hawk species' nest sites.

	Discriminant function		
	I	II	III
Eigenvalue	4.983	0.726	0.165
Percentage of eigenvalue associated with the function	84.8	12.4	2.9
Canonical correlation	0.913	0.649	0.376
Chi-square statistic	115.7	32.5	7.1
Significance (degrees of freedom)	$P < 0.001$ (21)	$P < 0.001$ (12)	$P > 0.05$ (5)
Standardized discriminant function coefficients			
PERSLOP	0.1387	0.2368	
WATER	0.5173	−0.0829	
DISFOROP	0.3146	−0.3541	
DBH2650	−0.1592	0.2079	
BASAL	0.0201	−0.5185	
DBH	0.0197	−0.3714	
PNSTHT	0.4297	0.1756	

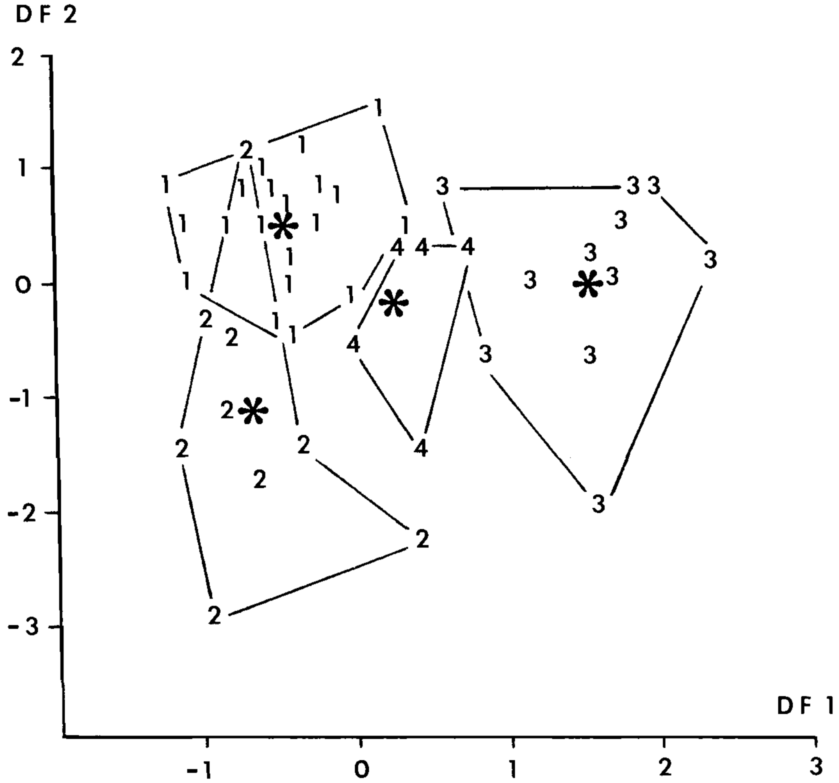

Fig. 1. Two-dimensional plots of discriminant scores indicating the nest-site habitat distributions among four species of hawks (1 = Broad-winged Hawk; 2 = Red-shouldered Hawk; 3 = Red-tailed Hawk; 4 = Cooper's Hawk; * = centroid for each species; the total number of cases for each species may not add up to the total sample size for that species, because one point may represent more than one case).

To measure the power of the discriminating variables in achieving group separation, the number of correct classifications of the individual cases was determined. The overall correct classification of species was high (87%), as was kappa, which showed a correct classification 81% above chance classification based on group sizes. Twenty-one of 24, 8 of 10, 11 of 13, and 6 of 6 nest sites were correctly classified for the Broad-winged, Red-shouldered, Red-tailed, and Cooper's hawks, respectively. No nest sites were misclassified as Red-tailed Hawk nest sites.

Broad-winged Hawk compared to random samples.—With only two groups, one discriminant function exists, and it must account for all of the discriminating power (Table 6). The associated chi-square statistic indicates that this function is highly significant. The standardized discriminant function coefficients indicate the relative power of the variables to discriminate Broad-winged Hawk nest sites from the available forested habitat. The two variables with the highest weighting indicate that Broad-winged Hawks place nests closer to water and closer to some forest opening than would be expected. Eighteen of 100 random samples were misclassified as Broad-winged Hawk nest sites. This was the largest percentage misclassification of random points for any of the hawk species (K_w = 61%), which suggests that the total available habitat has many suitable nesting areas for this species.

Red-shouldered Hawk compared to random samples.—The eigenvalue, canonical correlation, and associated chi-square statistic were higher in this analysis than for any of the other three listed in Table 6. More variables (eight) contributed to this function than to any of the others, with shrub density and distance to water showing the highest weighting. The higher basal area, more large overstory trees, and a well-developed mature understory stratum reflect the old-growth timber used by Red-shouldered Hawks as nest sites in this study. Red-shouldered Hawks had a much lower misclassification (4 of 100) and a higher kappa (K_w = 76%) than any of the other species. Based on this discriminant analysis, one might conclude that suitable nesting areas for the Red-shouldered Hawk are relatively uncommon on the study areas.

Red-tailed Hawk compared to random samples.—The sites upon which nests of Red-tailed Hawks were found had a higher percentage slope, a higher number of large trees, a higher shrub density, and a lower percentage canopy cover than did the random sites (Table 4). A moderate amount of overlap occurred with the random habitat samples, and 12 of 100 random samples were misclassified as Red-tailed Hawk nest sites (K_w = 39%).

Cooper's Hawk compared to random samples.—In comparison with random habitat samples, the nest sites of Cooper's Hawks were found in areas of larger overstory trees, a more mature understory stratum, a dense ground-cover layer, and a higher site index. Both the eigenvalue and the canonical correlation were low, indicative of relatively weak discriminating power. Seventeen of 100 random samples were misclassified as Cooper's Hawk nest sites, and kappa was low (K_w = 24%). The small sample size and the large range of discriminant scores for this species made an assessment of habitat patterns difficult.

Discussion

The four hawk species appear to select different nest-site habitats in the central Appalachians. No other studies have compared the nest sites of all these species in sympatry, although some studies have assessed one or two of these species. Bednarz (1979) quantitatively compared the nest sites of Red-shouldered and Red-tailed hawks in Iowa. Although his study was in an area of intensive agriculture, many of his results concerning nest sites were similar to those found in this study. Common separating variables included percentage nest height, dbh of the nest tree, percentage slope, and distance to water. The variables associated with Red-tailed Hawk nest sites in both this study and that of Bednarz indicated the possible importance of accessibility to the nest site. These results support the idea offered by Orians and Kuhlman (1956) that some unobstructed access to the nest is common for Red-tailed Hawks. Mader (1978) reported similar results for Red-tailed Hawks in Arizona. The 78.5% nest height for Red-tailed Hawks in this study was very similar to the 81% value found in Minnesota by Bohm (1978) and the 77% value reported by Bednarz (1979). By placing their nests high in trees and on steep slopes, the Red-tailed Hawk insures that the downslope side of the nest is usually free of obstructions.

The Red-tailed Hawk nest sites in this study were all located in relatively continuous forest and were no closer to forest openings than would be expected from the random samples. In this respect, our sample differs from most previous Red-tailed Hawk studies, which have been conducted in largely agricultural areas (Orians and Kuhlman 1956, Gates 1972, Cornman 1973, Misztal 1974, Howell et al. 1978, Bednarz 1979).

TABLE 6. Summary of four stepwise discriminant random habitat samples compared with each hawk species' nest sites.

	Broad-wing vs. random		Red-shoulder vs. random		Red-tail vs. random		Cooper's vs. random	
Eigenvalue	0.653		0.926		0.553		0.178	
Canonical correlation	0.629		0.693		0.589		0.389	
Chi-square statistic	59.8		68.1		46.5		16.7	
Significance (degrees of freedom)	$P < 0.001$ (6)		$P < 0.001$ (8)		$P < 0.001$ (4)		$P < 0.01$ (4)	
Standardized discriminant function coefficients								
	WATER	0.5571	PERSLOP	0.1552	PERSLOP	0.5358	SITINDX	−0.3075
	DISFOROP	0.3983	WATER	0.4008	SHRUBDEN	0.4907	GRNDTOT	−0.4444
	SITINDX	−0.3271	SITINDX	−0.1605	CANTOT	−0.1460	UNDGT9	−0.4503
	UNDTOT	−0.2858	UNDTOT	−0.1810	DBHGT50	0.5183	DBHGT50	−0.4946
	SHRUBDEN	−0.2748	SHRUBDEN	−0.4689				
	DBHLT25	0.1584	UNDGT9	−0.3299				
			DBHGT50	−0.2143				
			BASAL	−0.2652				

Comparing Red-shouldered and Red-tailed hawk nest sites, Bednarz (1979) was able to classify all nest sites correctly, using discriminant analysis. The same relationship held in this study, as neither species was misclassified as the other and variables such as percentage nest height and proximity to water separated these two species. Red-shouldered Hawks usually nested much farther below the top of the canopy than did the Red-tailed Hawk, as indicated by the 53.2% nest-height value calculated in this study and 66.8% and 50.2% calculated from the values given by Bednarz (1979) and Portnoy and Dodge (1979). The association of Red-shouldered Hawks with mature, moist areas was first described by Bent (1937) and Stewart (1949).

The Broad-winged Hawk is probably the most common nesting hawk in forested areas of the central Appalachians. This species appears to select sites in association with wet areas. While Burns (1911), Matray (1974), and Keran (1978) also noted the apparent association of nest sites with wet areas, they did not assess the proximity of these wet areas to random points in the forest. Burns (1911) and Keran (1978) also described the association of nest sites with some type of forest opening, and we found this relationship to be significantly different from the proximity of random samples to openings.

Nest sites have been shown to be limiting for some falcons and large eagles (see reviews by Newton 1976, 1979). Although no studies have suggested this for forest hawks, most trees are probably not suitable for nest placement, and nest trees may be a limiting factor in some otherwise suitable habitats. This is suggested in this study by the very low percentage of random sites misclassified as Red-shouldered Hawk nest sites.

The temporal aspect of habitat selection compared to the time of habitat assessment has been discussed by Whitmore (1979). He presented limited data to demonstrate changes in habitat-use overlap for pairs of grassland species based on time of habitat sampling. These changes are directly related to the specific variable(s) measured and may be more important in grassland situations, where seasonal changes in structure are proportionately greater than in forested habitats. The habitat variables measured in this study may be proximate and/or ultimate factors of habitat selection (Svärdson 1949, Hildén 1965). For example, Red-tailed Hawks were nesting more than 1 month prior to leaf-out (Janik 1980), while canopy cover at the nest site was assessed during mid-summer. In this sense canopy cover might be an ultimate factor in that it may provide shelter and protection for the young from adverse weather or from predation, while branch density or other structural features may provide the proximate cue.

As a final cautionary note, the method used to locate hawk nest sites may result in a biased sample of the population. This potential bias has been largely overlooked in other studies and may, for example, lead to the conclusion that some species are associated with forest edge simply because this is the easiest place to find nests. In this study, the 13 nests found in association with driving were significantly closer to forest openings (mainly roads or fields) than 10 nests found by systematic searching on foot ($t = 3.99$, $P < 0.001$). Systematic searching is less efficient (in terms of finding nests) than looking in "typical" nesting areas. To avoid bias and gain a better understanding of raptor-habitat relationships, however, a systematic approach to nest searching is necessary.

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The **Meandarra Ornithological Field Study Unit** (MOFSU) was formally established as a research group of the University of Queensland, Australia, in December 1980. MOFSU is active in field research in the area of Meandarra, 300 km west of Brisbane. Major emphasis is on the behavior and ecology of communally breeding species. MOFSU welcomes visitors and volunteer field assistants in its program. MOFSU is not in a position to provide financial support for students pursuing degrees, but may accept them for work on field projects. For further information contact **Dr. Douglas D. Dow, Director, MOFSU, Department of Zoology, University of Queensland, Brisbane, Australia 4067.**

THE TAXONOMY OF ROUGH-WINGED SWALLOWS (*STELGIDOPTERYX*; HIRUNDINIDAE) IN SOUTHERN CENTRAL AMERICA

F. GARY STILES

Escuela de Biologiá, Universidad de Costa Rica, Ciudad Universitaria, Costa Rica

ABSTRACT.—Based on morphological and distributional information, it appears that two species of *Stelgidopteryx* swallows breed in Costa Rica: the northern and highland *serripennis* (represented by the race *fulvipennis,* if one recognizes subspecies at all), and the southern and lowland *ruficollis* (represented by *uropygialis* on the Caribbean versant and *decolor* on the Pacific). In general, the forms of *ruficollis* have larger bills, shorter wings, brighter throats, and paler rumps than do those of *serripennis.* Overlap without demonstrable hybridization occurs between *uropygialis* and *fulvipennis* locally along the northern and eastern foothills of the central highlands of Costa Rica. Previous accounts of hybrids, intergrades, etc. have failed to take into account the amount of individual variation and migratory behavior of all forms. Appropriate English vernaculars for the species *serripennis* and *ruficollis* would be Northern and Southern Rough-winged Swallow, respectively. *Received 10 June 1980, accepted 24 September 1980.*

THE Rough-winged Swallows of the genus *Stelgidopteryx* are fairly small (ca. 15 g), brownish swallows, adult males of which possess short, stiffened barbs with sharp recurved tips on the outer web of the outermost primary; these produce the "rough" or "saw-toothed" feel to the leading edge of the wing that gives the birds their English and Latin names. Virtually all recent systematic discussions (e.g. A.O.U. 1957, Mayr and Short 1970) consider the genus monotypic, the single species *S. ruficollis* being divided into numerous races distributed from southern Canada to Argentina. In the past, however, two to four species were often recognized (e.g. Ridgway 1904). The presence of two of these forms in Costa Rica, apparently breeding sympatrically (Skutch 1960 and pers. comm.) prompted me to reexamine the relationships of these birds. In the process, I have examined virtually all specimens of *Stelgidopteryx* from southern Middle America in major museums and investigated breeding distributions in the field. The major conclusion to emerge is that there do appear to be two species of Rough-winged Swallows breeding in Costa Rica, with only slight geographical overlap and no conclusive evidence of hybridization.

HISTORICAL REVIEW

Most of the forms of *Stelgidopteryx* discussed here were described within a short period: the North American breeding race *serripennis* from South Carolina by Audubon in 1838, the southern Mexico-northern Middle American *fulvipennis* from Jalapa, Veracruz by Sclater in 1859, and the southern Middle American-northern South American *uropygialis* from central Panamá by Lawrence in 1863 (original citations in Ridgway 1904). The fact that the original description of *fulvipennis* was based on a juvenal bird led to confusion: in 1904 Ridgway (1904) named what turned out to be the adult of this form as a new species, *salvini* (type locality Dueñas, in the central Guatemalan highlands), and in the process synonymized *fulvipennis* with *serripennis.* Ridgway considered "*salvini*" closest to *serripennis* (but distinct) and considered *uropygialis* to be a representative of the South American *S. ruficollis* complex. He distinguished "*salvini*" from *serripennis* on the basis of its darker crown, brighter throat (these characters showing some approach to the condition in *uropygialis*), and white-tipped tertials (but had only four adult male specimens of *"salvini"* available), but noted that juvenals of the two forms were similar. *Uropygialis* was distinguished from both of the preceding by having a still blacker crown and brighter throat, a pale rump, yellowish belly, and boldly black-tipped under tail coverts; the juvenal plumage differed from that of *serripennis* and *"salvini"* but resembled that of *ruficollis* in most respects.

Bangs (1906) noted variability in several of the characters cited by Ridgway, particularly in a series of *Stelgidopteryx* taken by Underwood in southwestern Costa Rica. He questioned the distinctness of several forms and recommended that *"salvini"* be considered a subspecies of *serripennis* (a suggestion subsequently followed by virtually all authors).

The prevailing modern treatment of *Stelgidopteryx* took shape in a review by Griscom (1929). He too found that not all *uropygialis* had strongly black-tipped under tail coverts, whereas some *serripennis* and *fulvipennis* had dark crissal markings, and that very fresh-plumaged *serripennis* had buff-tinged throats. He noted that birds from southwestern Costa Rica and adjacent Chiriquí Province, western Panamá, were extremely variable but averaged paler than adjacent forms, and he described them as a new race, *decolor*. He also named a paler race of *serripennis* from southwestern U.S.A.-northwestern Mexico as *psammochrous*. In surveying the genus as a whole, he noted a general trend from darker, more brightly patterned birds in South America to progressively paler, more uniformly colored birds in North America. Hypothesizing that the eastern South American *ruficollis* was the ancestral form, he interpreted this pattern as a "progressive northwards dilution of ancestral characters" and recommended lumping all forms into *S. ruficollis*.

Subsequent treatments of these forms have essentially followed Griscom's arrangement, adding distributional information as more specimens were collected (e.g. Brodkorb 1942, Miller 1957, A.O.U. 1957, Monroe 1968, Mayr and Short 1970, Wetmore MS). Hellmayr and Cory (1935) went a step further and sank *decolor,* in essence considering it a hybrid swarm between *fulvipennis* and *uropygialis*; its status has remained in doubt ever since (e.g. Slud 1964, Wetmore MS). In a discussion of the validity of *psammochrous,* Phillips et al. (1964) called attention to the great amount of variability in specimens of *Stelgidopteryx* due to plumage wear, *post mortem* foxing, and individual variation, a caution that I find applicable to *all* forms of *Stelgidopteryx*. In any case, no authors seriously questioned Griscom's basic premise, that there was but a single species of *Stelgidopteryx*. Skutch (1960 and pers. comm.) however, observed sympatric breeding of dark-rumped and light-rumped birds (= *fulvipennis* and *uropygialis*) in the Pejevalle Valley, Costa Rica, without apparent interbreeding; he found burrows of the two forms only a few meters apart. Slud (1964) noted that specimens of *fulvipennis* and *uropygialis* in breeding condition had been taken in the same areas, but, beyond adding some distributional information, he did not attempt a critical evaluation of the status of these forms and did not rigorously define breeding distributions. Therefore, the time seems ripe for a careful reexamination of the available specimens, and precise documentation of breeding distributions, in order better to evaluate the status of the various forms of Rough-winged Swallows in Costa Rica.

METHODS

The bulk of the data presented here derives from an examination of 296 museum specimens of *Stelgidopteryx,* many of them recently taken and thus not available to earlier revisers of the genus. It proved surprisingly difficult to obtain adequate sample sizes for some forms, especially *fulvipennis, decolor,* and *serripennis* on their winter range: evidently collectors in the tropics prefer to collect more easily shot and "tropical" species than Rough-winged Swallows! For each specimen, measurements were taken with dial calipers of exposed culmen length (corrected insofar as possible for feather distortion) and wing chord; notes were taken on plumage coloration, wear, and molt; and gonad data were noted when available. For purposes of analysis I grouped specimens of the southern races into putatively "sympatric" and "allopatric" populations (i.e. separated specimens taken within and outside the known ranges of other forms) and also measured a sample of breeding *serripennis* from different parts of North America to compare with migrants of this form from southern Middle America. In all I examined 41 specimens of *decolor,* 89 of *uropygialis,* 55 of *fulvipennis,* and 111 of *serripennis.* In addition, on 11–12 April 1980 I mist-netted 17 *serripennis* during their northward migration at Chomes, Provincia de Puntarenas, Costa Rica and measured them as described above. Twelve of these birds were banded and released; five were collected and subsequently remeasured as specimens. Mean measurements of these netted birds were in close agreement with those of the sample of *serripennis* specimens from Costa Rica, and measurements of the five latter birds in the field and as specimens differed by no more than 0.2 mm (bill) or 1 mm (wing). Hence, I have included these mist-netted birds in the sample of *serripennis,* raising to over 300 the total number of birds included in the study.

Breeding distributions of the forms were examined in the course of my travels in Costa Rica between 1977 and 1980 and from specimen data; wherever possible the composition of breeding colonies was determined by observation or collecting. I have been unable to make long-term observations on particular pairs or colonies; hence, the present paper will deal mainly with specimen and broad distributional data.

PLUMAGE COLORATION

There appears to be considerable variability in plumage coloration in *all* populations of *Stelgidopteryx* (Table 1). Much of this is evidently due to age and plumage wear, but even subtracting these, a good deal of individual variation remains. Thus, there are practically no plumage characters that can in themselves distinguish all forms consistently (at least in museum specimens). It is virtually always possible, however, to distinguish *serripennis* or *fulvipennis* from *uropygialis* or *decolor* by color characters alone; within each of these pairs, some specimens are very difficult to assign to race without distributional data.

The most distinct form, in terms of coloration, is *uropygialis,* but a fair proportion of this race consists of rather pale-colored individuals virtually indistinguishable from many *decolor.* This has been taken as evidence for hybridization with *fulvipennis* by some, but because such pale birds have been taken during the putative breeding season (see below) in eastern Panamá, far from the range of *fulvipennis,* I think it more reasonable to consider this as simply individual variation. It could also be argued that this reflects widespread introgression of *fulvipennis* genes, but were this the case one should find a high frequency of hybridization and intermediate individuals in the zone of contact; in my experience, such is not the case (see below).

Considerable color variation occurs in *decolor,* especially in the rump, throat, and crissum: the more strongly-marked individuals are scarcely distinguishable from many *uropygialis.* The often less contrasting rump, less heavily marked crissum, and/or paler throat of many *decolor* have also been interpreted as evidence of hybridization with *fulvipennis,* but again these variants occur commonly throughout the range of *decolor,* including populations far from the range of *fulvipennis* (see below). For instance, a series of 6 birds that I collected from a breeding colony on the Río Tigre, Península de Osa included 4 with boldly black-tipped crissum feathers, 1 with bold dusky subterminal spots in each web, and 1 with only faint dusky smudges. All *decolor* in fresh plumage that I have seen have a distinct contrast between rump and back, although the pale area of the former may consist of feather-edgings that nearly or quite wear away in the course of a year (particularly due to abrasion in the nest burrow). Also, all *decolor* have the throat distinctly rusty to pale cinnamon, the chest and sides distinctly brownish. Overall, the color scheme of *decolor* resembles that of *uropygialis,* bleached or washed out to a varying extent. This is sufficiently consistent that I have no hesitation in recognizing this race; I fail to find any evidence of hybridization with *fulvipennis.* The two forms are apparently not even in contact at the present time. Of course, the coloration of *decolor* could represent the residue of extensive contact and hybridization between *fulvipennis* and *uropygialis* (?) sometime in the past. Measurements fail to disclose any indication of the intermediacy of *decolor,* however (see below).

The two most similar forms of *Stelgidopteryx* in Costa Rica are undoubtedly *fulvipennis* and *serripennis.* The former is, on the average, more heavily pigmented and contrastingly colored, but these differences become exceedingly difficult to discern in birds with worn plumage or in some old specimens. Many worn *fulvipennis,* including a nesting pair I collected near Turrialba in April 1977, have, at most, a faint buff tinge on the throat, less than many fresh *serripennis* (including one of the five collected at Chomes in April 1980). One of these latter also has distinct dusky smudges on the longest under tail coverts, a condition much more frequent in *fulvipennis* (Table 1). Without taking molting season into account (July–October for *fulvipennis,* evidently later for *serripennis,* as the migrants netted at Chomes were all in fresh plumage), it would be very difficult to assign many specimens to race.

The fairly bright throats and dark-spotted crissa of some *fulvipennis* might again be taken as evidence for introgression of *uropygialis* genes (although I have never seen a *fulvipennis* with a distinctly pale rump). Among the very brightest-throated *fulvipennis* I have seen, however, are the type series of "*salvini*" from Guatemala; in my experience, Costa Rican *fulvipennis* are, if anything, duller-throated than those of northern Middle America; they also tend to have very poorly defined dark caps. Were introgression the cause of this variation, one would expect the reverse tendency, with the southern birds the most brightly colored. I can see no clear-cut trend whatever in the extent of dark spotting on the crissum: this feature seems to be highly variable in all populations of *fulvipennis.*

A further factor to consider is the possible presence in Costa Rica of wintering birds of the pale form *psammochrous,* as Wetmore (MS) and Phillips (MS) cite specimens from central Panamá. I consider *psammochrous* to be a poorly marked race at best, however: I am unable to distinguish many breeding specimens of *psammochrous* from paler individuals of *serripennis* or, for that matter, of *fulvipennis*, as *psammochrous* tends to have a brighter throat than *serripennis*, approaching that of *fulvipennis* in the southern part of its range (Phillips MS). Most available data suggest that *psammochrous* winters north of Costa Rica. I have yet to see a definite Costa Rican specimen of this form and suspect that the Panamanian *psammochrous* may be merely a very pale *serripennis,* or at best a stray. In measurements, *psammochrous* appears similar to *serripennis* and *fulvipennis* (cf. Griscom 1929, Brodkorb 1942, Phillips et al. 1964); even if it were subsequently shown to winter in Costa Rica, this would not affect the major conclusions drawn here.

I have examined too few juvenals of any of the forms to evaluate the degree of individual variation in this plumage. There appear to be two basic types of juvenal plumage, however, one shared by *fulvipennis* and *serripennis,* the other by *uro-*

TABLE 1. Plumage description of four races of *Stelgidopteryx* swallows found in southern Middle America.

	serripennis	*fulvipennis*	*uropygialis*	*decolor*
Adults				
Back	Medium greyish-brown	Medium greyish-brown	Medium to dark greyish brown	Medium to fairly dark grey-brown
Crown	± concolor with back	Concolor to distinctly darker than back	Blackish; usually distinctly darker than back	Slightly to definitely darker than back
Tertials (fresh plumage)	Edged pale greyish	More broadly edged greyish white	Sharply edged whitish	Edged pale greyish to greyish white
Throat	Very pale grey-brown, tinged buff (faint; most strongly on chin) when *very* fresh	Pale greyish brown, usually strongly tinged cinnamon to buff *when fresh*	Cinnamon-rufous to pale cinnamon, fading with wear	Fairly bright to pale cinnamon; fading to rusty-buff with wear
Chest and sides	Very pale grey-brown; sides sometimes browner with dark shaft-streaks	Pale greyish brown, usually with dark shaft-streaks	Medium grey-brown; feathers of center of chest often with dark centers and shaft-streaks	Pale grey-brown, usually with dark shaft-streaks; feathers sometimes with dark centers on chest
Belly	Dull whitish to creamy white	Dull whitish to creamy white	Yellowish white to pale yellow	Whitish, usually tinged yellow, sometimes strongly so
Crissum	White, faily often with dark shaft-streaks, occasionally with indistinct dusky subterminal spots or smudges	White, usually with dark shaft-streaks; fairly frequently with dusky subterminal spots in each web; these usually faint, sometimes large and bold	White, with faint dark shaft-streaks; usually with central feathers boldly tipped black or dusky, narrowly edged white; sometimes with large dusky subterminal spots in each web	White, with faint darker shaft-streaks; usually with central feathers boldly tipped black or dusky, narrowly edged white; sometimes with large dusky subterminal spots in each web; rarely with small, faint spots

TABLE 1. Continued.

	serripennis	*fulvipennis*	*uropygialis*	*decolor*
Rump	Concolor with back; feathers very narrowly edged paler, so in very fresh plumage may appear slightly paler and greyer than back	Concolor with back; feathers narrowly edged paler, so in very fresh plumage may appear slightly paler or greyer	Usually whitish, contrasting sharply with back feathers edged/tipped broadly whitish; contrast reduced with wear	Usually greyish white to pale greyish, slightly to distinctly paler than back; feathers less broadly edged paler; occasionally no contrast in worn birds
Juvenals				
Dorsum	Dull grey-brown, feathers broadly and indistinctly edged or suffused dull cinnamon or tawny; tertials broadly edged dull buff, greater coverts dull cinnamon	Dull grey-brown feathers, broadly and indistinctly edged cinnamon to tawny; tertials broadly edged dull buff, greater coverts dull cinnamon-rufous	Dull dark grey-brown; feathers of back and especially wing-coverts distinctly edged cinnamon to buffy; tertials broadly and sharply edged buffy white to pale buff; rump pale brown to white	Dull grey-brown; feathers of back and wing-coverts distinctly edged dull buff; tertials sharply edged dull buffy to whitish; rump pale grey-brown to whitish
Venter	Throat and chest pale grey-brown, more or less washed with cinnamon; belly creamy white, crissum white, immaculate	Throat and chest grey-brown usually strongly washed cinnamon; belly dull creamy white; crissum white, immaculate to (rarely) faintly spotted	Throat and chest pale dull rufous to cinnamon, sides browner; belly dull white with slight yellowish wash; crissum white less heavily spotted than adult, sometimes nearly immaculate	Throat and chest pale to fairly bright cinnamon to cinnamon-buff; belly dull white with (sometimes) faint yellowish wash; crissum usually indistinctly spotted, often nearly immaculate

TABLE 2. Summary of measurements of *Stelgidopteryx* swallows from Middle and North America.

	Exposed Culmen				Wing chord			
	n	Mean	SD	Range	*n*	Mean	SD	Range
Males								
serripennis								
Central and eastern U.S.A.	21	6.78	0.34	6.2–7.5	23	108.87	2.83	103.8–112.4
Western and northwestern U.S.A.	25	6.75	0.42	6.1–7.6	25	110.22	2.88	105.0–116.4
Costa Rica-Panamá	13	6.74	0.25	6.3–7.3	14	109.38	2.73	104.6–113.3
Total	59	6.76	0.35	6.1–7.6	62	109.55	2.79	103.8–116.4
fulvipennis								
Northern Middle America	18	6.72	0.26	6.3–7.1	17	110.87	3.51	105.2–116.3
Costa Rica-Panamá	15	6.67	0.28	6.3–7.2	15	110.84	3.55	105.5–116.7
Total	33	6.70	0.27	6.3–7.2	32	110.86	3.53	105.2–116.7
uropygialis								
Honduras-Costa Rica	26	7.26	0.37	6.6–8.0	26	107.88	2.22	102.4–111.6
Panamá	24	7.27	0.32	6.7–8.1	22	106.47	2.28	103.2–111.8
Total	50	7.26	0.35	6.6–8.1	48	106.80	2.24	102.4–111.8
decolor								
Southwestern Costa Rica	12	7.50	0.38	6.9–8.3	12	106.85	3.00	100.6–110.7
Chiriqui-Veraguas	8	7.40	0.45	6.9–8.2	8	106.96	2.65	103.0–110.6
Total	20	7.46	0.41	6.9–8.3	20	106.89	2.82	100.6–110.7
Females								
serripennis								
Central and eastern U.S.A.	17	6.75	0.36	6.2–7.4	17	102.33	3.16	98.2–108.4
Western and northwestern U.S.A.	22	6.85	0.38	6.3–7.7	22	104.58	2.67	99.7–110.6
Costa Rica-Panamá	23	6.85	0.34	6.3–7.6	23	102.77	2.20	99.2–107.2
Total	62	6.83	0.35	6.2–7.7	62	103.32	2.81	98.2–110.6
fulvipennis								
Northern Middle America	14	6.71	0.31	6.3–7.2	13	102.92	2.64	99.2–107.7
Costa Rica-Panamá	10	6.75	0.37	6.2–7.4	10	104.93	3.11	98.7–109.3
Total	24	6.73	0.33	6.2–7.4	23	103.76	2.96	98.7–109.3
uropygialis								
Honduras-Costa Rica	19	7.38	0.39	6.7–7.9	19	99.58	2.80	93.4–103.8
Panamá	21	7.23	0.28	6.7–7.8	22	99.36	2.38	95.7–103.7
Total	40	7.30	0.33	6.7–7.9	41	99.46	2.55	93.4–103.8
decolor								
Southwestern Costa Rica	12	7.51	0.55	6.6–8.4	12	99.59	3.04	93.5–103.3
Chiriqui-Veraguas	8	7.29	0.39	6.8–8.0	9	99.79	2.47	95.7–102.6
Total	20	7.41	0.48	6.6–8.4	21	99.67	2.76	93.5–103.3

pygialis and *decolor* (Table 1). These types were first clearly described by Ridgway (1904). In general, young birds have the crissum less heavily and/or less frequently marked with dusky or black than do adults; whether this holds for birds in first basic plumage is conjectural.

MEASUREMENTS

All forms of *Stelgidopteryx* considered here are sexually dimorphic in wing length, with males averaging very significantly larger than females ($P < 0.01$ in all cases by t-test). In no form is there significant dimorphism in bill (exposed culmen) length. Thus, given the possibility of mis-sexed specimens, bill length is probably a better measure with which to compare forms. On this basis, the four races break into two

TABLE 3. Results of *t*-tests of differences in measurements of four races of *Stelgidopteryx* swallows.[a]

SPECIMENS FROM COSTA RICA AND ADJACENT AREAS

A. *Exposed culmen*

		Males			
		serripennis	*fulvipennis*	*uropygialis*	*decolor*
Females	*serripennis*		0.189	3.429**	4.097***
	fulvipennis	0.742		5.370***	6.153***
	uropygialis	3.196**	4.184***		1.750
	decolor	2.761*	3.440**	0.720	

B. *Wing chord*

		Males			
		serripennis	*fulvipennis*	*uropygialis*	*decolor*
Females	*serripennis*		1.135	2.750*	2.109*
	fulvipennis	2.287*		4.182***	3.206**
	uropygialis	4.128***	4.601***		0.269
	decolor	3.545**	3.870***	0.171	

GEOGRAPHIC VARIATION WITHIN FORMS OF *STELGIDOPTERYX*

	Exposed culmen		Wing chord	
	Males	Females	Males	Females
Costa Rica-Honduras *vs.* Panamá *uropygialis*	0.096	0.670	0.934	0.487
Costa Rica *vs.* Panamá *decolor*	0.551	0.693	0.179	0.103
C.R.-Panamá *vs.* Northern Middle America *fulvipennis*	0.592	0.271	0.095	1.830
C.R.-Panamá *vs.* Eastern + Central U.S.A. *serripennis*	0.340	0.903	0.493	0.515
C.R.-Panamá *vs.* Northwestern + Western U.S.A. *serripennis*	0.020	0.011	0.821	2.466*
Eastern + Central U.S.A. *vs.* Northwestern + Western U.S.A. *serripennis*	0.072	0.652	1.653	2.410*

[a] * = significant at $P < 0.05$; ** = significant at $P < 0.01$; *** = significant at $P < 0.001$.

well-defined groups: short-billed *serripennis* and *fulvipennis*, and long-billed *uropygialis* and *decolor* (Table 2). The two in each group are similar in bill length, but all intergroup comparisons give highly significant differences (Table 3A).

The same breakdown occurs with respect to wing length, but the picture is slightly less clear-cut (perhaps due to occasional mis-sexed specimens). In general, *serripennis* and *fulvipennis* are long-winged; *uropygialis* and *decolor* are short-winged. Geographic variation within *serripennis* complicates the picture: birds from the western and northwestern U.S.A. are longer-winged than those of the eastern and central regions (Table 2). This difference is significant in females, but not in males. The Costa Rican-Panamá sample of *serripennis* is intermediate in wing length but closer to the eastern-central group, especially in the females (Table 3). Thus the *serripennis* that migrate through southern Middle America probably breed in the central U.S.A. and adjacent south-central Canada. There is no appreciable geographic variation in any other form (Tables 2, 3). Particularly pertinent here is a series of *decolor* taken by Wetmore in Chiriquí; evidently following Hellmayr and Cory (1935), he considered them hybrids or intergrades between *fulvipennis* and *uropygialis* (Wetmore MS). In both plumage and measurements, however, these specimens agree perfectly with the series of *decolor* from southwestern Costa Rica (Tables 2, 3) and actually provide strong support for the validity of this form.

DISTRIBUTION

The distributional picture in *Stelgidopteryx* is complicated by the fact that *all* the forms considered here are migratory to some degree. Following breeding, part or all of most populations desert the breeding grounds; I have repeatedly visited breeding sites of *uropygialis, decolor,* or *fulvipennis* 1–6 months after the young fledged, to find no *Stelgidopteryx* present or to find a different form from that known to breed there. Thus, it becomes critical to distinguish between breeding and nonbreeding distributions of the forms in question.

I have used two procedures in delimiting breeding distributions: noting the locations of all nests or colonies at which I was able to identify the form(s) in question, and considering specimens taken during the months of the observed breeding season, especially those with gonad data indicating breeding. Skutch (1960) noted egg-laying in March virtually throughout Middle America. My own observations indicate a wider span, roughly from early March through mid- to late May. As stated by Skutch, however, all populations appear to be single-brooded. Thus, specimens taken between March and June should represent breeding birds, with two possible exceptions: early breeders may have left the nesting area by June, and it is often difficult to distinguish many worn, faded *fulvipennis* from many individuals of *serripennis*. Because the latter have been taken as late as mid-May in Costa Rica, and I have observed Rough-wings presumably of this race migrating north with other swallows in early May, I have excluded from the sample any doubtful birds without gonad data.

The resulting list of breeding localities for the three forms is plotted in Fig. 1. The conclusions are clear-cut: *fulvipennis* is a montane form breeding as low as 300–400 m locally, but mostly above 600 m, occasionally as high as 1,800 m; it does *not* breed south of the central highlands of Costa Rica. *Uropygialis* is essentially confined to the Atlantic lowlands, but on the northern and eastern slopes of the central highlands it may breed up to at least 1,000 m locally, thus overlapping with *fulvipennis*. The southwestern form *decolor* breeds north to near the Golfo de Nicoya; it may overlap with *fulvipennis* in the hills above Parrita, but I presently lack data from this area. Certainly at numerous localities in the far southwest, typical *decolor* breed at elevations that would be occupied by *fulvipennis* farther north, e.g. a breeding pair I collected at Las Alturas (1,600 m) in April 1980.

Outside the breeding season I have seen occasional pale-rumped birds (presumably *uropygialis*) in Guanacaste and around San José, Costa Rica, although most birds in both areas are dark-rumped. Dark-rumped birds are also common in the Caribbean lowlands of Costa Rica during the nonbreeding season, and I have seen dark-rumped, pale-throated birds in the southwestern lowlands on several occasions between August and March.

The present distributional picture seems to indicate that these forms are essentially allopatric in their breeding ranges but that widespread mixing occurs outside the breeding season. In the narrow zone of overlap between *fulvipennis* and *uropygialis* occasional hybridization might not be unexpected, but I can find no entirely conclusive evidence for its occurrence. I have yet to see a specimen that is not clearly one form or the other. My own observations in the zone of overlap are limited but tend to support the hypothesis that assortative mating exists and that hybridization is rare if it occurs at all. In April 1979 I traveled most of the roads in a zone of overlap in the Sarapiquí drainage in north-central Costa Rica, between Virgen del

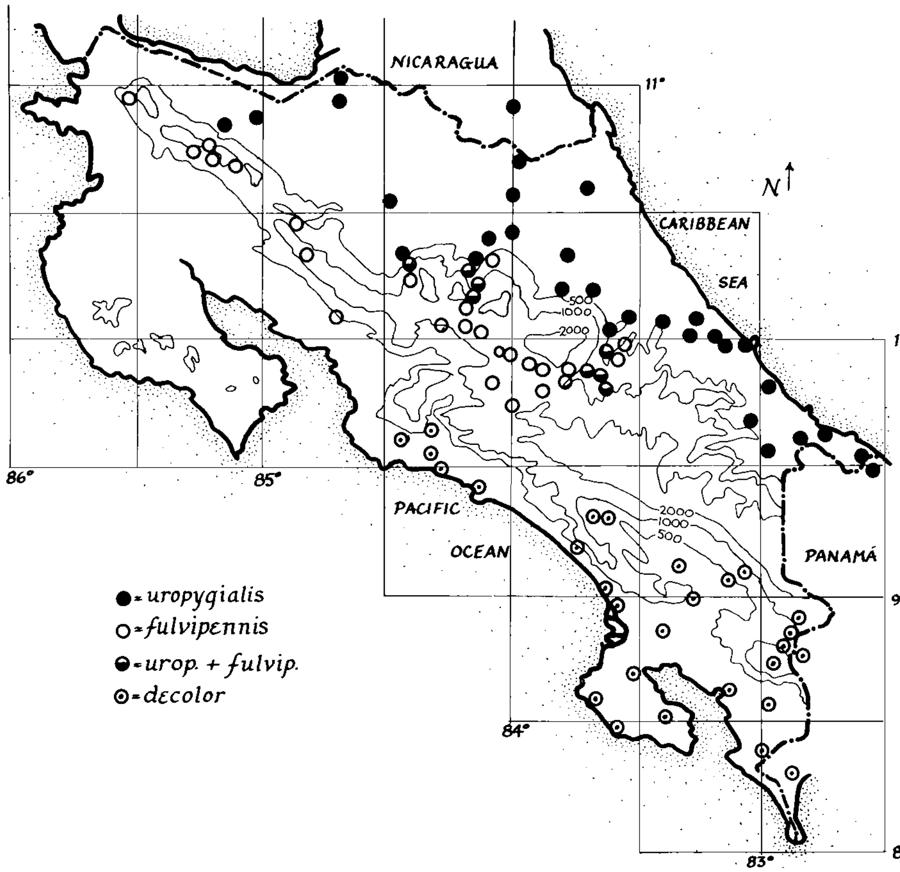

Fig. 1. Known breeding distributions of three races of *Stelgidopteryx* swallows in Costa Rica.

Socorro and Cariblanco (ca. 1,000 m) and San Miguel and Colonia Carvajal (300–400 m). In this area *fulvipennis* and *uropygialis* tend to form loose "pure" nesting colonies in roadbanks, rather than mixed colonies (although isolated pairs are not uncommon). Above about 700 m most birds seen were *fulvipennis*; below this elevation most were *uropygialis*. In all I found 37 "pure" *fulvipennis* pairs, 2 "pure" *uropygialis* pairs, and 2 possible mixed pairs (in both cases, involving the only *uropygialis* individuals I saw around the respective colonies of *fulvipennis*) in the higher parts of this area. Between San Miguel and Carvajal, I counted 18 "pure" *uropygialis* pairs, 4 "pure" *fulvipennis* pairs, and at most 1 possible mixed pair. In several cases I found pairs of the two forms breeding within 50–100 m. On a visit to Virgen del Socorro a month later, I was unable to find either putative mixed pair, though most "pure" pairs were located with young; the mixed pairbonds might not have persisted through egg laying. As colony locations tend to shift somewhat from year to year, such mixed pairs might include one bird whose previous nest site was now closer to or within the area occupied by a colony of the other form. More observations are clearly needed from this overlap zone to quantify the frequency and success of mixed pairs and to obtain comparative behavioral and ecological data.

Outside of Costa Rica, *fulvipennis* breeds north and west through Middle America, principally in the highlands, to the Petén in Guatemala and Veracruz and Chiapas in México. *Uropygialis* breeds north on the Atlantic slope of Middle America to southeastern Honduras; whether it overlaps with *fulvipennis* outside of Costa Rica is unknown. Southeastwards, *uropygialis* breeds on the Atlantic versant of western Panamá and on both slopes of eastern Panamá; it also ranges across northern South America from Ecuador to Venezuela and Trinidad; at least in Middle America, it is essentially a lowland bird in all areas. The breeding range of *decolor* extends eastward on the Pacific slope of Panamá at least into Veraguas; little is known regarding the situation further east, especially with respect to possible intergradation with *uropygialis*.

DISCUSSION

Data on morphology and distribution convince me that there are two breeding species of Rough-winged Swallows in Costa Rica. The northern/highland species, *serripennis,* is represented by the race *fulvipennis,* the southern/lowland species, *ruficollis,* by the races *uropygialis* and *decolor* on the Atlantic and Pacific slopes, respectively. Appropriate English vernacular names for the species *serripennis* and *ruficollis* would be Northern and Southern Rough-winged Swallow, respectively.

Geographical variation within the genus *Stelgidopteryx* as a whole must be reassessed in the light of this conclusion. In general, variation within the species *serripennis* is not great and is basically clinal in nature, making strict delimitation of subspecies difficult. A weak cline of increasingly contrasting markings exists from *serripennis* (*sensu stricto*) through *psammochrous* to *fulvipennis*; superimposed upon this cline is a tendency towards paleness in the hotter, drier areas of the southwestern U.S.A. and northwestern Mexico (*psammochrous*). A cline in size exists across North America, with wing length increasing toward the northwest, doubtfully justifying recognition of the race *aphractus*; size also increases slightly from north to south. Given the gradual nature of this variation, the broad areas of integradation, and the considerable individual variation in all forms, I feel that no great violence would be done to the facts by considering the species *serripennis* to be monotypic. I should note in passing that two very large, dark races of Roughwings, *ridgwayi* and *stuarti,* found from Yucután to Chiapas and Veracruz, will not be considered here, as they do not occur in Costa Rica; based upon sympatric breeding (with *fulvipennis*) and clear-cut size differences, they probably constitute a third species of *Stelgidopteryx* (A. R. Phillips pers. comm.).

In *S. ruficollis,* the same tendency toward a paler form in a (seasonally) drier area is seen in comparing the Pacific *decolor* with the Caribbean *uropygialis*; in Central America the dry season is more pronounced on the Pacific slope. Both forms have pale rumps, a feature not found in nominate *ruficollis.* Thus, although certain kinds of variation recur in both *serripennis* and *ruficollis,* I can find little justification for considering variation in the complex as a whole to represent simply a "progressive northward dilution of ancestral characters." In fact, if Phillips et al. (1964) are correct in considering *Stelgidopteryx* to be closely allied to *Riparia* (regardless of whether one wishes to lump the two genera or not), there is good reason for questioning the supposedly ancestral status of *ruficollis* on geographical grounds.

With regard to possible isolating mechanisms between *uropygialis* and *fulvipennis,* the differences in throat, crown, and especially rump color could certainly serve as visual features promoting assortative mating. In addition, I found that with practice I was able to distinguish the voices of the two forms. Although the vocal repertoires seem fairly similar overall, the calls of *uropygialis* seem lower-pitched, mellower, more rolling and liquid than do the harsher, drier corresponding ones of *fulvipennis*. In February 1977, prior to the actual breeding season, I repeatedly noted "pure" groups of both forms gathering in dead trees or on other conspicuous perches at Virgen del Socorro. Birds in these groups vocalized loudly and persistently. It is not unlikely that such groups function in pair formation, in which case the aforementioned vocal differences may be important as isolating mechanisms.

The difference in bill size between *S. serripennis* and *S. ruficollis* could indicate an ecological difference, perhaps in size of preferred prey. This would make an interesting study, as the question of ecological compatibility is a dynamic one. Distributions of birds like *Stelgidopteryx* swallows are very likely in a state of flux at present due to man and his roadbuilding and deforestation activities, which tend to produce new nesting and foraging habitat, respectively, in areas where neither existed before. Rough-winged Swallows are probably more numerous and evenly distributed in Middle America at present than ever before, and this seems a good point in time to undertake a detailed study of their ecology.

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INTRINSIC FACTORS IN THE SELECTION OF FORAGING SUBSTRATES BY PINE WARBLERS: A TEST OF AN HYPOTHESIS

JOHN T. EMLEN AND MICHAEL J. DEJONG

Department of Zoology, University of Wisconsin, Madison, Wisconsin 53706 USA

ABSTRACT.—This paper describes a test of an hypothesis recently proposed to explain a difference in foraging behavior observed in Pine Warblers (*Dendroica pinus*) on two neighboring Bahama islands. The hypothesis, that the members of the two populations were using different intrinsic preference patterns in selecting their foraging substrates, is supported by observations of different substrate responses in captive birds from the two islands in a common test situation. We interpret intrinsic preferences as expressions of stereotyped response patterns selected for during episodes of stress and active competition in fluctuating environments and becoming detectable as deviations from currently optimal patterns (matching the local resource distribution) during periods of resource abundance and reduced or suspended competition. Intrinsic preferences are difficult to recognize in nature, and we believe that they may be much more common than generally suspected. *Received 22 September 1980, accepted 16 December 1980.*

THE adaptive plasticity of foraging behavior in birds seen in recent studies of optimal foraging (Pyke et al. 1977, Krebs 1978) is, of course, invariably constrained by the morphological and physiological specializations of the species. The possibility that purely behavioral specializations may similarly constrain a bird in its foraging activities in nature has received little attention (but see Morse 1971) because of the difficulties inherent in detecting and identifying behavioral preferences and aversions outside of experimental contexts where extrinsic factors of food availability and interference can be controlled.

In a recent field study one of us (Emlen in press) demonstrated that during the breeding seasons of 1971, 1976, and 1978, Pine Warblers (*Dendroica pinus*) on Grand Bahama Island foraged almost exclusively on pine foliage, while those in closely similar situations on neighboring Andros Island divided their foraging activity about equally between foliage and bark. After measuring the distribution of insects on bark and foliage and examining the potential role of direct interference from community associates on the two islands, he concluded that the birds were not responding to the extrinsic factors of food abundance or substrate accessability but to intrinsic factors of substrate preference, i.e. that the two populations were phenotypically different with respect to this behavioral characteristic. Emlen's hypothesis, paraphrased in more specific terms, states that: if presented with a choice of bark and foliage in a neutral setting, birds from Grand Bahama will confine their searching activity almost entirely to foliage, while those from Andros will search on both substrates.

In May 1980 we tested this hypothesis by presenting freshly caught Pine Warblers from each island with a choice of bark and foliage in a portable observation tent, timing the number of seconds each bird spent searching on each of the substrates in 30-min observation sessions. We also measured the bills and feet of all test birds on the premise that the divergent substrate preferences might reflect small and previously undetected differences in size or proportions.

METHODS

Birds of both sexes (10 from Grand Bahama and 12 from Andros) were lured into mist nets on their territories by play-backs of taped songs and, in most cases, by caged live birds serving as decoys. After capture the birds were held in small individual cages with food (meal worms plus a high-protein mash) and water. During transportation between islands they were held in small paper cones for up to 4 h at a time.

The portable observation tent, made from translucent, green-dyed bed sheets and measuring 1.6 m × 1.6 m × 2.3 m high, was set up in the forest with a foliage-bearing pine tree segment serving as the central tent pole. Bark/foliage ratios were roughly standardized for each setting by selecting trees with good foliage in the central portion and cutting the 2.3-m segment of trunk between the 6.0-cm and 3.5-cm diameter points. Foliage on the 10–15 lateral branches in these segments was trimmed to 46 needle clusters in all sets. Observations were made from a small darkened blind at one side of the tent through a one-way milar window.

Each bird was tested twice in the observation tent, first on sterile substrates (thoroughly sprayed with Diazinon insecticide) in order to control the possible effects of response reinforcement, and a few days later on untreated substrates (residual native insects intact) from the other island as a check against differences of potential significance in the two insect faunas. Released quickly into the tent from the hand after a 1–4-h period of food deprivation, each bird typically flew to the central or upper part of the tree, peered around, fluffed and preened, and started foraging within 3–10 min. Activity, categorized as searching in the needles, searching on the bark, searching on the ground, quietly resting, and restlessly flying about, was monitored with a stop watch in hand for 30 min or longer, and the number of seconds of each of the five activities was recorded. A few birds failed to search the substrates; these and those that spent less than 30 s of searching in the 30-min observation period were disqualified from the record.

RESULTS

The number of seconds of searching on needles and bark in the two tests is presented in Table 1. The results in both cases support the prediction of the hypothesis that the proportion of bark foraging would be appreciably higher in the Andros than in the Grand Bahama birds. The proportions in these tests were all lower than those obtained for free-ranging birds in the field, but this may simply reflect a lower availability of bark relative to foliage in the test situation and does not appear to invalidate in any way the conclusion of an island-specific preference difference.

Several additional insights on foraging behavior may be drawn from the observations of the birds in the tent:

1. Some of the birds searched the available foliage and bark surfaces, systematically working downward from the top or upward from the bottom with little or no backtracking, then stopped searching. Others were quite haphazard in covering the available surfaces and continued to search to the end of the observation session. Individuals tended to follow similar searching routines on successive tests.

2. Some birds moved almost continuously through the branches and foliage as though using a short visual search range; others advanced less frequently and in longer hops. The former pattern appeared to be more common in the Grand Bahama birds, the latter in the Andros birds.

3. None of the birds searched the three available substrates (foliage, bark and ground) sequentially with indications of an order of preference. Some did considerable ground searching; others did none. Bark searching was interspersed with foliage searching as the birds moved about.

The behavioral differences between the Andros and Grand Bahama populations were associated with slight differences in morphology. The Andros birds in the test series averaged significantly smaller than the Grand Bahama birds in five of the

TABLE 1. Proportion of bark searching to total searching in two test situations: A—on sterile (insecticide-treated) native substrates, and B—on untreated foreign substrates. Values are seconds of searching activity for each bird.

A—TESTS ON STERILE (NATIVE) SUBSTRATES[a]

Grand Bahama birds				Andros birds			
Bird number	Bark	Foliage	Prop on bark	Bird number	Bark	Foliage	Prop on bark
1	0	340	0.00				
2	0	440	0.00	1	39	41	0.4875
3	5	650	0.0076	3	20	59	0.2532
6	13	313	0.0399	4	30	330	0.0833
7	2	233	0.0085	7	14	60	0.1892
8	0	367	0.00	8	52	259	0.1672
				10	37	75	0.3304
				11	1	65	0.0152
				12	4	293	0.0135
	($\bar{x}$ = 0.0093 ± 0.0155)				($\bar{x}$ = 0.1924 ± 0.1629)		

B—TESTS ON UNTREATED FOREIGN SUBSTRATES[a]

Bird number	Bark	Foliage	Prop on bark	Bird number	Bark	Foliage	Prop on bark
2	5	707	0.0071	1	15	33	0.3125
5	0	153	0.00	3	14	203	0.0645
6	25	375	0.0625	4	37	151	0.1968
7	15	180	0.0769	5	43	261	0.1414
8	5	190	0.0250	6	2	55	0.0351
9	3	161	0.0183	8	21	9	0.7000
10	0	154	0.00	12	17	72	0.1910
	($\bar{x}$ = 0.0286 ± 0.0309)				($\bar{x}$ = 0.2345 ± 0.2249)		

[a] Differences significant at 5% level (*t*-test).

seven measurements recorded (Table 2). Although not recognized as taxonomically distinct, the Andros population has been suspected of being slightly smaller (James Bond pers. comm.). At this time we see no basis for a functional relationship between these morphological divergencies and the behavioral divergencies under consideration.

DISCUSSION

These results confirm our prediction that captive representatives of the Pine Warbler populations of Grand Bahama and Andros islands would retain their distinctive response characteristics both in a neutral choice situation (sterile substrate) and when

TABLE 2. Bill and foot measurements (cm) for the test birds captured on Grand Bahama and Andros islands. (Culmen measurements are omitted for six birds with cage-damaged foreheads, foot measurements for one bird with diseased feet.)

	Grand Bahama	Andros
Culmen[a]	1.23 ± .030 (5)	1.18 ± .029 (7)
Gonys	0.78 ± .044 (7)	0.78 ± .036 (11)
Gape[a]	1.62 ± .085 (7)	1.52 ± .051 (11)
Nostril to tip	0.86 ± .075 (7)	0.82 ± .042 (11)
Tarsus[a]	2.02 ± .047 (6)	1.87 ± .089 (11)
Hind toe + claw[a]	1.21 ± .033 (6)	1.12 ± .047 (11)
Hind claw[a]	0.62 ± .019 (6)	0.55 ± .028 (11)

[a] Differences significant at 5% level (*t*-test).

presented with the natural substrates of the opposite island. This, in turn, supports our underlying hypothesis that the substrate responses observed in the field in these two populations reflected intrinsic response tendencies (genetically or culturally inherited) rather than extrinsic factors.

As with habitat selection (Lack 1937, Hildén 1965), or foliage selection (Klopfer 1965, Partridge 1974), any expression of substrate preference will, according to prevailing evolutionary theory, be maladaptive unless it coincides with the currently optimum response. A preference that would restrict a bird's freedom to exploit portions of otherwise available resources, as appears to be the case in the Grand Bahama birds that bypassed bark insects and the Andros birds that bypassed foliage insects, would, on this basis, be maladaptive and untenable. Departure from the current optimum may be adaptive, however, where environmental conditions fluctuate and specialization on a subset of the available substrates is advantageous during critical phases of the fluctuations (Wiens 1977). Species living in fluctuating environments thus have a choice between two evolutionary strategies: plastic responsivity to the changing conditions, or stereotyped specialization for conditions encountered during the most critical phase of the fluctuations. We propose that the apparent maladaptions in the substrate selections of Pine Warblers in this study reflect stereotyped response patterns adapted for conditions of intense competition and observed by us only during periods of reduced or suspended competition when food supplies exceeded the local community's demands. On Grand Bahama, where the Pine Warblers occurred with two species of bark-gleaning specialists (Emlen 1977), competition during food crises would presumably favor foliage-gleaning specialists over generalists, while on Andros, where there were no bark-gleaning specialists, no such selective pressure for specialization would occur.

The direct observational techniques that enabled us to detect these differences in foraging behavior in the Pine Warblers on the two islands also revealed significant foraging differences in the two Blue-gray Gnatcatcher (*Polioptila caerulea*) populations (Emlen in press). We suspect that further studies of this type would reveal additional examples of local foraging specialization attributable to intrinsic factors wherever environmental conditions fluctuate and resources are incompletely exploited during periods of resource superfluity.

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REVIEWERS FOR *THE AUK*, 1979–1980

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EFFECTS OF DENERVATION OF THE TRACHEO-SYRINGEAL MUSCLES ON FREQUENCY CONTROL IN VOCALIZATIONS IN CHICKS

RICHARD E. PHILLIPS AND ORLAN M. YOUNGREN
Department of Animal Science, University of Minnesota, St. Paul, Minnesota 55108 USA

ABSTRACT.—Audiospectrograms of chick twitter, peep, and trill vocalizations showed that denervation of the extrinsic syringeal muscles reduced frequency ranges and amplitudes of all three calls but that appreciable frequency modulation remained. Electromyograms from freely moving, awake chicks showed that the abominal (expiratory) muscles twitch and relax for each sound pulse of trills (up to 40–50/s). Comparison of these results with reports for songbirds supports the idea that the extrinsic syringeal and expiratory muscles play similar roles in both groups. *Received 10 June 1980, accepted 6 October 1980.*

ALTHOUGH anatomical and some physiological studies strongly suggest that the extrinsic syringeal muscles play an important role in the production and modification of avian vocalizations (Miskimen 1951, Brockway 1967, Peek 1972, Andrew 1973), several have failed to support such a role for them (Gross 1964, Smith 1977, Brackenbury 1978a). The persistence not only of sound production but also of appreciable frequency modulation after sectioning of the muscles raised the possibility that the correlations reported between vocalizations and EMG activity (Youngren et al. 1974, Gaunt and Gaunt 1977) were somehow spurious and that the muscles played no necessary role in vocal control. The present experiments were designed to test this hypothesis more thoroughly.

METHODS AND MATERIALS

Chicks.—Chicks (*Gallus gallus*) were hatched in our laboratory from a cross between Rhode Island Red cocks and Barred Rock hens. They were hatched and housed in groups except during surgery and recording.

Surgery.—All chicks were anesthetized with 1.8–2.4 mg of veterinary pentobarbital sodium (Diabutal, Diamond Laboratories, Inc.) injected into a leg muscle (gastrocnemius). Surgery was performed under a Zeiss operating microscope with coaxial light source.

Experimental groups.—(1) To test the effects of total denervation of the syrinx, the muscle and attached nerve (cervicalis decendans superior or c.d.s.) were removed bilaterally from 6–8 tracheal rings just caudal to the glottis in six chicks (Cut XII-High). In adults this procedure severed the only innervation of the two pairs of muscles (m. tracheolaterlis, m. sternotrachealis), eliminating their activity (Youngren et al. 1974). In all these experiments, we have assumed that these muscles have no innervation in chicks that is absent in adults: careful dissection has revealed none. In six sham-operated controls from the same hatch, the neck skin was incised and sutured as a control for anesthetic and trauma affects (Operated Control).

(2) To test for effects of denervation on m. sternotrachealis, the muscles and nerves were removed from the 6–8 tracheal rings immediately cephalad of the interclavicular air sac membrane (Cut XII-Low). This left most of m. tracheolateralis functional but, based on our anatomical studies of adults (Youngren et al. 1974), completely denervated m. sternotrachealis without interfering with the interclavicular air sac membrane or with any passive mechanical action of the muscle upon the syrinx. The six sham-operated chicks from (1) above (Operated Control) served as controls for this group also.

(3) To compare the effects of direct interference with m. sternotrachealis to those of denervating it, the interclavicular air sac was opened in six chicks, and the sternotrachealis muscles were severed bilaterally at their insertion on the trachea. Their free ends were allowed to drop into the sternal cavity (Cut Muscles). To control for possible effects of rupturing the interclavicular air sac membrane, the sacs were

opened to the same extent as in the experimental birds in six control chicks, but the sternotrachealis muscles were left intact (Rupture Air Sac). In both of these groups the neck skin was sutured tightly to prevent air leakage. A group of six intact chicks that were never anesthetized was tested as the others to provide normal calls for comparison (Intact Control).

(4) In six additional chicks a third pair of muscles, m. ypsilotrachealis, was sectioned and effects on vocalizations analyzed. In four of these, m. sternotrachealis and m. tracheolateralis were denervated as well (by sectioning c.d.s. high in the neck). In only two was m. ypsilotrachealis alone affected.

Eliciting and recording vocalizations.—Three types of calls that Andrew (1963) described and named were studied; peeps, twitters, and trills. These three types of calls include the entire range of frequency modulations that occur in a chick's vocal repertoire. Examples of each from intact chicks are displayed under the PRE headings of Fig. 1. Chicks were deprived of food for 3–5 h prior to recording, then put into an oval test pen 76 cm by 56 cm with 38-cm-high solid walls lined with 12 mm of foam. The floor was padded, and the whole pen was housed inside a sound isolation room (Industrial Acoustics Co., Inc.) that eliminated noise from other birds and activities in the bulding. The pen was lighted by an overhead, 100-W incandescent bulb. The recording microphone was hung 8 cm above the center of the pen floor. Calls were recorded at a tape speed of 19 cm/s (7½ ips) on a Sony TC 353 D tape deck, and the chicks were monitored either through a one-way mirror in the sound isolation room wall (peeps) or by the experimenter in the room itself (twitters and trills). Peeps were evoked simply by leaving the chick alone in the test pen. A few chicks that failed to peep with the room lights on did so quickly when the lights were turned off. Twitters were reliably evoked by talking softly to the chick and/or by placing a hand in the test cage near it. Hungry chicks nearly always responded to this by feeding and twittering. Trills were elicited by suddenly picking up a feeding or twittering chick by one leg or, better, by first getting the chick to feed, then pulling it sideways by one wing. This didn't disturb the chick enough to cause peeping unless the action persisted. Trills were difficult to evoke if the chicks were peeping or showed other signs of being frightened.

All three types of calls were recorded from each of the experimental and sham-operated control chicks on the second day after surgery. Comparable recordings were made from six intact controls.

Verification of nerve and muscle section.—Following testing the experimental chicks were killed and their tracheae examined under a dissection microscope.

Measurement of frequency modulations.—Samples of four to six calls from each chick from each test period were visualized with the audiospectrograph (Sona-Graph 6061B, Kay Elemetrics), and measurements of maximum and minimum frequency of the fundamental frequency and of its duration were made. Harmonics were not included in the measurements. Peeps were sampled just after peeping had reached its loudest as judged subjectively. Twitters were sampled just as the hungry chick discovered food, a time when the calls were loudest and most rapidly uttered. The loudest and longest trills from each chick were selected for analysis.

Treatment effects on each measure were evaluated with one-way analysis of variance with individual *t*-tests for all possible pairs where significance for the overall comparison exceeded 0.05. Primary attention was paid to comparisons between Operated Controls and the two Cut XII groups. In addition, a Fisher Exact Probability Test for equality of proportions in independence of treatment and call-not-call was used to test the probability that the number of birds that trilled in the Low-cut group was the same as that for controls (Operated Controls).

The chicks recovered from the anesthesia and surgery very quickly: they fed and drank as soon as they could stand, and by the next day they seemed completely normal. Only the data from the second day after surgery are analyzed here.

Electromyograms.—To determine whether the expiratory muscles contributed to the trills that persisted after muscle or nerve section, a pair of enamel-insulated nichrome wires 0.127 mm in diamter, with 1-mm bare tips bent into hooks, were implanted in the abdominal oblique muscle of each of two 14-day-old female chicks. When the chicks had recovered from anesthesia, EMG's were recorded on one channel of a Sony stereo tape recorder (after amplification by a Tektronix P-122 pre-amplifier), and calls were simultaneously recorded via a microphone connected to the other channel. Tape speed was 9.5 cm/s. The records were visualized by photographing the face of a dual-beam oscilloscope with a Grass oscillographic camera at a film speed of 100 mm/s.

RESULTS

Post mortem examinations showed that section of the appropriate nerves or muscles was complete in all experimental chicks.

Cutting the nerves (Cut XII-High) to the tracheal muscles (m. tracheolateralis,

TABLE 1. Characteristics of peep vocalizations in control and experimental groups of chicks.

	Intact Control	Operated Control	Cut XII High	Cut XII Low	Rupture Air Sac	Cut Muscles
Maximum frequency						
Mean	5,190^{a}	4,920^{ab}	4,010^{c}	2,970^{c}	4,420^{bc}	3,150^{d}
SE	200	130	130	70	190	110
Minimum frequency						
Mean	1,810^{a}	1,900^{a}	2,180^{a}	1,880^{a}	1,890^{a}	1,900^{a}
SE	50	50	120	100	120	50
Range (maximum–minimum)						
Mean	3,380^{a}	3,010^{a}	1,830^{c}	1,100^{d}	2,540^{b}	1,250^{d}
SE	220	160	100	50	170	100
Number of chicks peeping	6	6	6	5	6	6

[a] All six chicks of each group were tested for each measure in this and the following tables. All numbers in a horizontal row of this and subsequent tables that have different superscripts differ ($P < 0.05$). Those with the same superscript do not differ ($P > 0.05$).

m. sternotrachealis) reduced, but did not abolish, the frequency range of all three of the call types (Table 1–3; Fig. 1B), primarily by reducing the highest frequencies in the calls. The effects were more severe with the low cuts that selectively inactivated m. sternotrachealis (Cut XII-Low, Tables 1–3; Fig. 1C). These chicks appeared unable to produce low-intensity calls, and two of the six did not produce twitters at all (Table 2). Those that twittered did so only in the initial feeding bouts after food deprivation, a time when chicks twitter most loudly and frequently. By gently placing a finger on the throat of those chicks that failed to twitter (even though they went through the motions), one could feel the trachea moving cephalad with each attempted, but silent, "vocalization." Furthermore, slightly stronger finger pressure that prevented the movement of the trachea resulted in audible sounds with each calling movement. The calls of the chicks in which the tracheal muscles had been denervated were noticeably less loud than those of controls, and they were absent in situations in which low-intensity twitters were normally given, but no quantitative measurements were made of sound level. Durations of peeps were also reduced in the Cut-Low group. Cutting the sternotrachealis muscles (Cut Muscle, Table 1–3) had effects very similar to those of denervating them, in that it reduced the maximum frequency and the range of frequencies in all three types of calls. The results from this group and its control (Rupture Air Sac) rule out incidental damage to m. tracheolateralis or general trauma as explanations for the relative severity of

TABLE 2. Characteristics of twitter vocalizations in control and experimental groups of chicks.

	Intact Control	Operated Control	Cut XII High	Cut XII Low	Rupture Air Sac	Cut Muscles
Maximum frequency						
Mean	4,400^{a}	4,080^{a}	3,710^{a}	2,520^{b}	3,700^{a}	2,630^{b}
SE	160	150	320	100	180	80
Minimum frequency						
Mean	2,470^{a}	2,490^{a}	2,240^{a}	1,760^{b}	2,220^{a}	1,850^{b}
SE	120	200	140	90	150	60
Range (maximum–minimum)						
Mean	1,930^{a}	1,590^{ab}	1,470^{b}	760^{c}	1,480^{b}	780^{c}
SE	130	190	210	50	120	50
Number of chicks twittering	6	6	6	4	6	5

TABLE 3. Characteristics of trill vocalizations in control and experimental groups of chicks.

	Intact Control	Operated Control	Cut XII High	Cut XII Low	Rupture Air Sac	Cut Muscles
Maximum frequency						
Mean	5,060[a]	5,140[a]	3,980[b]	2,840	4,460[a]	3,180[c]
SE	150	250	200	—	180	100
Minimum frequency						
Mean	2,400[a]	2,330[a]	2,770[a]	1,880	2,470[a]	1,940[b]
SE	50	80	120	—	160	70
Range (maximum–minimum)						
Mean	2,650[a]	2,810[a]	1,710[b]	960	1,980[b]	1,240[c]
SE	150	300	110	—	100	120
Number of chicks trilling	5	6	6	1	6	4

the vocal loss after partial (Cut XII-Low) vs. total (Cut XII-High) denervation of the syringeal musculature. The reduction in frequency range of calls in the Rupture Air Sac control group, although not as severe as that in the nerve section groups, is consistent with earlier demonstrations (Gaunt et al. 1973, Youngren et al. 1974) that vocalizations depend on pressurization of the interclavicular air sac: although the incision in the neck skin was tightly closed, the air sac was not, and air could leak into the subcutaneous space to alter the dynamics of pressure changes external to the syringeal membranes.

The call of the chicks with m. ypsilotrachealis denervated, either alone or with the other two muscles, did not differ from the Operated Control and Cut XII-High groups, respectively, in any measure. Like the chicks of these two groups, however, their peeps contained significantly greater frequency excursions than those of Cut XII-Low chicks ($P = 0.007$, paired t-test). These results from chicks resemble those from adult hens in that, although m. ypsilotrachealis is often activated during vocalization (Youngren et al. 1974, Gaunt and Gaunt 1977), it does not seem to play a major role in controlling the brief types of vocalizations that we have studied.

All three types of calls were preceded by a burst of EMG activity in the abdominal (expiratory) muscle, and each amplitude-frequency peak within a trill was preceded by a well-defined burst of EMG activity that commenced 15–30 ms (mean of 40 measurements in 20 trills 22.1 ± 3.4 ms) before the sound (Fig. 2). These bursts all occurred during a single period of expiratory activity of the muscles, and activity briefly ceased between bursts within a trill. The EMG activity immediately preceding each sound, even the weakest, consistently included much larger spikes than did normal, even excited but silent, exhalation, suggesting that different sets of muscle fibers are involved in breathing and in vocalizing (fast-twitch alpha fibers for the large spikes associated with vocalizing and slower, beta fibers for the smaller spikes seen during breathing?). Because muscle fiber types are determined by their motor neurons, this suggests partial differentiation of nerve fibers for calling and for respiration.

Calls tended to occur during exhalations rather than interrupting inhalations, but several calls could be given on a single exhalation. Brackenbury (1978a: Fig. 8C) has shown the same. His figure shows strikingly that the respiratory rhythm is not reset by the calls.

Fig. 1. Audiospectrograms illustrating the three types of chick vocalizations analyzed in this investigation and the effects of the experimental treatments on them. **A.** Operated Control, skin of upper ventral neck cut and sutured. **B.** Cut XII-High, bilateral section of ramus cervicalis decendens superior of N. XII near its cephalic end. **C.** Cut XII-Low, bilateral section of ramus cervicalis decendens superior of N. XII just cephalad of its entry into the interclavicular air sac. **D.** Rupture Air Sac, incise skin, and rupture interclavicular air sac to same extent as in "E" below, as control for damage to the air sac. **E.** Cut Muscles, cut both sternotrachealis muscles free from the trachea close to their insertions on it. "Pre" columns contain examples of normal vocalizations prior to surgery, "Post" columns contain examples of vocalizations 48 h after surgery. Each horizontal calibration mark at the left of the figure represents 1 Khz (from 1 through 8).

DISCUSSION

All three types of calls were produced by the chicks after complete denervation of the tracheal muscles (Cut XII-High group), but the range of frequencies spanned by calls was significantly reduced. Selectively denervating (Cut XII-Low group) or cutting the sternotrachealis muscles had more drastic effects, eliminating all soft

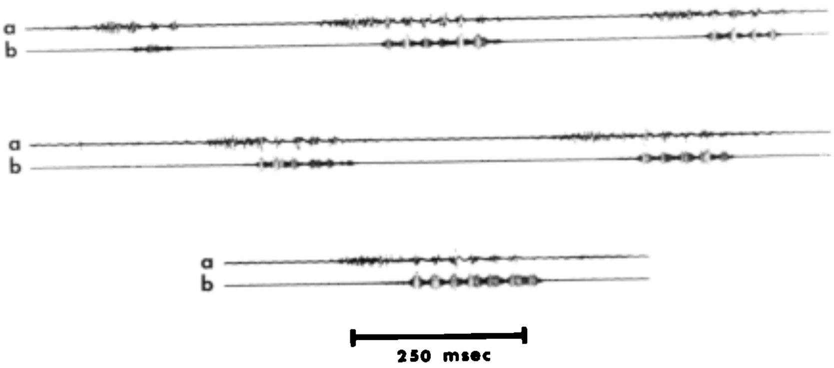

Fig. 2. Electromyograms of the expiratory muscle m. obliquus abdominis externus referenced to vocalization. A. expiratory muscle EMG. B. vocalizations (trills). Time scale, 250 mm/s.

calls and reducing the frequency ranges of the calls even more. We found the same in adults (Youngren et al. 1974); selective denervation of m. sternotrachealis altered vocalizations much more than did inactivation of both it and m. tracheolateralis together. In both young and adults reduction in frequency range was accompanied by a loss of amplitude, indicating that in chicks, as in songbirds (Greenewalt 1968, Stein 1968, Gaunt and Wells 1973), amplitude and frequency modulation are intimately linked. Our results with chicks apparently differ from those of Allen (1970, cited in Andrew 1973), who reported loss of all frequency modulation after cutting m. sternotrachealis in chicks, for we saw some modulation, although admittedly not much, after such surgery, even in the trills (Fig. 1). The literature for adult fowl is scant: aside from our report, Gross (1964) simply said that the operation failed to silence chickens, and Brackenbury (1978a) that "In their essential features, clucking and crowing remained unchanged." Miskimen (1951) reported that her two cocks eventually crowed loudly but with altered sound.

We interpret these results with domestic fowl to indicate that the coordinated actions of the extrinsic syringeal muscles play an important facilitatory role in the production and modulation of the birds vocalizations. The importance of their coordination is most apparent in the greater vocal losses in Cut XII-Low and Cut Muscle groups than in the Cut XII-High group. In addition, air pressure events controlled primarily by the expiratory musculature and pressure-flow dynamics of the system are sufficient both to produce and to modulate amplitudes (and so frequencies) of sounds in both chicks and adults.

This conclusion is strongly supported by our findings (1) that recognizable trills persist after denervation of the extrinsic syringeal muscles of chicks, and (2) that the expiratory muscles produce separate EMG bursts for each sound peak of a trill. Both audiospectrographs and oscillograph records show that a trill is a continuous sound, not a series of sounds separated by brief silent intervals as Canary (*Serinus canaria*) trills seem to be (Calder 1970). This suggests that chicks produce trills by superimposing brief, added expiratory muscle pulses (whose effects are reinforced by activities of the extrinsic syringeal muscles) to an exhalation and not by "mini-breaths" as proposed by Calder (1970) for Canary song. They thus seem to conform to the pulsatile input model (No. 4) of Gaunt et al. (1976).

The average rate of pulsing that we measured in 16 trills was 40.3 ± 6.8 (maximum 63) pulses/s. This is very close to the rate of trills in mini-breaths (37/s) that Calder (1970) reported for his Canaries and to the pulse rate of 52/s that Brackenbury (1978b) observed in the songs of *Locustella.* It is far higher than the frequency of panting, 6.25/s, that the same author has reported for a 15-day-old chick (Brackenbury 1978a). Clearly, pulsatile contractions of the respiratory muscles can play an important part role in amplitude modulations of the vocalizations of both passerine and nonpasserine birds up to repetition rates of 40–60 Hz.

Although the respiratory and vocal systems are linked to the extent that they use the same peripheral apparatus for moving air and are further related by the fact that vocalizations occur only on exhalations, their neuromuscular controls differ in several important ways. Vocalizations do not result simply from sudden, forceful exhalations, even at the level of abdominal muscle control. Our EMG data on chicks hint that different types of muscle fibers, and thus of motor neurons, may be involved in ventilatory and vocal exhalations (Fig. 2). Air-sac pressure records of both Gaunt et al. (1976: Fig. 4) and Brackenbury (1978a: Fig. 8) show that, at least some times, ventilatory rhythms are not reset even by multiple, rapidly repeated calls. This implies the existence of at least two pattern generators capable of producing independent rhythms.

Comparison of denervating and of severing m. sternotrachealis in domestic fowl and in other species suggests some basic similarities as well as some striking differences. Denervating the syrinx produces more severe vocal deficits in adult songbirds than in (infant) chicks (Nottebohm 1971, Peek 1972, Smith 1976), but the degree of loss reported in the latter ranges from the "virtually aphonic" of Nottebohm and the "mute" of Peek to "species atypical sounds" of Smith. Brockway (1967) also reported loss of species typical sounds but not muting after denervation of the syrinx in Budgerigars (*Melopsittacus undulatus*). In adult fowl, sectioning the nerves has had little effect on vocalizations (Gross 1964, Brackenbury 1978a). Clearly, denervation of syringes with intrinsic musculature more seriously impairs their capabilities than it does those of chickens, which lack intrinsic muscles. Ability to make vocal sounds persists even in some songbirds (apparently fairly loud ones in Smith's birds), suggesting a difference in degree rather than in kind from chickens.

Some role for the extrinsic muscles in songbirds is suggested by the loss of song that Miskimen (1951) reported after cutting the sternotrachealis muscles in four Cardinals (*Cardinalis cardinalis*), but Smith (1977) reported normal songs in three species of songbirds after 2 weeks for recovery. His results clearly show that the muscles are not essential for loud sounds, a result very similar to those with cock crows. Our results with chicks and adult fowl, however, suggest that the softer vocalizations of songbirds might be more severely affected: the lower air pressures associated with these softer calls would be less likely able to bow the vocal membranes into the air stream sufficiently to produce sound. This would be consistent with the demonstrated roles of the extrinsic muscles in other forms and with their persistence in song birds.

In conclusion, we suggest that the vocal mechanisms of songbirds share the basic respiratory-pump and extrinsic syringeal muscle controls that are present in chickens. Superimposed upon this, they have evolved further syringeal muscles and structures that seem to increase greatly their vocal efficiency (Gaunt and Wells 1973, Brackenbury 1979) and range of frequencies (Greenewalt 1968).

ACKNOWLEGMENTS

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LABORATORY STUDIES OF FORAGING IN FOUR BIRD SPECIES OF DECIDUOUS WOODLAND

VIRGINIA PIERCE[1] AND THOMAS C. GRUBB, JR.[2]
Department of Zoology, The Ohio State University, Columbus, Ohio 43210 USA

ABSTRACT.—In an indoor aviary containing 60 American elm branches of 6 different diameters (0.5, 1.0, 2.5, 5.0 ,10.0, 20.0 cm), Carolina Chickadees, Tufted Titmice, male and female White-breasted Nuthatches, and male and female Downy Woodpeckers were allowed to forage singly under controlled circumstances. Each species had a particular and unique preference for branch size and branch surface. Variation occurred among the individuals of each species or sex, and differences between the sexes were found in branch sizes used by woodpeckers and branch surfaces selected by woodpeckers and nuthatches. Nuthatches alone seemed partially to select branch size by total available surface area; they also showed the greatest diversity in use of the three branch surfaces (top, sides, bottom). Differences among species in their use of different branch sizes and surfaces and in the extent to which their behavior changed with experience generally supported Morse's (1974) hypothesis that socially subordinate species are behaviorally more plastic in thier foraging and occupy a broader fundamental niche. *Received 29 February 1980, accepted 8 October 1980.*

WHY do birds look for food the way they do? In studies of wild birds in nature, various workers have shown that foraging behavior can be controlled by variation in food distribution and abundance (e.g. Gibb 1954, Charnov et al. 1976), habitat type (Morse 1970), weather (Grubb 1975, 1977, 1979; Austin 1976), interspecific social environment (Morse 1974), season of the year (Travis 1977), and time of day (Rubenstein et al. 1977). How proximity of predators might influence avian foraging has not been studied systematically, but foraging activity in other taxa (e.g. crayfish, Stein and Magnuson 1976; fish, Milinski and Heller 1978) changes in the presence of predators. An important consideration is that each of these studies emphasizes only one or two of the many environmental factors that might be influencing foraging but does not control any of the others.

Concurrently, a large literature has accumulated concerning the ways by which avian communities partition resources (e.g. Willis 1966; Root 1967; Cody 1968, 1974; Willson 1970; Austin and Smith 1972; Alatalo and Alatalo 1979). The general thrust of these studies has been to explain such competition-reducing mechanisms among species as horizontal and vertical stratification of foraging sites, temporal differences in foraging activity, variation in foraging rates, and disparities in parts and sizes of vegetative substrates used. Such works about competition and realized niches (*sensu* Hutchinson 1957) have usually not considered the likelihood that factors other than the composition of their foraging guild could significantly control the food-seeking techniques of species.

Field observations of avian foraging behavior could be confounded by such uncontrolled variables as sex, age, presence of conspecifics and competitor species, hunger state, food distribution and abundance, habitat type, weather, proximity of

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[1] Present address: Department of Biology, University of Pennsylvania, Philadelphia, Pennsylvania 19104 USA.

[2] Send reprint requests to second author.

predators, time of day, and season of the year (Grubb 1979). Laboratory studies present the opportunity to control such variables, and the more elegant of these have offered birds different quality foods (Gass 1978) or food hidden in different places (Partridge 1976a, b).

The winter foraging behavior of four species resident in Ohio woodlands, the Carolina Chickadee (*Parus carolinensis*), Tufted Titmouse (*P. bicolor*), White-breasted Nuthatch (*Sitta carolinensis*), and Downy Woodpecker (*Picoides pubescens*), was studied in an indoor aviary in which all the above variables, except age and, in two species, sex, were known and controlled. Records were taken on branch sizes and branch surfaces (top, sides, bottom) selected by a bird searching for food.

The objectives of this study were to determine: (1) whether individuals within a species (chickadee and titmouse) or within a sex (nuthatch and woodpecker) differ in their foraging behavior; (2) whether sexes of a species differ in foraging; (3) whether species differ in their foraging behavior; (4) whether species select substrates on which to forage on a random basis or choose particular substrates; and (5) whether foraging changes with time in the absence of food reinforcement.

MATERIALS AND METHODS

Between 16 January and 1 March 1978, 10 Carolina Chickadees (CC) and 10 Tufted Titmice (TT) were captured in hardware-cloth treadle traps. Ten male and 10 female White-breasted Nuthatches (WBN) and 7 male and 7 female Downy Woodpeckers (DW) were captured between 3 January and 10 March 1979, using radio-controlled traps and Graves tree traps, respectively. Only 4 male and 4 female woodpeckers could be tested because of deaths during confinement (2 males) or refusal to forage in the aviary.

Chickadees and titmice cannot be sexed externally, and the birds in this study were not sacrificed or laparotomized, so for analysis the chickadees were considered one group, the titmice another, and the nuthatches and woodpeckers were divided into male and female groups. All birds tested were at least 6 months old and had had at least 8 weeks' experience foraging in deciduous woods during the no-leaf season.

Each bird was observed singly in an aviary constructed in a windowless cement-block building on The Ohio State University campus, Columbus, Ohio. Aluminum pipes formed the supports of the 3.1 × 4.3 × 2.8-m-high aviary, which was enclosed with polypropylene netting and lined with opaque black plastic. Two rows of three 40-W fluorescent lights provided illumination inside the aviary. At one end of the aviary was a 3.1 × 1.0 × 2.8-m-high annex, separated from the main aviary by netting only; its outside walls were also lined with plastic. A 5-cm × 3.1-m American elm (*Ulmus americana*) branch extended across the annex 1.5 m from the floor and could be seen but not reached by birds in the main chamber. The annex was empty throughout this study, but we anticipate using it in future studies when it will hold conspecifics, competitors, or predators.

The "habitat" inside the aviary consisted of 60 0.75-m-long American elm branches suspended on strings from the ceiling at 45° angles with their midpoints 0.9 m from the floor (Fig. 1). All branches were cut from live trees after leaf-fall in 1977. Six branch diameters were employed, measured midbranch: 0.5 cm (n = 15), 1.0 cm (n = 15), 2.5 cm (n = 9), 5.0 cm (n = 9), 10.0 cm (n = 6), and 20.0 cm (n = 6). Each branch was randomly assigned a position in a 5 × 12 matrix and a left or right 45° inclination. Further characteristics of the branches are shown in Table 1.

Inside the aviary, the "weather" conditions of temperature, light intensity, wind, and precipitation were held constant or within narrow ranges, and food, conspecifics, competitors, and predators were absent. Temperature in the aviary ranged from 23–28°C for the chickadees and titmice and from 19–23°C for the nuthatches and woodpeckers. To ensure that the aviary was devoid of prey items, we carefully examined each branch and removed from bark crevasses the insect adults, larvae, and eggs we found. Then we let pretest birds of each species search the branches for 2 h. No bird was seen to find any food during testing.

To standardize hunger, each bird was fasted for 1–2 h after capture, with water *ad libitum,* then introduced singly into the aviary between 0900 and 1200. The longer fasting times occurred when two birds were tested in one morning. As fasting intervals were similar for all species, the effect of food

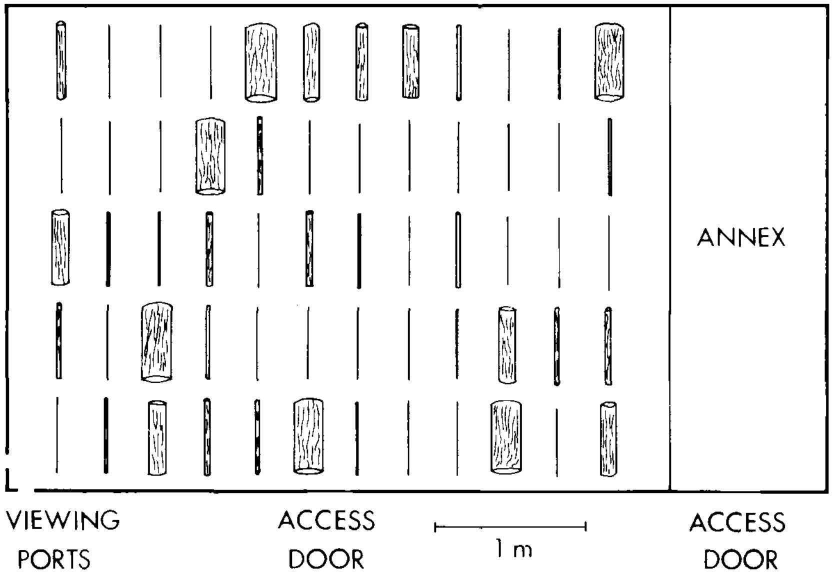

Fig. 1. Overhead view of the aviary showing the 60 branches of six diameter classes. Ceiling lights and the strings supporting branches are not shown. Although the branches appear horizontal in the figure, they were hung at 45° angles (see text).

deprivation was probably more severe for chickadees, which weighed about 10 g, than for the nuthatch (about 21 g), titmouse (about 24 g), or woodpecker (about 25 g). The chickadees and titmice were tested on the day of their capture; nuthatches and woodpeckers were held overnight and tested the following morning.

Behavior in the aviary was observed through two 1 × 5-cm slits in the plastic lining, and observations were tape-recorded at a whisper. Birds appeared unaffected by our presence during their testing. After a bird had landed on the branches 200 times, or after 60 min, it was removed from the aviary, weighed, banded, and released at the site of its capture. Each individual was used only once. After each test, bark flakes dislodged from the branches by the foraging bird were removed by vacuuming the cement floor of the aviary.

For each branch on which a bird looked for food, records were taken on diameter class and branch surface (top, sides, or bottom). Branches were divided visually into top, side and bottom quadrants, where the top side faced the ceiling and the bottom side faced the floor. A bird was recorded as foraging in one of the quadrants when its head and feet were in that quadrant. The landing point on each branch was taken as the measure of a bird's preference for foraging site. When, periodically, a forager moved around a branch to search for prey in an additional quadrant, this behavior was not recorded. Thus, our records of branch surface selection are subject to some degree of error.

Analyses were accomplished using Chi-square tests (Runyon and Haber 1971), and we accepted significance at the 0.05 level.

TABLE 1. Characteristics of the American elm branches in the aviary.

Diameter (cm)	Number	Total length (m)	Length ratio	Total surface area (m^2)	Area ratio
0.5	15	11.25	2.5	0.18	1.0
1.0	15	11.25	2.5	0.35	1.9
2.5	9	6.75	1.5	0.53	2.9
5.0	9	6.75	1.5	1.06	6.0
10.0	6	4.50	1.0	1.41	8.3
20.0	6	4.50	1.0	2.83	17.8

RESULTS

Within 2 min of their introduction into the aviary, the nuthatches and woodpeckers commenced searching the branches for food. Chickadees and titmice delayed somewhat longer, but all began foraging within 15 min. Detailed descriptions of each bird's foraging behavior may be found in Pierce (1979).

Differences among individuals.—During the course of 200 landings, the 10 Carolina Chickadees selected significantly different sets of branch sizes ($P < 0.01$). Members of this species also differed significantly in the proportions of landings on sides and bottoms of branches (the two branch-surface categories were lumped because they were so seldom used) and on the tops ($P < 0.01$; Table 2).

Significant differences in branch size selection occurred among the 10 Tufted Titmice ($P < 0.01$). As all 10 titmice virtually ignored the sides and bottoms of the branches, there were no significant differences among individuals in surfaces scanned for food ($P > 0.30$; Table 2).

Viewed intrasexually, individual male White-breasted Nuthatches selected significantly different sets of branch sizes ($P < 0.01$), as did the females ($P < 0.01$). Because several nuthatches moved too rapidly for us to record their branch surface selections accurately, we have complete records for only seven males and eight females of this species. During 200 landings on branches, the seven male nuthatches showed no significant variation in selection of branch surfaces ($P > 0.30$). By contrast, female nuthatches differed significantly in their choices of branch surfaces ($P < 0.01$; Table 2).

Individual male Downy Woodpeckers selected significantly different sets of branch sizes ($P < 0.01$), as did individual females ($P < 0.01$). Male ($P < 0.01$) and female ($P < 0.01$) woodpeckers also differed intrasexually in selection of branch surfaces (Table 2).

Differences between sexes.—There were no significant differences in branch size selection by male and female nuthatches ($P > 0.50$). The sexes varied significantly in their use of branch surfaces ($P < 0.01$), however, the males preferring the bottoms and the female preferring the sides (Fig. 2).

Male and female Downy Woodpeckers differed significantly in branch size selection ($P < 0.01$). The cells for 5- and 20-cm branches in the Chi-square contingency table contributed 92%of the χ^2 value, indicating strong sexual variation in preference for these branch sizes. Females used the 5-cm branches and males the 20-cm branches much more than did the opposite sex. The sexes also differed in their use of branch surfaces ($P < 0.01$), with the males spending more effort on sides and bottoms.

Differences among species.—Intraspecific variation notwithstanding, the four species selected branch sizes that differed significantly in the aggregate ($P < 0.01$). Examination of the values in the 4 (species) × 6 (branch sizes) contingency table showed that each species used one unique size markedly more than expected. These pairings, evident in Fig. 3, were Carolina Chickadee—1.0 cm, Tufted Titmouse—2.5 cm, Downy Woodpecker—5.0 cm, and White-breasted Nuthatch—20.0 cm.

There was considerable variation among the four species with respect to use of the three surfaces of the branches ($P < 0.01$; Fig. 2). Responses ranged from the nearly total dependence on branch tops by the titmouse to only about two-thirds of landings there in the nuthatch.

Table 2. Branch surfaces selected by each individual Carolina Chickadee, Tufted Titmouse, male and female White-breasted Nuthatch, and male and female Downy Woodpecker, shown as percentages of landings.

Species	Branch surface	Individual										χ^2 (df)	*P*
		1	2	3	4	5	6	7	8	9	10		
CC	Top	85	87	93	92	93	90	87	99	92	98	45 (9)	<0.01
	Sides	12	8	6	7	6	7	11	1	7	2		
	Bottom	3	5	1	1	1	3	2	0	1	0		
TT	Top	100	99	100	100	100	99	100	100	99	98	10 (9)	>0.30
	Sides	0	1	0	0	0	1	0	0	0.5	2		
	Bottom	0	0	0	0	0	0	0	0	0.5	0		
♂ WBN	Top	61	69	70	69	65	65	66				5 (6)	>0.30
	Sides	24	25	26	24	26	23	25					
	Bottom	15	6	4	7	9	12	9					
♀ WBN	Top	62	77	69	74	71	39	54	48			109 (7)	<0.01
	Sides	29	20	25	20	24	38	32	41				
	Bottom	9	3	6	6	5	23	14	11				
♂ DW	Top	58	75	62	69							15 (3)	<0.01
	Sides	30	22	27	28								
	Bottom	12	3	11	3								
♀ DW	Top	96	87	72	74							35 (3)	<0.01
	Sides	4	12	25	21								
	Bottom	0	1	3	5								

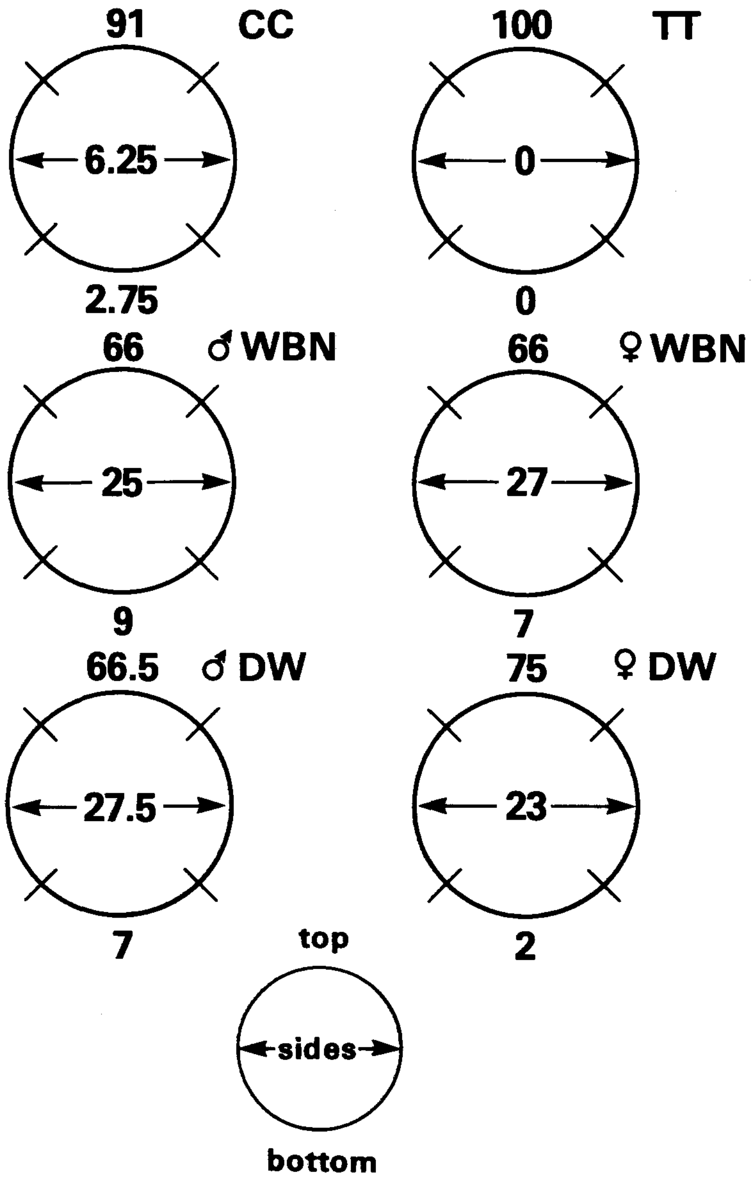

Fig. 2. Branch surfaces selected by Carolina Chickadees, Tufted Titmice, White-breasted Nuthatches, and Downy Woodpeckers.

Comparison with random selection.—If these four species normally forage without preference for particular branch sizes, branch-size selection in the aviary should have been proportional to the total lengths or total surface areas of the six branch sizes. Branch length and surface area ratios are given in Table 1. For each of the four species the distribution of landings differed significantly from that expected based on total lengths of the various branch sizes ($P < 0.01$; Fig. 4). Chi-square comparisons of landings expected from the ratio of branch surface areas with those

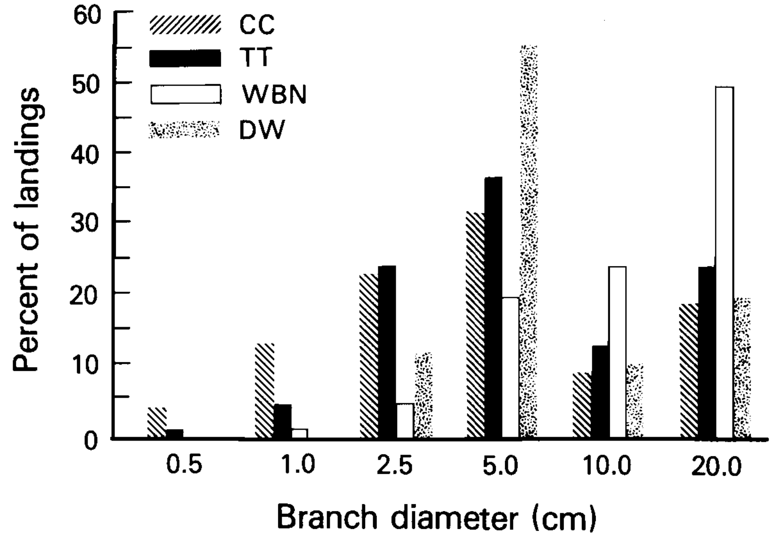

Fig. 3. Branch sizes selected by Carolina Chickadees, Tufted Titmice, White-breasted Nuthatches, and Downy Woodpeckers, shown as median percentages of the total landings.

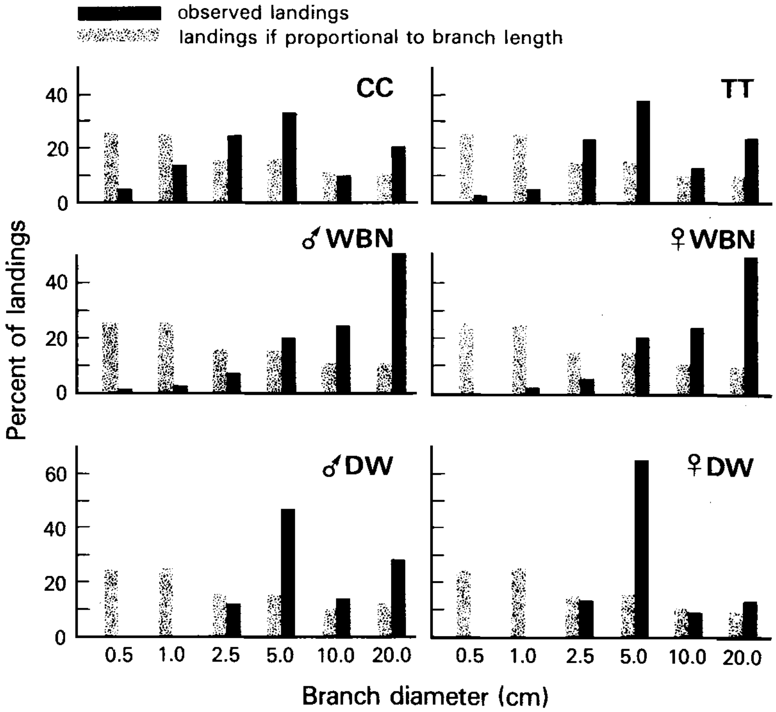

Fig. 4. Comparison of observed selection of branch size, shown as percentages of all landings, with that expected if landings had been proportional to branch lengths.

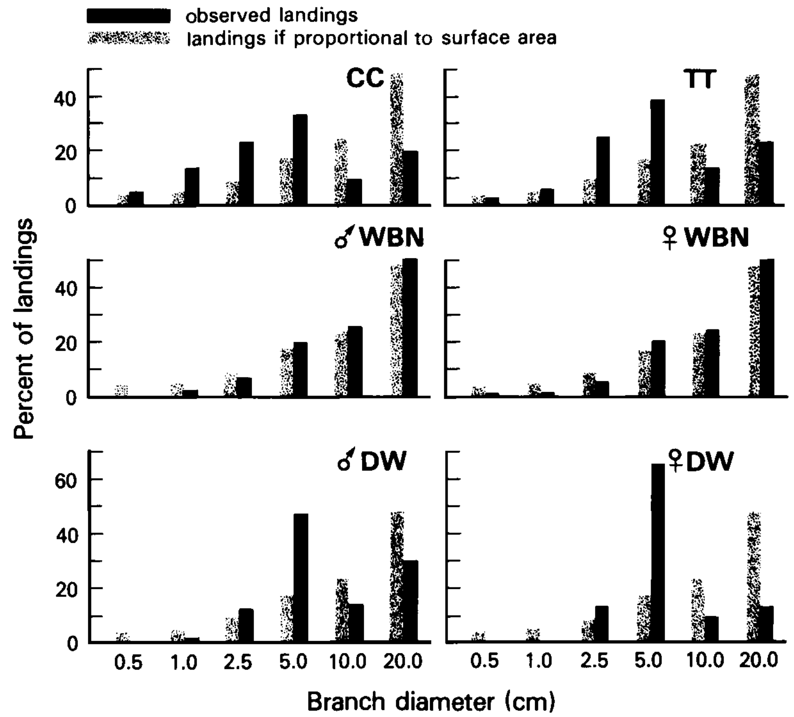

Fig. 5. Comparison of observed selection of branch size, shown as percentages of all landings, with that expected if landings had been proportional to branch-surface area.

observed also showed statistical significance for all species (P's < 0.01). While it is clear from Fig. 5 that chickadee, titmouse, and woodpecker landings in no way resemble the proportions of surface areas, however, the nuthatch landings do. We found in the contingency table for this last species that 72% of the χ^2 value came from the cells for 0.5- and 1.0-cm branches. Figure 5 also suggests that, while they avoided these small branch sizes, the nuthatches used the four larger diameters proportional to their surface areas.

If the birds had no foraging preference for a particular branch surface, landings should have been proportional to the relative areas of tops (25%), sides (50%), and bottoms (25%). This was clearly not the case, as over the course of 200 landings all four species preferred to forage on the top surfaces (all P's < 0.01; Fig. 6).

Variation with experience.—As the branches were devoid of prey, it was possible to determine, by comparing use of the six branch sizes during the first and last sets of 50 landings, whether birds responded to the lack of food reinforcement by changing their selection of branch sizes and surfaces. The chickadees, titmice, and nuthatches all significantly changed their branch-size preferences between landings 1–50 and 151–200 (P's < 0.01). These species moved with experience toward the large diameters (Fig. 7). By contrast, branch-size selection in the Downy Woodpecker appeared unaffected by experience ($P > 0.50$).

The χ^2 values obtained (df = 5) can be used to compare the magnitude of the

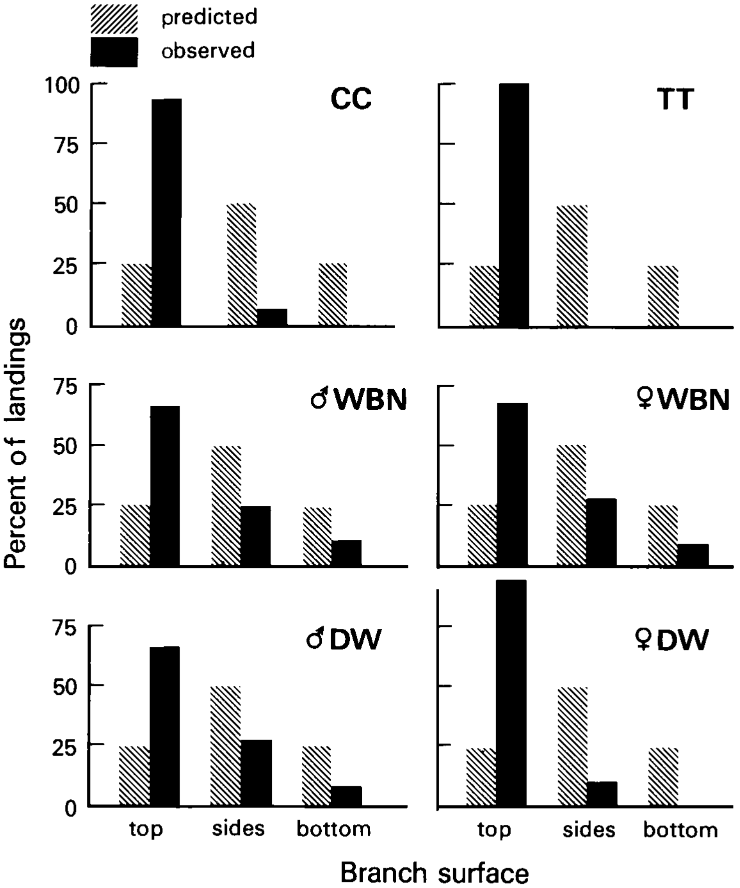

Fig. 6. Comparison of the observed percentages of landings on the three branch surfaces with percentages expected if birds had been responding proportional to available surface area.

shift with experience in the four species: these were 96, 49, 34, and 4, respectively, in the chickadee, nuthatch, titmouse, and woodpecker.

Changes in branch-surface preferences between landings 0–50 and 151–200 could be analyzed only for three species; titmice virtually ignored branch bottoms and sides (Fig. 3), so for this species the condition of the Chi-square procedure that all cells have expected values greater than or equal to 5 when df = 1 could not be met (Runyon and Haber 1971). Chickadees and woodpeckers shifted their preference for foraging surface significantly (*P*'s < 0.01; Fig. 8), but the nuthatch did not ($P > 0.50$; Fig 8). Chi-square values of 15, 10, and 0.18 for the chickadee, woodpecker, and nuthatch, respectively, indicate the magnitude of the shift in branch-surface preference for each species.

DISCUSSION

Individual differences.—Except for branch-surface selection by titmice and male nuthatches, significant differences occurred among the birds of each sex and each species in use of branch sizes and surfaces. This result is of interest, because field

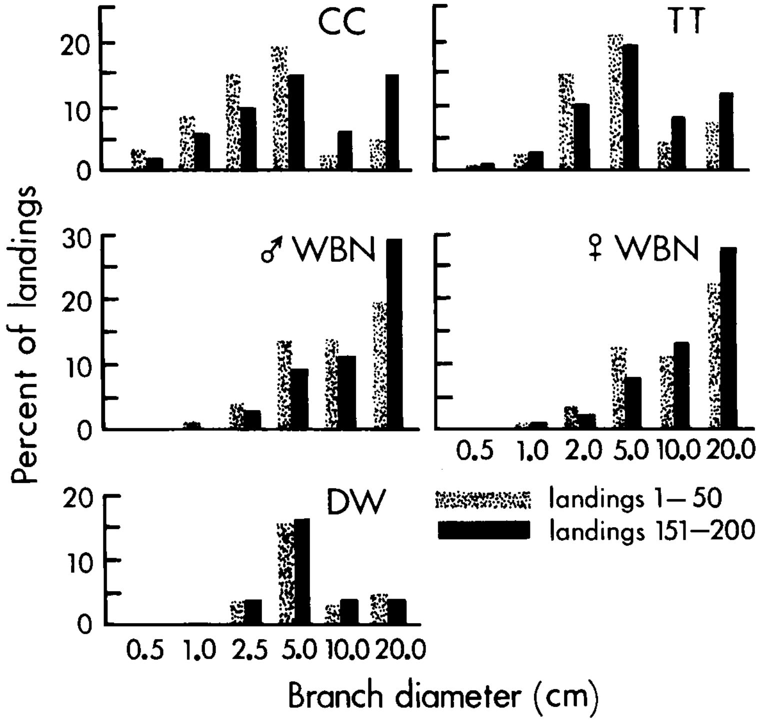

Fig. 7. Comparison of branch sizes selected during the first 50 and last 50 landings of Carolina Chickadees, Tufted Titmice, White-breasted Nuthatches, and Downy Woodpeckers.

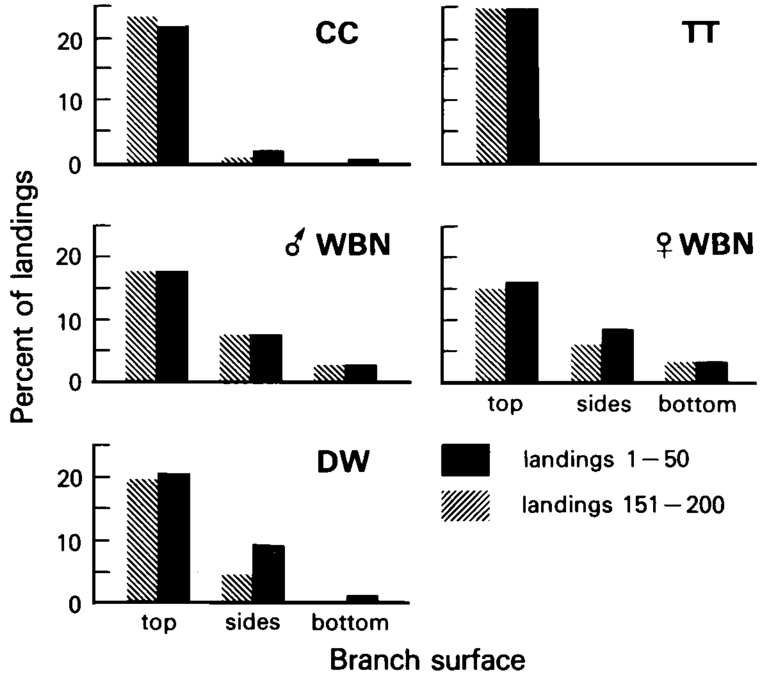

Fig. 8. Comparison of foraging on the three branch surfaces in the first 50 and last 50 landings of Carolina Chickadees, Tufted Titmice, White-breasted Nuthatches, and Downy Woodpeckers.

studies of avian foraging routinely deal with individually unidentified birds and lump all sightings of a species for analysis (but see Holmes et al. 1978). Several factors may have contributed to these individual differences. Although an attempt was made to standardize hunger state, the amount of food chickadees and titmice had ingested before capture was unknown, and the length of the pretrial holding period varied from 1–2 h. There appears to be no evidence of how hunger state might influence foraging of free-ranging birds, but food deprivation does seem to affect the behavior of Pigeons (*Columbia livia*) and Chickens (*Gallus gallus*) (e.g. Levine 1974).

From field studies of readily sexed birds, we know that males and females can differ in such foraging techniques as branch-size selection (e.g. Downy Woodpeckers, Jackson 1970, Kilham 1970, Kisiel 1972, Williams 1975; and White-breasted Nuthatches, McEllin 1979). Carolina Chickadees and Tufted Titmice cannot be sexed externally, and, as the birds were not sacrificed or laparotomized, the question remains whether sex differences contributed to the observed variations among individuals in the two parids.

In some quite different birds, foraging techniques and success change with age (e.g. pelicans, Orians 1969; herons, Recher and Recher 1969). All the animals we tested were at least 6 months old and had had at least 8 weeks' experience foraging in deciduous woods during the no-leaf season. They could not be aged, however, and the possibility exists that birds of the year may have differed behaviorally from their elders.

Differences between sexes.—The nuthatch sexes selected the same proportions of branch sizes in our aviary, while McEllin's (1979) field results show males foraging on large diameter substrates and females on smaller branches. Because our birds foraged alone, while McEllin's did so in the company of the opposite sex, social dominance effects may account for the disparity.

In the aviary, the Downy Woodpecker sexes differed significantly in branch-size selection, with females using small (5 cm) and males the largest (20 cm) branches. Field studies (Jackson 1970, Kilham 1970, Kisiel 1972, Grubb 1975, Williams 1975) in other parts of North America have found sex-specific foraging in this species, but with males, not females, preferring smaller substrates. While our small sample size calls for caution in interpreting our laboratory results, we do note that also in the congenic Three-toed Woodpecker (*Picoides tridactylus,* Hogstad 1976) males use large substrates and females the smaller ones. We are currently examining the behavior of free-ranging Downy Woodpeckers here in Ohio (Peters and Grubb in prep.), with an eye to resolving this inconsistency between laboratory and field results.

Differences between species.—Partridge (1976b) watched isolated Blue Tits (*Parus caeruleus*) and Coal Tits (*P. ater*) search for food items contained in five types of artificial containers arranged on an indoor experimental tree made of dowels. The deciduous-dwelling Blue Tits and the conifer-dwelling Coal Tits have different foraging techniques in the field and maintained those differences in her laboratory study. Each species preferred to use the foraging technique that it employs in the field, and each was more efficient than the other at its preferred foraging technique.

The behavior of the four species we studied in controlled surroundings lends additional support to the model that avian species living together have different inherent preferences. Each species specialized more than expected on a different branch size, and the four used different proportions of branch sides and bottoms.

Morse (1974) hypothesized that interspecific social behavior is an important determinant of fundamental niche (*sensu* Hutchinson 1957) breadth. He proposed that social dominance among species frequently plays a major role in resource partitioning among mobile animals, that subordinates have considerably broader fundamental niches than their dominants, and that specialist dominants and high levels of niche overlap should result in guilds whose members show an inverse relationship between dominance rank and fundamental niche breadth.

The interspecific dominance hierarchy in this guild is Downy Woodpecker > White-breasted Nuthatch > Tufted Titmouse > Carolina Chickadee (Morse 1970). If we assume that a broad fundamental niche is indicated by a large number of preferred branch sizes and wide use of all branch surfaces, then this study supports Morse's hypothesis (Fig. 2). The parids displayed the most attributes of species with a broad fundamental niche and are subordinate to the nuthatches and woodpeckers. The blurring of distinctions with regard to niche size between the two parids and between the nuthatches and woodpeckers may have resulted from the absence of social influence while the tests were conducted.

Differences from random foraging.—Our statistical procedure indicated that all four species actively selected certain branch sizes and surfaces on which to forage. Results for the White-breasted Nuthatch (Fig. 5), however, lead us to an alternative premise, that, while this species avoids branch sizes $\leqq 1$ cm in diameter, it uses all larger substrates in proportion to the abundance of their surface areas in the habitat.

In a temperate deciduous woodland, large diameter tree trunks and branches may comprise the greatest proportion of available surface area for foraging. For species such as American elm, tulip (*Liriodendron tulipifera*), oaks (*Quercus* spp.), and box elder (*Acer negundo*) bark furrowedness may be an important cue to the foraging insectivorous bird (Travis 1977). The rough-barked surfaces of trees are important places for insect larvae to overwinter (MacLellan 1959), and the significance of bark crevices as food sources for the Downy Woodpecker has been discussed by Jackson (1970) and Travis (1977). Nuthatches cache food in bark crevices (Bent 1948); perhaps bark furrowedness, as well as surface area, would be selected by nuthatches. Although no precise measurements were made of bark furrowedness, the relative abundance and depth of crevices seemed to increase with increasing branch diameter.

In nature it is not possible to ascertain whether use of a particular branch size differs from random or whether branch size selection is affected by social pressure from more dominant species in a foraging guild. Thus, comparison of the branch-size preferences demonstrated in this study with those reported from field observations may be informative.

The chickadees' avoidance of 0.5-cm branches was unexpected, because during the winter in Ohio woodlots this species uses substrates less than 1 cm almost exclusively (Grubb unpubl.). Extensive use of twigs by chickadees in nature may occur only because twigs are so abundant relative to larger diameter branches. Also, in nature, chickadees may be forced from preferred 1.0- and 2.5-cm branches by social pressure from the larger, dominant Tufted Titmouse (Morse 1970).

Willson (1970) reported greater use of small branches (<7.5 cm) by free-ranging White-breasted Nuthatches than occurred in our study, although in both cases large (>7.5 cm) branches were preferred. We do not know the relative abundances of various branch sizes in Willson's study area, however.

Differences with experience.—With lack of food reinforcement from the branches, all four species changed foraging preferences for the various branch sizes or surfaces. That subordinates should show more plasticity of behavior was among Morse's (1974) predictions of the effect of social dominance on foraging. If shifts in substrate preferences shown by the birds in this study are appropriate measures of behavioral plasticity, Morse's prediction is partially upheld. The magnitudes of the χ^2 values generated from comparison of branch-size selection between landings 0–50 and 151–200 show that, as predicted, the subordinate chickadee's searching behavior was most responsive to experience, the dominant woodpecker's foraging was least labile, and the nuthatch and titmouse were intermediate. The subordinate chickadee also changed branch-surface selection most with experience. While the reversal in plasticity of surface selection between the nuthatch and woodpecker was counter to prediction, the small number of woodpeckers tested could have been responsible.

The degree of correspondence between behavior in the artificial environment of our aviary and that of free-ranging birds is open to question. It is clear that additional field study checking the validity of these laboratory findings will be necessary.

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FORAGING BEHAVIOR OF THE RED-COCKADED WOODPECKER IN SOUTH CAROLINA

ROBERT G. HOOPER AND MICHAEL R. LENNARTZ
USDA Forest Service, Southeastern Forest Experiment Station, Department of Forestry, Clemson University, Clemson, South Carolina 29631 USA

ABSTRACT.—Foraging Red-cockaded Woodpeckers (*Picoides borealis*) selected live pines (96% use; 71% availability) over hardwoods (1% use; 25% availability). Use of recently dead pines (3%) was the largest departure from use of live pines. Mast was rarely consumed, although abundant at times. Live pine stems greater than 23 cm in diameter at breast height represented only 19% of the available pines but received 65% of the use. The sexes exhibited strong divergence in foraging behavior. Most important was the partitioning of foraging sites on live pines. Males foraged on dead and live limbs of the crown and midtrunk 54% of the time and females only 4%. On the lower trunk, females foraged 38% of the time and males only 3%. On the midtrunk, females foraged 29% and males 12%. On the trunk-in-crown, females foraged 28% and males 32%. Mean foraging height of males was 14.1 m and that of females 8.7 m ($P < 0.001$). The sexes used tree sizes, tree types, and methods for capturing prey with similar frequencies. Within each sex, there were between-season differences in use of foraging sites and in methods used at each site. *Received 9 July 1980, accepted 5 January 1981.*

ENDEMIC to mature pine forests of the southeastern United States, the Red-cockaded Woodpecker (*Picoides borealis*) is considered endangered due to loss of nesting habitat. Its use of mature, live pines for nesting and roosting cavities is well known (Jackson et al. 1979). The scarcity and decline of suitable pines for cavity excavation is the major reason the species was classified as endangered (Federal Register, 13 October 1970, 35, 199: 16047). Red-cockadeds also use large areas of 30–100 ha and more of pine and pine-hardwood forests for foraging (Baker 1971a, Skorupa and McFarlane 1976, Wood 1977, Nesbitt et al. 1978, Sherrill and Case 1980, Hooper pers. obs., G. W. Wood pers. comm.). Because of the extensive areas used for foraging and the fact that forest management continually alters foraging habitats, information on the species' foraging behavior is critical to its management and prospects for survival.

We report year-round observations made on foraging Red-cockadeds in coastal South Carolina. Prior to our work, Ligon (1968) studied foraging behavior of the Red-cockaded in Florida, and Morse (1972) looked at foraging during winter in Louisiana. Contemporaneously with our study, Skorupa (1979) and Ramey (1980) examined year-round foraging behavior in South Carolina and in Mississippi and South Carolina, respectively.

METHODS

Study area.—The study was conducted on the Francis Marion National Forest, Berkeley County, in coastal South Carolina. This area was chosen because of its large population of Red-cockaded Woodpeckers, an indication of good habitat. Oscar Stewart (pers. comm.) estimates at least 400 breeding groups on about 64,000 ha of habitat. Hooper (pers. obs.) found 22 groups on 1,000 ha, the most dense population thus far examined. The study area was also chosen for its diversity of habitat. Pine stands were interspersed with mixed stands of gum (*Nyssa* spp.), cypress (*Taxodium* spp.), oaks (*Quercus* spp.), red maple (*Acer rubrum*), and other species. Loblolly (*Pinus taeda*) and longleaf (*P. palustris*) were the most common pines. Since 1944, the pine stands have been periodically control burned; they have been under even-age timber management since 1950. Ages of pine stands ranged from less than 1 to 100 yr.

Sampling of foraging behavior.—From early May 1976 to mid-March 1977 we quantified foraging behavior of 6 adult females, 6 breeding males, and 3 adult helper males in 6 separate groups. Red-cockaded groups are family units consisting of a mated pair, their offspring of the year, and, in some groups, auxilliary adult male helpers. All birds were uniquely marked with colored plastic leg bands. Although four of the groups had juvenile birds during at least part of the study period, we collected data only on adults. Red-cockadeds with little or no human contact respond to human presence and act wildly. The birds we studied were conditioned by periodic exposure to humans, however, and we do not believe our presence affected foraging behavior.

An electronic metronome, modified from Wiens et al. (1970), giving an audible tone each minute, was used to determine a possible instant for recording foraging behavior. Recordings were seldom made every minute for any extended period, because movement of the birds created problems in identifying bands. Red-cockadeds commonly foraged at several sites on the same tree and changed both foraging height and method as they moved over the tree. Direct contact was temporarily lost with specific birds when we measured foraging heights and tree diameters. Also, foraging was frequently interrupted by other behavior, and considerable time was involved merely in following and maintaining contact with the birds. If we had identified a bird and could judge its activity at the tone, we recorded the following: (1) foraging method, (2) foraging site, (3) foraging height measured with range finder and clinometer, (4) tree species, (5) tree condition, and (6) tree diameter at breast height (dbh, 1.4 m) measured with a caliper. A total of 3,172 observations was made on 69 different days. An average of 17 and maximum of 81 observations per bird were made per day. A group was followed for several hours each day, and observations were spread throughout the period.

Analyses.—Because several observations were made of the same bird on a given day, we cannot assume all observations to be independent. Consequently, only subsets of observations assumed to be independent were used for statistical comparisons. The subsets of observations assumed to be independent were derived as follows. Table 1 and Fig. 1 are based on one foraging observation for each individual tree used for foraging (about 50% of the total observations). Subsequent or additional foraging observations from the same tree are not included. Chi-square tests were made on numerical values, not the percentages shown in Table 1 and Fig. 1. Data in Table 2, and associated comparisons on foraging heights and diameters made in the text, were derived by randomly selecting one observation for a male and one for a female for each of the 69 sample days (about 4% of the total observations). Because such data are commonly treated as independent observations, we made χ^2 and t-tests on these data in numerical form. Cells with zero entries were deleted for χ^2 tests. Division of the total observations for other comparisons results in samples too small to compare reliably with the χ^2 test. Thus, in Figs. 2, 3, and 4 and Tables 3, 4, and 5 and for some means in the text, we included our total observations and presented the frequency data without statistical comparisons.

We calculated overlap in foraging behavior of males and females with Schoener's (1970) equation:

$$\% \text{ overlap} = 100(1 - 0.5\,\Sigma\,|P_{x,i} - P_{y,i}|),$$

where $P_{x,i}$ and $P_{y,i}$ are the respective frequencies for males and females in each class for a given type of behavior. An overlap of 100% indicates that the sexes acted identically in regard to the type of behavior examined, whereas 0% overlap indicates completely different behavior.

General observations.—From May 1976 to April 1979, we followed the activity of birds in 18 different groups (6/yr) for 2,300 h. These observations served as a check on the validity of our sampling of apparently rare foraging behavior, e.g. use of hardwoods, fruit, and water.

Tree availability.—We determined the density of trees within the six territories used for the quantitative study. Vegetation was stratified into stands of similar species composition, age, and density. Depending on stand size, 3–20 plot centers were located systematically from a random starting point. At each plot center, stems equal to or greater than 3 to less than 13 cm dbh were recorded by species and dbh on a 0.02-ha plot. Stems equal to or greater than 13 cm dbh were sampled with a 1-m factor wedge prism. Trees selected by the prism were recorded by dbh and species. Availability values in Table 1 and Fig. 1 were adjusted by multiplying the number of stems for each diameter class or tree type in a territory by the proportion of foraging observations made in the territory.

RESULTS

Comparison of breeding and helper males.—Two groups we studied had helper males in addition to breeding males. A comparison of breeding and helper males showed nearly identical foraging behavior. The mean sizes of live pines selected by

TABLE 1. Types of trees ($\geq$13 cm dbh) used by foraging Red-cockaded Woodpeckers and availability of trees ($\geq$13 cm dbh) in the territories, May 1976–March 1977.

		Pine		Hardwood		Cypress
Sex	n	Live	Dead	Live	Dead	Live
		Percent of stems selected[a]				
Female	944	96.0	3.4	0.3	0.0	0.2
Male	756	96.0	2.9	0.9	0.0	0.1
		Percent of stems available[b]				
	21,861[c]	71.3	2.8	24.6	0.4	1.9

[a] No significant difference in the frequency with which males and females foraged on live and dead pines ($\chi^2 = 0.3$, $P > 0.50$). Overlap in use of tree types by sexes = 99%.

[b] Sexes pooled, dead hardwoods and cypress excluded: the frequency with which tree types were selected differed significantly from the availability of tree types ($\chi^2 = 584.7$, $P < 0.0001$).

[c] Value is adjusted n, see text. Actual estimate of total number of stems in the six territories was 143,157.

breeders and helpers were 28.1 cm (n = 172) and 28.3 cm (n = 108), respectively. Foraging heights were 13.9 m and 14.3 m for breeders and helpers. Use of sites on live pines for breeders and helpers were: limbs = 58% and 58%; trunk-in-crown = 27% and 28%; mid-trunk = 13% and 12%; lower trunk = 2% and 2%. We thus lumped data on breeding and helper males in all the following comparisons.

Trees selected for foraging.—Red-cockadeds showed a strong preference for living pines as a foraging substrate (Table 1). Although there were only 3 times more live pines than live hardwoods within the territories, pines were selected 163 times more frequently than hardwoods. If observations made after the quantitative study are included, Red-cockadeds foraged 18 times on oaks, 7 on gum, and 2 on sweetgum (*Liquidambar styraciflua*). Cypress was rarely foraged upon by the six groups in the quantitative study (Table 1). Later, for 140 h, we followed a group that spent about 12% of its foraging time on cypress. That group had considerably less pine available than groups we observed during the quantitative study.

Males and females foraged on living pines with similar mean diameters of 29.5 cm and 29.8 cm, respectively (df = 136, $t = 0.2$, $P > 0.5$). There was no difference in the frequency with which tree sizes were used by the sexes (Fig. 1). Both sexes showed a strong preference for pines greater than 23 cm dbh and avoidance of pines less than 13 cm (Fig. 1). Red-cockadeds generally avoided stands of trees with diameters less than 11 cm and foraged on trees of that size mostly in stands of larger trees.

The next most frequently used trees were dying or recently dead pines, most of which had been struck by lightning (Table 1). Most of these trees still had dead needles and bark. Dead pines with extensively exposed wood were avoided, except once when three birds foraged on a long-dead pine that had only 50% of its bark. The frequency of use of live and dead pines was similar for males and females (Table 1).

Foraging sites.—Combining all seasons or sampling periods, we found that males and females foraged at different sites on live pines with strikingly different frequencies (Table 2). Males spent a major part of their foraging time (58%) in the crown and generally avoided the lower trunk, where females did 38% of their foraging. Although both sexes used the midtrunk frequently (males, 39% of the time; females, 32%), each tended to select different specific foraging sites within that zone. Males foraged more on limbs (28%) than on the trunk (12%), while females foraged more

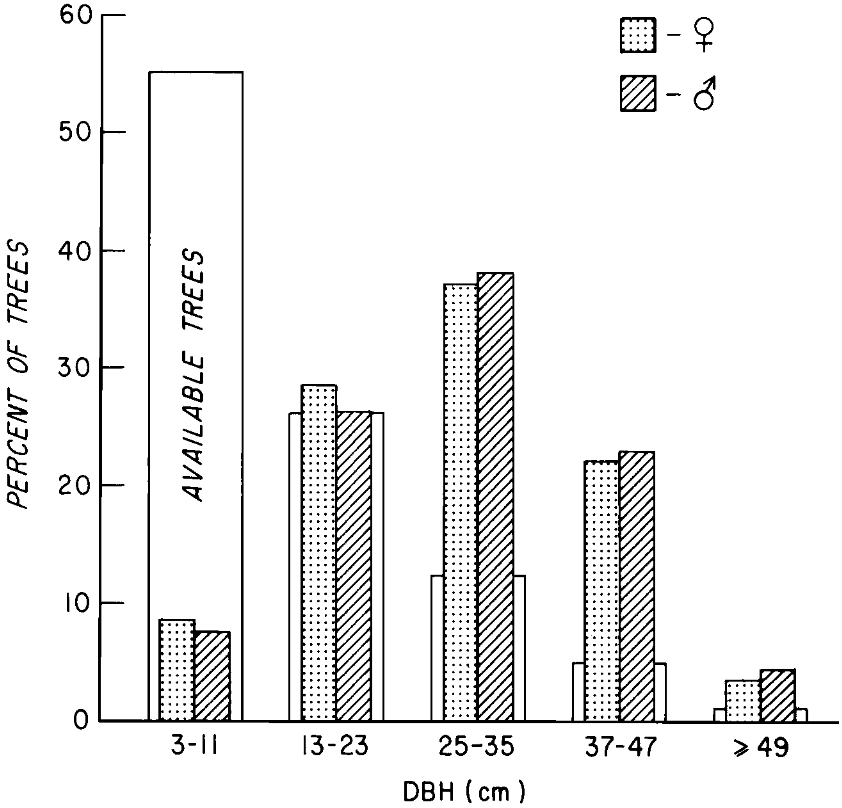

Fig. 1. Diameter (dbh) classes of live pines used by foraging Red-cockaded Woodpeckers compared to availability of diameters in the territories. By diameter class, there was no significant difference in the frequency with which males and females used trees of different sizes ($\chi^2 = 2.8$, $P > 0.5$). Sexes combined, the frequency with which trees were used, by diameter classes, differed significantly from the availability of trees within diameter classes ($\chi^2 = 2{,}758.6$, $P < 0.0001$); $n_{\text{males}} = 726$, $n_{\text{females}} = 906$. Overlap in use of tree diameters by sexes = 97%.

on the trunk (29%) than on limbs (3%). Females spent time within the crown (28%), but their foraging activities, as at the midtrunk zone, were primarily on the trunk. In contrast, males, when foraging in the crown, spent 45% of their time on limbs. The differential use of limbs and trunk by the sexes is more striking when observations of the crown, midtrunk, and lower trunk are combined. While males divided their foraging almost equally between limbs (46%) and the trunk (54%), females restricted their foraging almost exclusively to the trunk (94%).

Partitioning of foraging sites by the sexes was reflected in their relative foraging heights. On live pines males foraged at a mean height of 14.1 m and females at 8.7 m. Thus, the sexes were separated by a mean vertical distance of 5.4 m (df = 136, $t = 4.9$, $P < 0.001$). The range in foraging heights overlapped substantially, because both sexes used the same sites but at different frequencies. Females foraged from near ground level on the lower trunk to 29 m into the crown. Males foraged between 1 and 37 m. Occasionally females foraged higher than males, even when they were on the same tree. The foraging heights of females were skewed toward the lower height classes, but those of males were more symmetrically distributed about the mean (Fig. 2).

TABLE 2. Methods and sites used on live pines by foraging Red-cockaded Woodpeckers, May 1976–March 1977. Data (percentage of n) are from one randomly selected observation per day for each sex from 3,054 observations collected on 69 days ($n_{\text{males}} = 69$, $n_{\text{females}} = 69$).

	Method									
	Probe		Excavate		Scale		Glean		Site total[a]	
Site	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀
Crown										
Trunk	17.4	10.1	0.0	5.8	14.5	11.6	0.0	0.0	31.9	27.5
Live limbs	8.7	1.4	2.9	0.0	2.9	0.0	1.4	0.0	15.9	1.4
Dead limbs	1.4	0.0	8.7	0.0	0.0	0.0	0.0	0.0	10.1	0.0
Cones	0.0	0.0	0.0	1.4	0.0	0.0	0.0	0.0	0.0	1.4
Midtrunk										
Trunk	7.3	15.9	1.4	7.3	2.9	4.4	0.0	1.4	11.6	29.0
Live limbs	0.0	2.9	0.0	0.0	2.9	0.0	0.0	0.0	2.9	2.9
Dead limbs	4.4	0.0	20.3	0.0	0.0	0.0	0.0	0.0	24.7	0.0
Lower trunk										
Trunk	1.4	14.5	1.4	17.4	0.0	5.8	0.0	0.0	2.8	37.7
Method totals[b]	40.6	44.8	34.7	31.9	23.2	21.8	1.4	1.4	99.9	99.9

[a] Significant difference in frequency with which males and females used sites ($\chi^2 = 30.9$, 5 df, $P < 0.005$). Overlap in use of sites by sexes = 46%.

[b] No significant difference in frequency with which males and females used methods ($\chi^2 = 0.3$, 2 df, $P > 0.75$). Overlap in use of methods by sexes = 96%.

Within each sampling period, males and females differed in the frequencies with which they used sites on live pines (Fig. 3). Primary foraging sites for males in all periods were live and dead limbs and the trunk-in-crown. Females foraged primarily on the trunk, making negligible use of limbs. The lower trunk, a major foraging site for females, was usually avoided by males. The midtrunk and trunk-in-crown were important sites for both sexes and are the only two sites where there was considerable overlap in foraging activity between the sexes. The period of least overlap, or greatest separation of the sexes, was January–March (Fig. 3). During that period, females spent most of their foraging time (61%) on the lower trunk and only 12% of the time in the crown. In contrast, males spent most of their foraging time in the crown (57%) and on the midtrunk (42%) and little time on the lower trunk (2%). The greater separation of the sexes during January–March was also apparent in mean foraging heights. During January–March, females foraged lower ($\bar{x} = 5.1$ m) than in May–August ($\bar{x} = 8.1$ m) and September–December ($\bar{x} = 8.0$ m). Mean foraging heights of males differed little throughout the year (12.5 m, January–March; 13.2 m, May–August; and 12.7 m, September–December).

Within each sex, the frequency of foraging at sites on live pines varied between sampling periods (Fig. 3). Between periods, males varied the most in the frequencies with which they foraged on dead limbs, live limbs, and the trunk-in-crown. Between periods, females varied most in the frequencies with which they used the lower trunk and trunk-in-crown. The lower trunk was the principal foraging site for females during January–March and May–August. During September–December, however, the lower trunk received the least use, except for limbs, and the trunk-in-crown received the most use.

Both sexes avoided green loblolly cones. Males were seen on green longleaf cones nine times and females five times. Our general observations suggest that in some years both sexes made greater use of green cones. We suspect that birds were preying on coneworms (*Dioryctria* spp.).

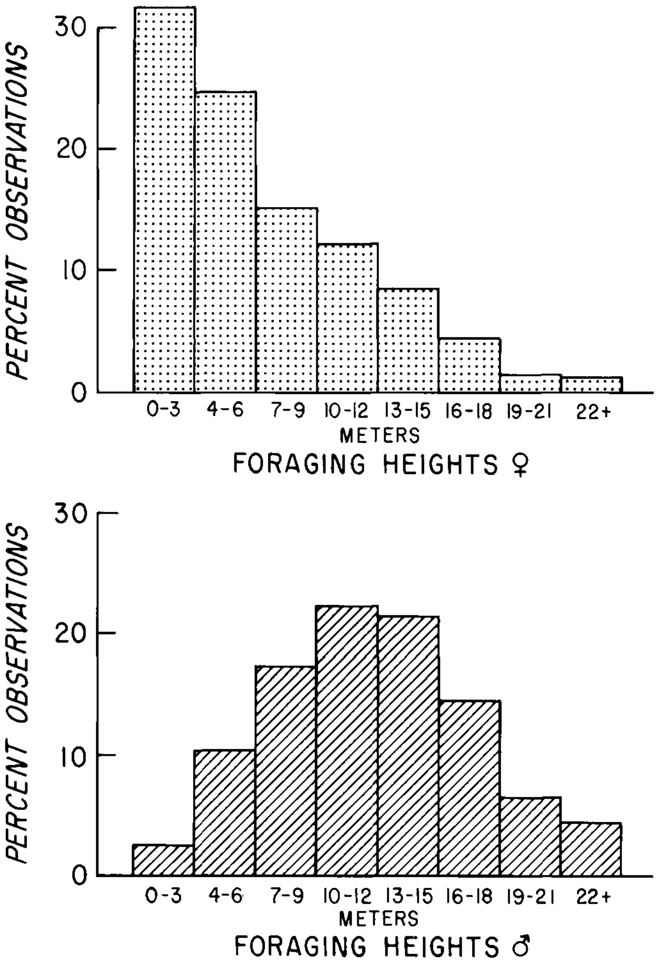

Fig. 2. Foraging heights of male and female Red-cockaded Woodpeckers on live pines, May–March; $n_{\text{males}} = 1{,}317$, $n_{\text{females}} = 1{,}737$. Overlap in foraging heights of sexes = 56%.

Males and females also differed in the frequency with which foraging sites on dead pines were used (Table 3). Their partitioning of sites on dead pines was similar to that on live pines, females using the lower and midtrunk more than males and males using the trunk-in-crown and limbs more.

During the quantitative study we did not see Red-cockadeds forage on the ground. Later, we saw a Red-cockaded foraging on a gravel road and suspect it was eating ants. We saw a group forage briefly on limbs cut from longleaf pines; Ligon (1968) reported similar behavior.

Foraging methods.—The sexes used methods with equal frequency for securing prey from live pines (Table 2). Also, when foraging on dead pines, males and females used foraging methods with similar frequencies (Table 3).

Four methods were used to capture prey: probing, excavating, scaling, and gleaning. We did not see Red-cockadeds flycatching. When probing, the birds hopped along trunks and limbs, appeared to inspect the surface visually, then probed be-

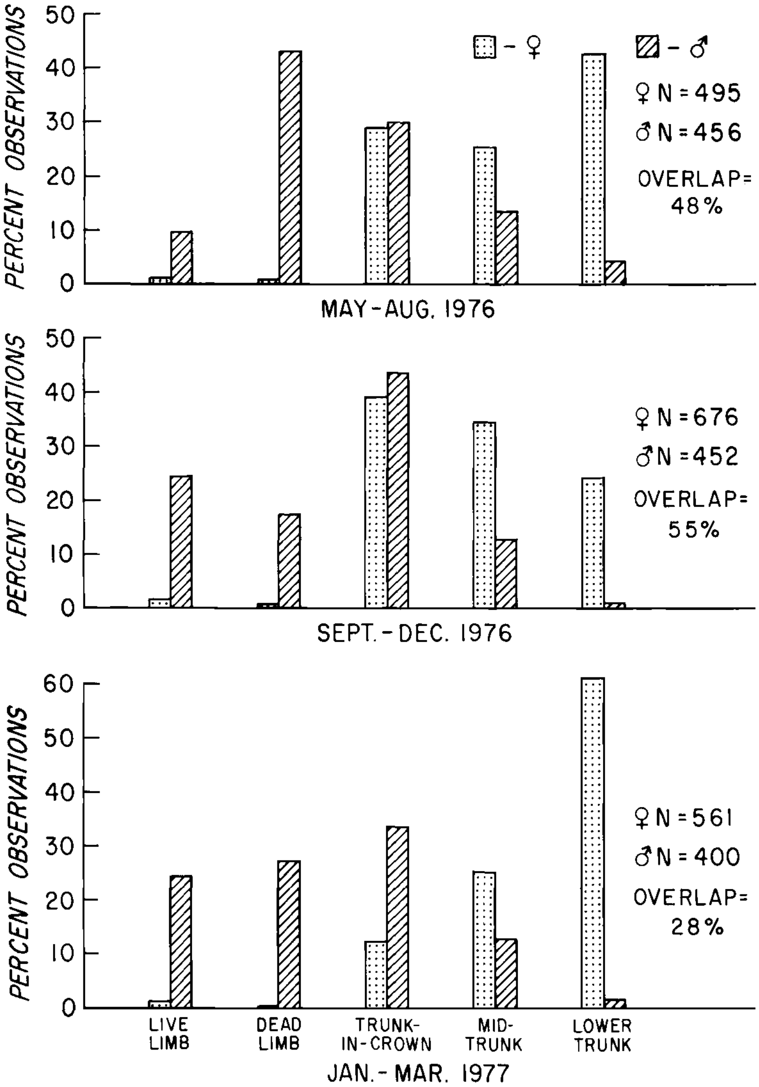

Fig. 3. Intersexual use of foraging sites on live pines by Red-cockaded Woodpeckers in different periods.

TABLE 3. Foraging activity of Red-cockaded Woodpeckers on dead pines, May 1976–March 1977.

		Method (% of n)[a]			Site (% of n)[b]			
Sex	n	Excavate	Probe	Scale	Limb	Trunk-in-crown	Mid-trunk	Lower trunk
Female	56	48.2	42.9	8.9	0.0	21.4	44.6	33.9
Male	41	56.1	36.6	7.3	22.0	41.5	17.1	19.5

[a] Overlap in use of sites by sexes = 50%.

[b] Overlap in use of methods by sexes = 92%.

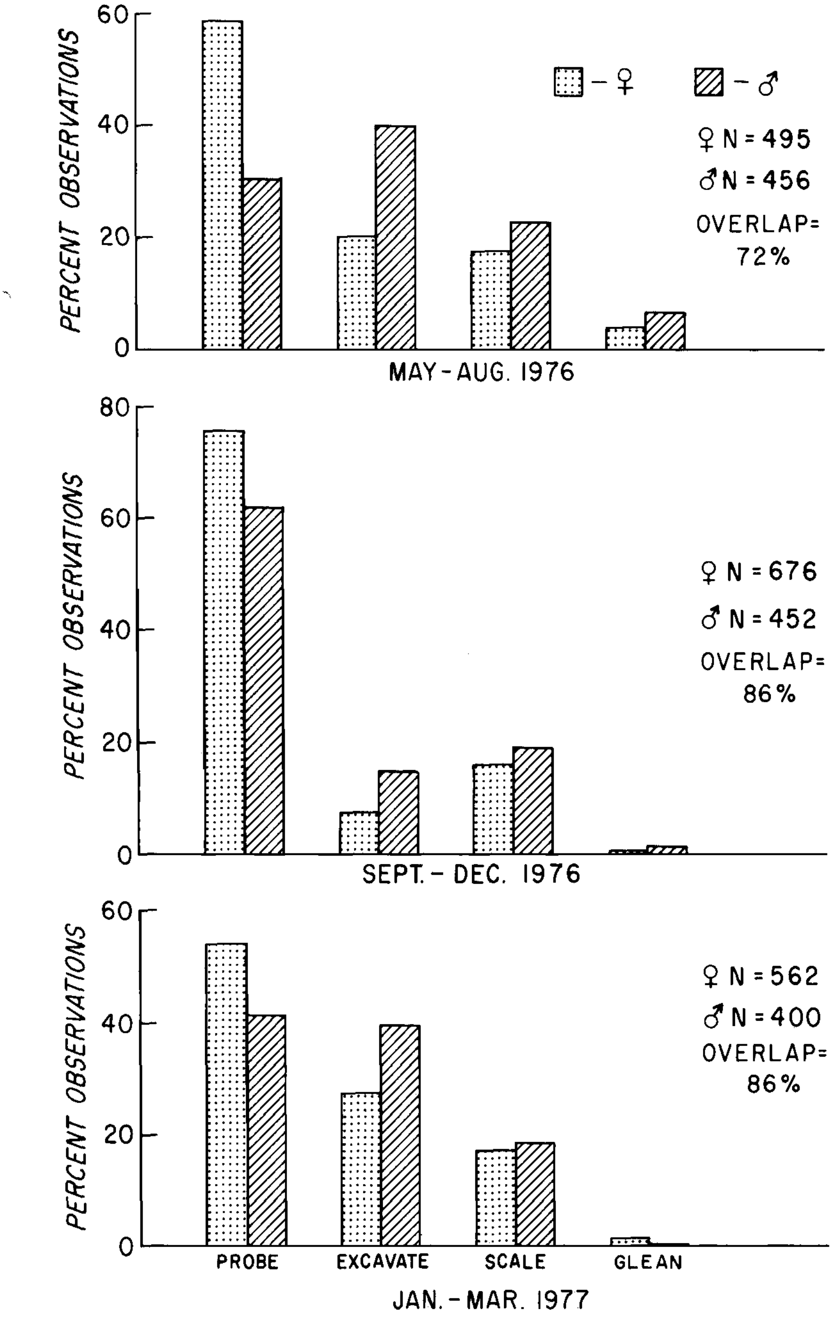

Fig. 4. Foraging methods used by male and female Red-cockaded Woodpeckers on live pines in different periods.

tween bark plates with their bills. Compared to scaling, only small amounts of bark were removed by probing. When probing, birds seemed to cover a larger area of foraging substrate per unit of time than when other methods were used. Year-round, probing was the most frequently used method of both sexes on live pines (Table 2)

TABLE 4. Relative use (percentages of *n*) of foraging methods by Red-cockaded Woodpeckers at foraging sites on live pines, May 1976–March 1977. Only sites receiving major use are considered.

	Male			Female		
Foraging method	May–August	September–December	January–March	May–August	September–December	January–March
			Trunk-in-crown			
Scale	48.9	28.8	23.7	32.2	23.4	32.4
Probe	35.8	61.6	60.7	49.6	68.7	52.9
Excavate	11.7	7.1	14.8	17.5	7.2	14.7
Glean	3.6	2.5	0.7	0.7	0.7	0
n	137	198	135	143	265	68
			Midtrunk			
Scale	42.6	8.6	21.6	15.7	15.4	31.2
Probe	41.0	82.8	51.0	61.4	77.2	51.8
Excavate	11.5	8.6	27.4	20.5	7.3	16.3
Glean	4.9	0	0	2.4	0	0.7
n	61	58	51	127	233	141
		Live limbs			*Lower trunk*	
Scale	18.6	21.6	31.6	8.3	3.0	7.0
Probe	46.5	71.2	46.9	63.4	87.2	56.4
Excavate	4.6	6.3	21.4	20.8	8.5	34.6
Glean	30.2	0.9	0	7.4	1.2	2.0
n	43	111	98	216	164	344
		Dead limbs				
Scale	0	0	0			
Probe	18.5	32.5	5.5			
Excavate	79.0	67.5	94.5			
Glean	2.6	0	0			
n	195	80	109			

and the second most used method on dead pines (Table 3). Red-cockadeds excavated in order to expose subsurface arthropods and eggs in bark and dead wood. On live pines, males and females excavated with near equal frequency, and it was the second most used method year-round (Table 2). On dead pines, excavation was the primary method used by both sexes (Table 3). Scaling involved concentrated removal of superficial flakes of bark with the bill. Both sexes scaled with nearly equal frequencies (Tables 2 and 3) and rarely gleaned prey from the surface of the bark without first scaling.

Within each sampling period, the sexes overlapped considerably when foraging on live pines in the frequencies with which methods were used (Fig. 4). Observed differences in seasonal use of methods were not of the magnitude found in similar comparisons of seasonal use of foraging sites (Fig. 3). Males and females tended to use methods with similar frequencies at the two sites they both used regularly (Tables 4 and 5).

At foraging sites receiving major use, there were differences between sampling

TABLE 5. Percentage overlap in methods used by foraging male and female Red-cockaded Woodpeckers at two sites on live pines used frequently by both sexes. See Table 4 for frequencies.

Site	May–August	September–December	January–March
Midtrunk	80	93	89
Trunk-in-crown	71	93	91

periods in the frequencies with which both sexes used the four methods for capturing prey (Table 4). For example, when on the midtrunk, males scaled five times more often during May–August than during September–December (Table 4). Females were as variable as males. For example, when on the lower trunk, females excavated four times more often during January–March than during September–December (Table 4).

Use of vegetable matter.—We saw Red-cockadeds take fruit only once during the quantitative study. Including other observations, we saw 17 cases of Red-cockadeds feeding on fruits and seeds: wax myrtle (*Myrica cerifera*), 7 times; blueberry (*Vaccinium* spp.), 4; longleaf pine, 3; sweetbay (*Magnolia virginiana*), 2; and poison ivy (*Rhus radicans*), 1. Both wax myrtle and blueberry produced abundant fruit in 1976–1978. Longleaf pine is a sporadic seed producer, with good crops about 5–7 yr apart (Wahlenberg 1946: 72). Seed yield was light during 1976–1978. Loblolly pine is a more consistent seed producer and had good yields in 1976–1977 but a light yield in 1978 (O. Gordon Langdon, pers. comm.). We did not see Red-cockadeds foraging on loblolly seeds.

Use of water.—We observed 14 cases of Red-cockadeds drinking water. On four occasions Red-cockadeds drank from hollows in hardwood trees and on one occasion from one of their flooded cavities. Birds drank water from puddles on the ground on seven occasions. In one case the birds were perched on the base of a tree, but in the others they stood on the ground. When drinking from the ground, both males and females would back down a tree trunk and step off onto the ground. Twice we saw birds licking dew from pine needles. Drinking was observed from October to April, with nine of the cases in November and December. During the hottest part of the year, 28 June–8 September, we followed groups for 9 full days and 53 partial days and did not see the birds drink. Water was probably available to the groups year-round, and it is possible that birds, on occasion, drank without being detected.

Interspecific conflicts.—Overt interspecific conflicts at foraging sites appeared to be rare. Red-cockadeds supplanted Downy Woodpeckers (*Picoides pubescens*) four times from foraging perches and were in turn supplanted once. Red-bellied Woodpeckers (*Melanerpes carolinus*) supplanted Red-cockadeds seven times. A Red-cockaded was supplanted once by a Red-headed Woodpecker (*M. erythrocephalus*). Yellow-bellied Sapsuckers (*Sphyrapicus varius*) were supplanted six times by Red-cockadeds and in turn supplanted a Red-cockaded once. One Brown-headed Nuthatch (*Sitta pusilla*) was supplanted by a Red-cockaded. Some of these interactions may have been harassment not associated with foraging competiton. In only one case did a Red-bellied Woodpecker forage at the usurped site. Another time the Red-bellied examined the site for a few seconds and then left, and the Red-cockadeds returned and resumed foraging. Red-cockadeds foraged at half the sites usurped from Downy Woodpeckers.

Intersexual conflicts.—Conflicts between adult members of Red-cockaded groups at foraging sites were rarely seen. Males and females commonly foraged close together on the trunk or passed each other with no overt aggression or other discernible interaction. The one case of intersexual conflict that might be related to foraging sites occurred when a breeding female, foraging on a limb in the crown, was jabbed and supplanted by her mate. Agonistic behavior among juveniles was fairly common. We saw adults take over the foraging sites of juveniles, but it was more common to see adults yield sites to juveniles with no overt signs of aggression.

DISCUSSION

Tree selection.—The Red-cockadeds we studied foraged almost exclusively on live pines. Birds did not avoid stands with a high percentage of hardwood trees, but in such areas they foraged on scattered pines. Other workers have not compared the frequency to the availability of trees foraged upon by Red-cockadeds, but they have reported extensive use of live pines in Florida (Ligon 1968, 1970; Nesbitt et al. 1978), Louisiana (Morse 1972), Oklahoma (Wood 1977), Virginia (Miller 1978), Mississippi (Ramey 1980), and South Carolina (Skorupa and McFarlane 1976; Skorupa 1979, Ramey 1980; G. W. Wood pers. comm.). Some use of hardwoods was reported by the above workers, except Nesbitt et al. (1978). Skorupa and McFarlane (1976) found exclusive use of pine in summer but 10% use of hardwoods in winter. Wood (1977) reported about 15% use of hardwoods, and Miller (1978) 4% use. Skorupa (1979) reported that only males foraged on hardwoods, 1% in summer and 3% in winter. In Mississippi Ramey (1980) reported 22% use of hardwoods by males but only 6% use by females, and in South Carolina the percentages were 12 and 1, respectively.

The major departure from foraging on live pines, albeit small, was in the use of recently dead or dying pines. Ligon (1970), Baker (1971b), Nesbitt et al. (1978), and G. W. Wood (pers. comm.) have also reported use of recently dead pines. We overestimated the avialability of dead pines suitable for foraging because unsuitable pines were included in the vegetation sample. Thus, selection for recently dead pines was probably strong, even though little use was made of them compared to live pines.

A group that occupied a territory from which much of the pine had been cut spent about 12% of their foraging time on cypress. While this seems to indicate some adaptability in the selection of foraging habitats, the data from groups that had the opportunity to forage on pine or other species indicated a clear preference for pines.

We found that Red-cockaded foraging on larger pines was disproportionate to the quantity available. Skorupa (1979) obtained similar results. Preference for larger trees could indicate more (or different) food per unit area because of thicker, more fissured bark and larger dead limbs. Use of larger trees might also be energy conservative in that more foraging area per tree could reduce time spent flying between trees.

Use of vegetable matter.—We saw very little use of fruit and seeds by Red-cockadeds. In the same study area Harlow and Lennartz (1977) likewise did not observe fruits and seeds being brought to nestlings. Beal et al. (1941), however, collected 99 stomachs representative of every month and found 14% of the diet to be vegetable matter. Pine seeds were found in 45% of the stomachs, constituting the major portion of the plant material.

Red-cockadeds we studied excavated green longleaf cones, presumably for larvae, but we never saw them on loblolly cones. The birds perched directly on longleaf cones when excavating for insects and when taking seeds; thus, the size of the cone may have influenced its use. Longleaf cones are 15–25 cm long, but loblolly cones are only 5–13 cm long. Perhaps Beal et al. (1941) collected stomachs during good seed years, and we might have seen greater use of pine seeds under similar conditions. Morse (1972), however, did not see Red-cockadeds make regular use of an unusually heavy longleaf seed crop, and one stomach contained only arthropods. Ramey (1980) saw only minor use of cones. Baker (1971b) reported that Red-cockadeds fed heavily on wild cherry (*Prunus serotina*) and wax myrtle. Our study area had almost no wild cherry. Wax myrtle was common and had good fruit yields but received little use. Blueberry had abundant yields and was common but likewise received little use. It appears that Red-cockadeds, on some occasions, make considerable use of fruit and seeds (Beal et al. 1941, Baker 1971b), yet on other occasions use is casual, even when mast is common (Morse 1972, this study). It seems possible that use of mast could be related to the relative abundance of arthropods.

Intersexual foraging differences.—Divergent foraging behavior between sexes has been reported for most North American *Picoides*: Hairy (*villosus*) (Kisiel 1972, others), Downy (Williams 1975, others), White-headed (*albolarvatus*) (Koch et al. 1970, but not Ligon 1973), Strickland's (*stricklandi*) (Winkler 1979, others), Nuttall's (*nuttallii*) (Jenkins 1979), Ladder-backed (*scalaris*) (Austin 1976, others), Red-cockaded (Ligon 1968, Skorupa 1979, Ramey 1980, but not Morse 1972), and Northern Three-toed (*tridactylus*) (Massey and Wygant 1954, but not Short 1974). No sexual difference in foraging was reported for Black-backed Three-toed (*arcticus*) (Short 1974).

Ligon (1968) found intersexual foraging differences in the Red-cockaded in Florida. Obtaining results similar to those of our study, he found that males foraged mainly on limbs and upper trunk of pines, while females foraged mainly on the lower trunk and, to a lesser extent, the upper trunk. Ramey (1980) reported similar partitioning of pine trees by Red-cockadeds in Mississippi. Working on an area in South Carolina where young trees predominated, Skorupa (1979) and Ramey (1980) found that females made greater use of limbs (9 and 15%, respectively) than in Mississippi (4%) or in our study (4%), where mature trees predominated. In addition, they found that females used the trunk above limbs more than the trunk below limbs, contrary to the Mississippi data and our study. In Louisiana, Morse (1972) reported no sexual differences in foraging behavior in winter. Unfortunately, Morse's data are inconclusive because he did not use banded birds, and Red-cockadeds cannot be sexed out-of-hand. Also, several birds are usually found together. Two birds in relatively close proximity are frequently an adult-juvenile combination or two adult males and not necessarily an adult male-female pair, as assumed by Morse. It appeared to Miller (1978) that there were no intersexual differences in foraging behavior of Red-cockadeds in Virginia. He pointed out, however, the limitations of his data due to his inability to sex unmarked birds consistently. Beckett (1971) reported no difference in feeding sites of the sexes in South Carolina but did not present data.

In our study area, male and female Red-cockadeds clearly exhibited divergent foraging behavior. Differential use of foraging sites, especially the limited use of limbs by females and the limited use of the lower trunk by males, appeared to be the most important factor in the sexual partitioning of foraging habitat. It is possible that selection of foraging sites was predetermined by the observed vertical stratification of males and females. Evidence against this hypothesis, however, is provided by Ramey (1980). She found that Red-cockadeds foraging in young habitat averaged only 1.2 m difference in foraging heights of males and females but that they still maintained a significantly different intersexual use of sites. We found little evidence of intersexual partitioning of foraging resources by the methods that were used for capturing prey. These results are similar to those of Ramey (1980).

Significance of divergent foraging behavior.—Intersexual foraging differences appear to be widespread among woodpeckers. The most frequently cited presumed advantages of this adaptive behavior are a reduction in intraspecific competition for food and concomitant reduction in intersexual aggression (Selander 1966, Ligon 1968, Wallace 1974, Jackson 1970, Hogstad 1978, others). These adaptive advantages may be of major significance to the Red-cockaded. This species is a cooperative breeder, and a group of 2–9 birds maintains a mutual all-purpose territory throughout the year. Group members forage together, and they cooperate in such activities as incubation, feeding nestlings and fledglings (Lennartz and Harlow 1979), excavating cavities, and territorial defense. In their daily activities, group members maintain close contact. As suggested by Wallace (1974) for other species, sexual partitioning of the foraging resource is possibly one mechanism facilitating the social organization of the Red-cockaded by reducing intersexual aggression and competition.

ACKNOWLEDGMENTS

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COURTSHIP BEHAVIOR AND REPRODUCTIVE ISOLATION BETWEEN WESTERN GREBE COLOR MORPHS

Gary L. Nuechterlein
Bell Museum of Natural History, 10 Church Street S.E., Department of Ecology and Behavioral Biology, University of Minnesota, Minneapolis, Minnesota 55455 USA

Abstract.—In a study of behavioral isolating mechanisms existing between light- and dark-phase Western Grebes (*Aechmophorus occidentalis*) in two sympatric populations near the Oregon-California border, opposite-sexed birds nearly always chose to display with members of their own color phase. Males of opposite phase, however, frequently engaged in mutual display sequences to attract females. Film analysis revealed no color-phase divergences in form, duration, or sequential ordering of the many visual courtship displays. There were differences, however, in "Advertising," a call used to attract potential mates prior to the pair formation sequences. Dark-phase birds had calls with two notes ("cree-creet"), while light-phase birds had one-noted calls ("creeet"). In playback experiments, courting males of the two color phases readily distinguished the two call-types and only approached or answered female calls of their own phase. This response reversed when an artificial gap was spliced into the light-phase stimulus calls. Films of feeding dives by birds of each color phase also suggested differences that may relate to mean diving depth and hence ecological segregation of the two morphs. When the same playback experiments were repeated in a region of dark-phase allopatry (Manitoba), however, courting males showed very poor discrimination. This suggests that the high degree of segregation in sympatry possibly results from a learning process, whereby individuals rapidly sharpen their discriminative abilities by association. *Received 15 September 1980, accepted 19 December 1980.*

In 1858, George N. Lawrence described two closely related species of the genus *Podiceps,* which he designated as *P. occidentalis* and *P. clarkii* (in Baird 1858: 894–895). Lawrence distinguished the two species by differences in bill coloration and by whether or not the black of the crown extended downward beyond the eye to the lores. Although Ridgway (1881) and Fannin (1891) accepted this classification, Coues (1874) and Henshaw (1881) believed that the two forms were varieties (i.e. color phases) of the same species. The first edition of the American Ornithologists' Union "Checklist of North American Birds" (1886) upheld the views of Coues and Henshaw, as have more recent editions of the checklist (1931, 1957) and Mayr and Cottrell's (1979) checklist. Presently, the Western Grebe (*Aechmophorus occidentalis*) is placed in its own monotypic genus, and Dickerman (1963, 1973) has distinguished *A. o. clarkii* as a smaller subspecies found on the Mexican Plateau and represented by members of both color phases. Mayr and Short (1970: 88) report the two color phases as a case of "scattered polymorphism."

The most detailed published description of the two color phases is that of Storer (1965). The most conspicuous difference, in the extent of black on the head, is especially striking in the field, where the brilliant eyes of the living bird draw attention to the facial region. The scarlet eyes of light-phase birds are surrounded by white feathers, in contrast to those of dark-phase birds, which are surrounded by a shroud of black facial feathers. The bills of light-phase birds are orange-yellow, those of dark-phase birds dull greenish-yellow.

Storer (1965) and Lindvall (1976) gave evidence of strong assortative mating within a sympatric population of the two color phases at Bear River Marsh, Utah, and a recent study by Ratti (1979) has confirmed that mixed pairs are rare (<3%) in Utah and California. Ratti (1979) also found spatial segregation within mixed flocks

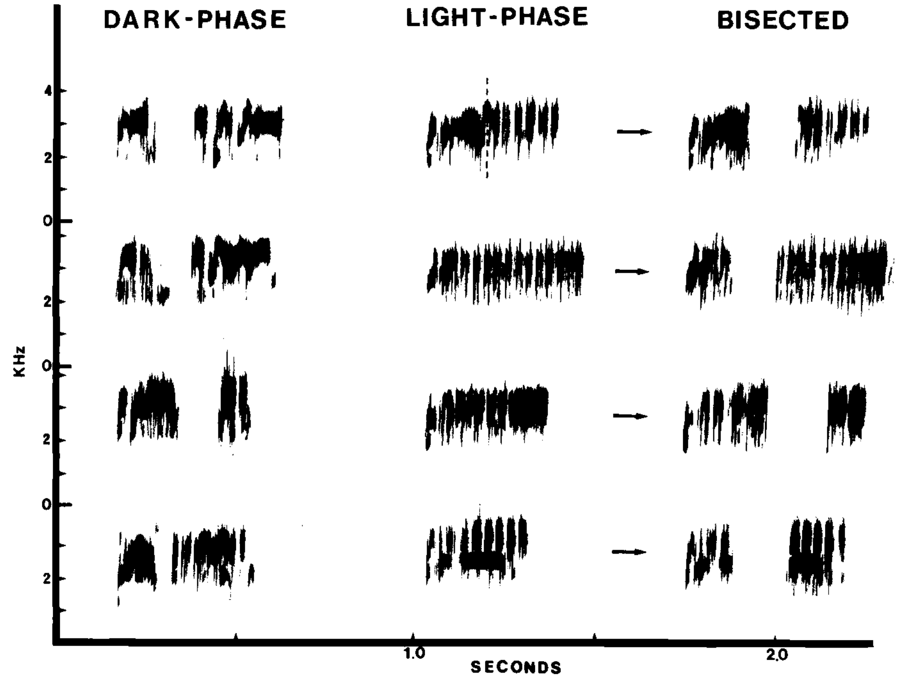

Fig. 1. Advertising calls of four dark- and light-phase Western Grebe females recorded at Tule Lake, California. Sonagrams are of the eight stimulus calls used in the reproductive isolation experiments. The importance of the call-gap to phase discrimination was tested by splicing a short segment of blank recording tape into each light-phase stimulus call and repeating the experiments.

of the two types at Utah and various locations in Nevada and California. My data confirm these observations for breeding populations in Manitoba (Marshy Point and the Delta Marshes of Lake Manitoba), Oregon (Upper Klamath Lake), and California (Tule Lake). Ratti (1979) recommends that the color phases be designated separate species and suggests "resurrection of *A. clarkii* as a separate species from *A. occidentalis,* as originally described."

To date, however, the specific reproductive isolating mechanisms important in segregating the two color phases have largely remained a matter of speculation. Storer (1965) suggested that imprinting on parental coloration could be involved, but Ratti (1977) was not able to confirm this with hand-reared chicks. Ratti's results were inconclusive, however, because his chicks apparently failed to imprint on any of the silent, stationary parental models used. I became interested in this problem during a study of variation in the Advertising call of Western Grebes. Recordings made during 1978 within several mixed-phase populations in Oregon, California, and Utah revealed a consistent and striking difference between calls of the two color morphs (Fig. 1). Advertising calls of dark-phase birds included two distinct notes ("cree-creet"), while those of light-phase birds consisted of a single, more drawn-out note ("creeet"). Advertising usually constitutes the first contact between two unpaired courting birds, and it seemed likely that this call difference might play a key role in reproductive isolation of the two color phases.

The basic objectives of the study were: (1) to analyze visual and vocal components of the courtship displays for differences between the color phases, (2) to determine the point in the extended pair-formation sequence at which isolation usually took place, and (3) to conduct playback experiments examining the extent to which differences in the Advertising call serve as a reproductive isolating mechanism. I also examined feeding-dive differences that may relate to ecological segregation between the two morphs. Display names used throughout this paper are those of Nuechterlein and Storer (in prep.).

METHODS

During April 1978 and April–May 1979, I watched courting Western Grebes in mixed-phase populations at the Klamath Basin National Wildlife Refuges (Tule Lake, Upper and Lower Klamath lakes), near the California-Oregon border. Display activity was particularly intense at Tule Lake Refuge, which is a major staging and breeding ground in this area. In 1979, grebe populations on Tule Lake peaked (estimated 2,000–3,000) during a stretch of windy, inclement weather in late March. On 5 April weather conditions became calm and sunny, initiating a period of very active courtship during which I recorded over 450 display sequences in a 7-day period. These sequences were dictated into a cassette recorder or recorded directly on data sheets.

For micro-analysis of display form, I obtained films and tape recordings of courtship sequences of both color phases. Films were made with a Beaulieu R16 16-mm movie camera and were examined frame by frame using a L-W Analyst Projector. A Uher 4000 Report-L tape recorder was used for all recording and playback of calls, and tapes were compared by use of a Spectral Dynamics real-time analyzer. Playback experiments were conducted during May 1979 at Upper Klamath Lake and were carried out from a small, camouflaged kayak on the edge of a channel frequented by courting males of both color phases. Tape loops used in the playbacks were spliced from tapes of Advertising calls of light- and dark-phase females recorded at Tule Lake, located 45 km away. This assured that males were reacting to phase-typical characteristics rather than individual features of calls of known females. The Advertising calls used for each experiment were chosen at random from tape loops of four females of each phase.

In all cases, the target bird was an actively courting, unpaired male that was swimming within 10–20 m of the tape recorder. Each male was tested three consecutive times with a single call variant. Positive responses were scored only if, within 5 s following the playback, he either (a) replied by giving the Advertising call ("Advertises") or (b) turned and approached the tape recorder ("Approaches").

RESULTS

DISPLAY DIFFERENCES BETWEEN THE COLOR PHASES

Although frame-by-frame film analysis of courtship sequences revealed many individual variants in courtship display movements and postures, none of these visual components of the displays was peculiar to either color phase. Sufficient films were obtained to analyze the form and mean duration of the four most frequent displays statistically, but no significant differences were found (Table 1). Comparisons of the postures and orientation of these and other displays similarly revealed no obvious differences. Finally, flow diagrams constructed from the 408 male-female courtship interactions observed at Tule Lake also showed no obvious differences between the two color phases in sequential ordering of the displays.

Vocal components of the following courtship displays were examined spectrographically: (1) Advertising, (2) Ratchet-pointing, (3) Tick-pointing, (4) Barge-trilling, (5) Neck-stretching, (6) Neck-arching, and (7) Copulation trilling. Although individual variations were common, there were consistent differences between members of the two color phases only in the Advertising call. Of 92 dark-phase birds observed Advertising at Upper Klamath Lake, 91 gave a distinctly two-noted call, while 76 of 77 light-phase birds gave one-noted Advertising calls ($\chi^2 = 161.0$, $P <$

TABLE 1. Mean duration of four courtship displays of light- and dark-phase Western Grebes filmed and analyzed frame by frame. Differences between the color phases were not significant for any of the displays.

Display name	Number of displays (individuals) analyzed		Mean duration[a] (S.D.) (s)		
	Dark-phase	Light-phase	Dark-phase	Light-phase	t-value
Dip-shaking	99 (19)	37 (24)	0.43 (0.04)	0.40 (0.05)	1.83
Rushing	12 (12)	20 (19)	3.41 (1.22)	3.96 (1.71)	1.04
Bob-shaking	16 (10)	12 (6)	0.50 (0.05)	0.48 (0.09)	0.53
Bob-preening	57 (12)	102 (12)	0.85 (0.16)	0.81 (0.19)	0.59

[a] These are the means of the mean values computed separately for each individual.

0.001). Repeated calls by the same bird were nearly identical, and no individual was heard to give calls of both types. This sharp distinction between the calls of dark- and light-phase birds was found in all other populations I examined. Because unpaired birds use the Advertising call to attract potential mates, these findings strongly suggest that differences in this call are partially responsible for the high degree of assortative mating observed in the field.

BEHAVIORAL ISOLATION OF THE COLOR PHASES

Male-female display sequences.—Observations of courtship interactions at Tule Lake from 1 to 22 April 1979 revealed almost total reproductive isolation between the color phases, even for preliminary displays of the pair formation sequence. Within this mixed population, comprised of approximately 22% light- and 78% dark-phase birds, 408 male-female courtship display sequences were recorded, of which only 13 (3%) involved members of both color phases. Frequency of inter-phase courtship varied from about 2–3% for early displays in the pair formation sequence (e.g. Dip-shake and Rush) to 0–1% for later displays of the sequence (Table 2).

The few sequences involving birds of both phases were usually aborted before or shortly following Rushing (8 of 12 cases). Of the remaining four sequences, two were unusual in that after Rushing, the pair reverted back to Dip-shaking, the first display of the pairing sequence. In only two instances did the sequence continue after Rushing, and in both the birds separated shortly after Bob-preening.

Male-male display sequences.—Unlike most other grebe species, two male Western Grebes frequently perform displays together, probably to attract the attention of females in the vicinity. Such male-male sequences frequently involved birds of opposite color phase. Of 94 interactions 16 (17%) involved males of opposite phase, a percentage that is significantly greater than that for male-female sequences ($\chi^2 = 22.4$, $P < 0.01$). In contrast to mixed-phase male-female sequences, those involving only males were not abbreviated, and in all respects they appeared to be similar to male sequences involving birds of the same phase. Frequency of inter-phase displaying varied from 17 to 20% (Table 2B).

The most common display was Barge-trilling, seen during 77 of 94 male-male interactions. Females in the vicinity of two displaying males frequently approached and then engaged in courtship with one of the males. In five such instances observed at Tule Lake, the females chose the male matching their own color phase. [These

TABLE 2. Chi-square analysis of assortative courtship displaying by dark- (D) and light-phase (L) Western Grebes on the Klamath Basin Wildlife Refuges. Displays are analyzed separately in their sequential order. (A) Male-female dyads, (B) Male-male dyads.

(A) MALE-FEMALE SEQUENCES

Courtship display	*n*	Number of dyads displaying D-D	L-L	D-L	L-D	χ^{2a}	Percentage mixed
Dip-shake	451	302	136	10	3	393.4	2.9
Rush	369	239	120	9	1	326.5	2.4
Bob-shake	248	165	82	1	0	243.5	0.4
Weed-dive	102	59	43	1	0	99.0	0.9
Weed-dance	27	17	10	0	0	27.0	0.0
Bob-preen	308	212	92	3	1	289.5	1.2
Arch-cluck	197	115	80	1	1	188.8	1.0

(B) MALE-MALE SEQUENCES

Courtship display	*n*	Number of dyads observed (expected) D-D	L-L	L-D	χ^{2b}	Percentage mixed
Dip-shake	50	31 (25.9)	9 (3.9)	10 (20.2)	12.8	20.0
Rush	54	35 (29.6)	9 (3.6)	10 (20.8)	14.7	18.5
Barge-trill	77	48 (38.6)	16 (6.5)	13 (31.8)	11.1	16.9

[a] For all values $P < 0.001$, df = 1.

[b] For all values $P < 0.01$, df = 2.

observations essentially constitute a natural female-choice experiment, $P = (½)^5 = 0.03$.]

Of 74 3-bird interactions observed on Tule Lake, 7 included birds of both phases. Such mixed-phase triads usually consisted of a female and one male of each color phase. Often their interactions appeared to be the result of confusion within dense courting groups, and in all cases, further displays were performed only between members of the same color phase.

PLAYBACK EXPERIMENTS WITH ADVERTISING CALLS

The field observations reported above showed that reproductive isolation occurs largely before birds reach the stage of close-range courtship interactions. Even Dip-shaking, the initial visual display of the pair-formation sequence, occurs only rarely between birds of different color phases. Evidence from continuously run, 30-min tapes recorded during April 1978 at Upper Klamath Lake suggested that Advertising may play a central role in isolating the two phases. Over a 7-day period I recorded 6.5 h of tape including 362 Advertising bouts, many of which consisted of two or more individuals engaging in short bursts of reciprocal calling. Because I could usually identify the color phase and sex of calling birds from the tapes, the tapes provided a valuable record of vocal interactions occurring within and between the color phases under natural conditions.

To provide an analytical framework for these data, I defined a "reply" as any Advertising bout occurring within 5 s of a preceding call bout. Each bout consisted of from 1 to 6 calls by the same individual, spaced 0.5–1.5 s apart. All recorded bouts were first divided into (1) those which received answers, and (2) those which did not. Answered bouts further consisted of (a) those answered by members of the same sex, and (b) those answered by members of the opposite sex. Calls too faint to distinguish from the tape with certainty were omitted from the analysis.

TABLE 3. Color phase composition of "replies" to (A) naturally occurring Advertising calls of each phase, and (B) playback calls broadcasted to a mixed population at Upper Klamath Lake, Oregon. Only heterosexual responses are tallied.

(A) NATURAL EXPERIMENT

First call	Advertising calls within 5 s[a]	
	Dark-phase	Light-phase
Dark-phase	36	6
Light-phase	4	61

(B) PLAYBACK EXPERIMENT

Stimulus call	Advertising calls within 5 s[b]	
	Dark-phase	Light-phase
Dark-phase	19	5
Light-phase	0	15

[a] $\chi^2 = 69.0$, $P < 0.001$, df = 1.
[b] $\chi^2 = 23.2$, $P < 0.001$, df = 1.

When summarized in this manner, these data essentially constitute a natural isolation experiment. If reproductive isolation by mating call type is occurring, heterosexual replies should come largely from individuals of the same color phase. Data from the analysis support this prediction. Of 137 recorded "replies," 107 followed a call by a member of the opposite sex. Of these 107 heterosexual replies, 91% followed individuals of the same phase type (Table 3A).

In early April 1979, I conducted a brief pilot experiment using playback calls. Female calls of each phase type were played to a mixed population of males at Upper Klamath Lake, and the phase of answering birds was recorded. Seventy-two trials were run, each 30 s apart, and a 5-s response period was allowed following each playback trial. Calls of each phase were alternated in 12-trial playback blocks. The results of this experiment suggest discrimination between morphs by Advertising call. Male "replies" to light-phase female playback trials were all from light-phase birds, while most replies to dark-phase female playbacks were from dark-phase males (Table 3B).

There were two difficulties with the interpretation of these results, however. Observations during the experiment indicated that some of the male "replies" were not given in response to the playback. Courting males often called spontaneously, apparently to attract the attention of nearby females. Active birds give such calls irregularly at 1–3 min intervals, and presumably some of these fall by chance within the 5-s playback response period. Also, nearby females (often of opposite color phase) sometimes happened to call simultaneously with the playback vocalization and elicited "inappropriate" male replies. But these sources of error were rare and presumably random with respect to the designated 5-s playback response periods, and both difficulties were largely eliminated in subsequent experiments by conducting several consecutive trials on individual males. When a male answered or approached within 5 s of two consecutive playbacks, I could be confident that the response was not spurious. When 3 consecutive playback calls were directed at each individual courting male, I scored a "positive" result only when the bird answered or approached after at least 2 of the 3 calls.

These three-trial playback experiments showed *complete* segregation of the color phases by Advertising (Table 4). Of 30 dark-phase and 26 light-phase males tested

TABLE 4. Reproductive isolation: number of (A) dark-phase and (B) light-phase males responding to playbacks of female Advertising calls of each color phase. Additional males were then tested with bisected, two-noted, light-phase calls having an artificial gap.

	Stimulus calls		
Playback response	Dark female	Light female	Light female (bisected)
(A) Dark males[a]			
Advertise/Approach	25	0	13
Negative response	8	30	4
(B) Light Males[b]			
Advertise/Approach	0	25	1
Negative response	26	4	11

[a] Significance tests for dark-phase males: (a) Dark versus light female calls, $\chi^2 = 37.7$ ($P < 0.001$); (b) Dark versus bisected light female calls, $\chi^2 = 0.003$ ($P > 0.75$).

[b] Significance tests for light-phase males: (a) Dark versus light female calls, $\chi^2 = 41.1$ ($P < 0.001$); (b) Dark versus bisected light female calls, $\chi^2 = 2.2$ ($P > 0.10$).

with calls of the opposite phase-type, none showed a positive response. In contrast, most dark males tested responded positively to playbacks of dark female calls, while light males tested responded positively to playbacks of light female calls (dark males: $\chi^2 = 37.7$, $P < 0.001$, light males: $\chi^2 = 41.1$, $P < 0.001$).

Mechanisms of call discrimination.—To examine the importance of the call gap to vocal segregation of the phases, a playback experiment with altered tapes was devised. Tapes of light-phase calls (copies of the same tapes used previously in the reproductive isolation experiments) were bisected with a scissors, and a short (1–2 cm) segment of blank recording tape was spliced into the middle of each call (Fig. 1). Both light- and dark-phase males showed complete reversal in responsiveness to the altered calls compared to the initial experiment (Table 4). Of 17 dark-phase males tested, 13 showed a positive response to the altered calls. Light-phase males, on the other hand, virtually ignored the calls with the exception of one male, which, for unknown reasons, responded vigorously to all three playback trials.

Geographical variation in discrimination responses.—A final playback discrimination experiment was conducted in Manitoba (Marshy Point) during May 1979, with somewhat surprising results. This experiment was a repetition of the color-phase discrimination playbacks initially performed at Upper Klamath. Procedures and tape loops were identical to those used in previous playbacks, except that only single-trial experiments were performed. Because light-phase birds are extremely rare (<0.5%) in this population, playbacks were limited to dark-phase males.

Table 5 compares the first-trial responses of Manitoba and Oregon males to the playback calls. Although Manitoba males did show some tendency to discriminate the two types of calls, segregation was not nearly as complete as it was for Oregon males. Chi-square statistical analysis suggests that this difference resulted largely from dark-phase Manitoba males showing more positive responses to light-phase female calls. In fact, nearly half of the 40 dark-phase males tested approached or Advertised. At the same time, males of the two populations showed little difference in responsiveness to dark-phase female calls.

OBSERVATIONS OF MIXED PAIRS AND PRESUMED HYBRIDS

Observations at Upper Klamath and Tule Lake confirmed Ratti's (1979) report of strong assortative mating within these mixed populations of the two color phases.

TABLE 5. Discrimination of dark- versus light-phase female Advertising calls by actively courting dark-phase males in areas of sympatry (Upper Klamath Lake, Oregon) versus allopatry (Marshy Point, Manitoba).

Stimulus call used	Response to call	Oregon males[a]	Manitoba males[b]
Dark-phase female[c]	Advertise and/or Approach	25	27
	No response	13	13
Light-phase female[d]	Advertise and/or Approach	1	19
	No Response	32	21

[a] Significance test for Oregon males: $\chi^2 = 30.0$, $P < 0.001$.
[b] For Manitoba males: $\chi^2 = 3.3$, $P = 0.07$ (N.S.).
[c] Significance test for differences in responsiveness to dark-phase calls: $\chi^2 = 0.03$, $P > 0.75$ (N.S.).
[d] For differences in responsiveness to light-phase calls: $\chi^2 = 18.0$, $P < 0.001$.

A pair count conducted on 2 April 1979 at Tule Lake yielded only one mixed pair out of a sample of 91 pairs (D-D: 71, L-L: 19, D-L: 1; $\chi^2 = 85.2$, $P < 0.001$). During my observations over a 2-week period at Tule Lake, I noted only two additional mixed pairs, which I differentiated by their individually distinct plumage patterns and Advertising calls (see Nuechterlein in press). While conducting playback experiments at Upper Klamath from 17 April to 10 May, I saw one additional mixed pair on several occasions. Observations of this dark-phase female interacting with her light-phase mate revealed that she had a *one-noted* Advertising call! This bird was the only dark-phase female I observed with such a call at Upper Klamath. Members of mixed pairs appeared to interact with their mates in a normal manner. The pair bonds seemed strong, and in one instance the male repeatedly defended his mate from intruders while engaging in mate-feeding. Eggs of the only mixed pair seen at Marshy Point, Manitoba were fertile and hatched successfully.

Birds with intermediate breeding plumage, probably progeny of such mixed matings, also were rare at both Upper Klamath and Tule lakes. Of a total of 18 individuals classified as "intermediates" (the black of the crown extending down to but not beyond the eye, Ratti 1979), 15 birds had orange bills (as in light-phased birds), while only 3 birds had dull greenish-yellow bills (as in dark-phased birds). Of 9 individuals with intermediate plumage observed Advertising, 6 gave one-noted calls and 3 gave two-noted calls. Repeated calls by a given individual were always of the same type. Thus, if these birds were indeed "hybrids," they were intermediate in facial coloration, but not call-type or bill coloration.

Six of the above intermediates were males observed while conducting playback experiments at Upper Klamath. Preliminary tests yielded positive responses from three of these birds, all responding to female playbacks of their own call-type. I was not able to perform the necessary control experiments on these individuals, however, so these data are only suggestive.

Observations of birds with intermediate plumage nesting within large colonies at Marshy Point, Manitoba, suggest that they are fertile, and eggs of one such female were observed hatching. Apparently, however, some intermediate birds, especially males, have difficulty obtaining a mate. Male-female courtship sequences at Tule Lake involving such males usually ended soon after Rushing (6 of 7 instances), though again male-male interactions involving intermediate birds (3 instances) were not so truncated. In two of these three instances, unpaired females approached and made a choice between the two displaying males; the nonhybrid individual was selected both times.

In Manitoba, birds with intermediate plumage appeared to be especially frequent in late-season courting groups of unmated birds. Such groups frequently contained individuals with obvious abnormalities, such as irregularities in their Advertising call. One late season courting male ("the voice-less male"), for example, had a hoarse, barely audible call, while another ("the clear-noted male") had a call consisting of very pure tones. A third bird, observed unpaired in July of two consecutive breeding seasons, had a three-noted call. Of the 18 intermediates observed at Upper Klamath and Tule Lake, only three were paired. One of these, an intermediate female with a one-noted call, was paired with a light male. The other two intermediates were paired with one another!

DIVING DIFFERENCES AND ECOLOGICAL SEGREGATION BETWEEN PHASES

Lawrence (1950) described four types of dives used by Western Grebes in different contexts. The "alarm dive" and "surface dive" were used in escape situations; the "feeding dive" and "springing dive" occurred during feeding. The latter differed in the extent to which the forepart of the body emerged from the water as the bird submerged. Although Lawrence did not attribute any special functional significance to the springing dive, he noted that it was more frequent in the ocean and in rough water.

Analysis of 49 dives filmed at Upper Klamath suggested that what I call "level dives" (="feeding dives" of Lawrence 1950) and "springing dives" probably represent extremes on a continuum of dive-forms used by Western Grebes while feeding. Level dives are the most common: the grebe sleeks its head and neck feathers, then propels itself smoothly forward beneath the water in a seemingly effortless, head-first motion. Neither the breast feathers nor the tarsi emerge from the water (Fig. 2A), and the bird submerges with scarcely a ripple. In springing dives, the grebe cocks its head backwards, after sleeking its feathers, then springs up out of the water while arching neck and body so as to enter the water more vertically. In its most exaggerated form, the entire body, including the feet and tarsi, emerge from the water as the head disappears under the surface (Fig. 2B).

I suspect that the bird goes deeper in springing dives than in level dives. Birds feeding far offshore at Upper Klamath during April 1978 frequently used springing dives, whereas those feeding close to shore used mostly level dives (Fig. 2B, $\chi^2 = 14.5$, $P < 0.01$). In a sample of 69 dives, dark-phase birds only once performed a full springing dive (breast and tarsus emerging from water), while light-phase birds did so frequently (Fig. 2A, $\chi^2 = 38.8$, $P < 0.01$). This probably was a result of spatial segregation of the two morphs during feeding. Light-phase birds generally tended to feed at a greater distance from shore than dark-phase birds. In shallow marshes such as Tule Lake, Bear River Marsh, and the Delta Marsh, I have only rarely observed springing dives, even by light-phase birds. Thus, I suspect that the critical factor determining the dive-type may be water depth rather than color phase *per se* and that light-phase birds may be more inclined to dive in deeper water when such areas are available. Ratti (pers. comm.) rarely observed light-phase birds in the shallow "borrow ditches" at Bear River Refuge that were commonly utilized by dark-phase birds. Further study of this topic is needed.

DISCUSSION

Ecological segregation.—Ratti (1979) suggests that morphologically and ecologically the two color phases are practically indistinguishable and that sympatric pop-

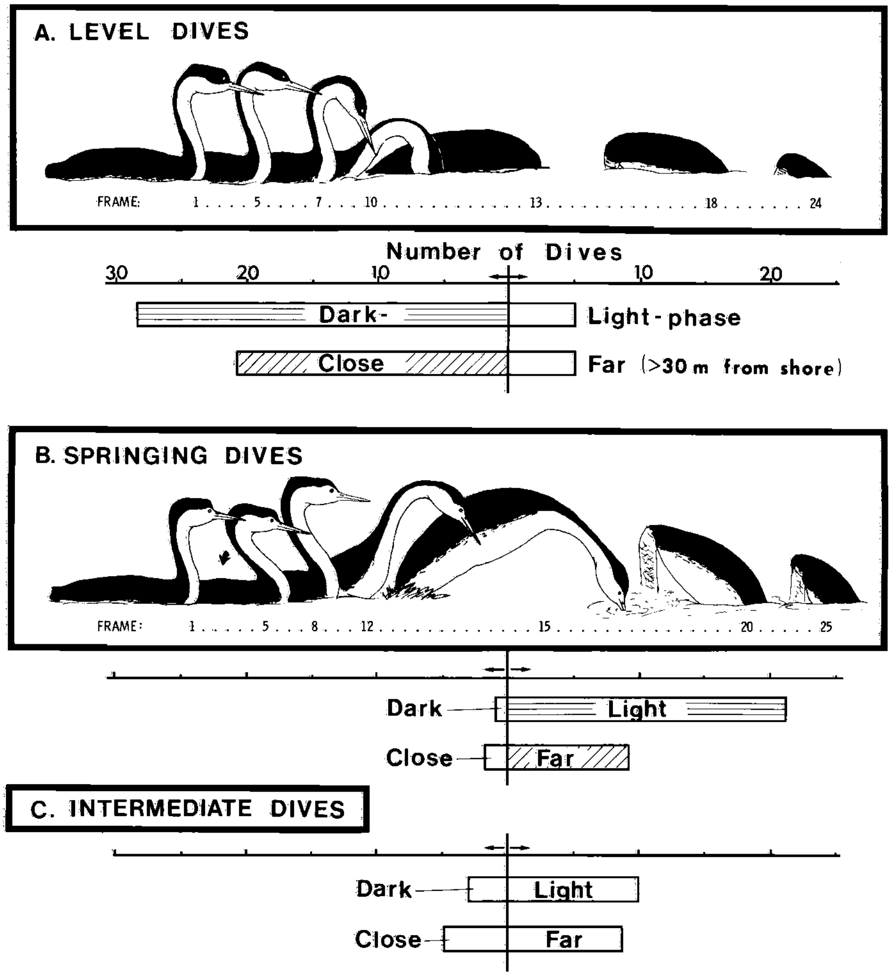

Fig. 2. Types of dives used by feeding dark- and light-phase Western Grebes at Upper Klamath Lake, Oregon. Dives were filmed at 25 frames/s; image size was used to determine relative distance from shore.

ulations may therefore represent one of the best avian examples of an exception to the competitive exclusion principle. My preliminary data on dive-types, however, suggest that the two color phases may be segregating behaviorally into two subtly different ecological forms specialized for feeding at different depths.

This is an important aspect of the speciation question in critical need of further study. Both Feerer (1977) and Ratti (1979) report that major differences exist in the proportion of light- and dark-phase birds comprising the breeding populations of neighboring lake systems within Oregon, California, and Mexico. For example, Ratti (1979) reports a large grebe population at Goose Lake, Oregon comprised of over 93% light-phase birds. This breeding population lies only 110 km east of Upper Klamath, Lower Klamath, and Tule Lake, all of which support predominantly dark-phase populations.

If the color phases are diverging ecologically with respect to mean diving depth, differences in the physiography of lake basins may be important in explaining many of the local irregularities that Feerer (1977) and Ratti (1979) report within the more basic north-south cline in color-phase frequencies described by Storer (1965).

Playback experiments.—For Western Grebes comprising sympatric populations of dark- and light-phase birds at Tule and Upper Klamath lakes, phase discrimination by call-type plays an important role in reproductive isolation. For most birds, call discrimination appears to be based largely on whether or not there exists a 20–200 ms gap dividing the Advertising call into two notes. There is no evidence of character displacement in gap length of calls recorded within mixed populations, but grebes in areas of sympatry do show increased discriminatory responses to the character difference.

Unfortunately, very little is known about the ontogeny of vocalizations or about the development of mating call preferences in Western Grebes. If these are both imprinting-like phenomena, results of the geographical variation experiment could suggest a sharpening or narrowing of the sexual imprinting process for birds within sympatric populations. Another explanation, however, is that individuals comprising sympatric populations discover through associative learning that birds having Advertising calls different from their own possess other traits making them less compatible as mating partners.

Most birds within the nearly allopatric populations of Manitoba may not have had ample opportunity to make the association. This is not true for all individuals, however. One marked dark-phase male, for example, responded positively to 16 of 20 dark-phase female calls played to him, but showed only one positive response to 20 playbacks of light-phase female calls.

Advertising songs and calls are probably important species recognition signals for many birds (Marler 1960). Among the songbirds (Passeriformes), for example, many closely related species-pairs have similar plumages but widely divergent Advertising songs, and Nottebohm (1972) suggests that song learning has played an important role in the group's rapid radiation. Although the importance of Advertising calls to reproductive isolation is well-established in other vocal species, such as the anurans (see reviews by Blair 1958, 1964; Littlejohn 1969) and orthopteran insects (Walker 1957, 1974; Perdeck 1958), the isolating role of birdsong has rarely been demonstrated (but see Szijj 1966, Payne 1973). This probably is because female songbirds usually fail to give easily quantified, overt playback responses in the field and, unlike anurans and orthopterans, are difficult to test in the laboratory. Unlike the grebes, most female songbirds have no Advertising calls of their own, and playback studies have largely been limited to male-male territorial responses.

In a series of extensive behavioral studies on hybridization and isolating mechanisms between Blue-winged (*Vermivora pinus*) and Golden-winged (*V. chrysoptera*) warblers, Gill and Lanyon (1964), Ficken and Ficken (1967; 1968a, b; 1969), and Gill and Murray (1972a, b) conducted reciprocal experiments, playing both types of Advertising song to territorial males of each species. Gill and Murray (1972b) summarize these data, which show song discrimination by both species. Further studies showed that, like Western Grebes, male Blue-winged Warblers in allopatric populations give weaker discrimination responses (Ficken and Ficken 1969, Gill and Murray 1972a). In contrast, Emlen et al. (1975) report that male Indigo Buntings (*Passerina cyanea*) and Lazuli Buntings (*P. amoena*), which defend interspecific territories, show more vigorous responses to calls of the other species within zones of sympatry. Authors of both studies suggest that these responses are learned by association. Gill and Murray (1972b) relate several instances of individually marked males eventually learning to discriminate song-types when their territories were bordered by members of both species.

This phenomenon of "response displacement" parallels character displacement in signal patterns but involves *individuals* of sympatric populations *learning* to alter their *responsiveness* to evolved signal differences, rather than *populations* genetically altering the *signals* themselves. Such learned discrimination responses to Advertising calls may have important bearing on the rate at which effective reproductive isolation takes place. Associative learning might explain, for example, the extremely rapid (within 10–20 yr) reduction in the frequency of cross-matings in Northern Oriole (*Icterus galbula*) subspecies reported by Corbin and Sibley (1977) and Corbin et al. (1979) in areas of recent sympatry.

Littlejohn and his associates have conducted numerous playback experiments showing the importance of male call differences to reproductive isolation of closely related anuran species (Littlejohn 1969, Blair 1974). In all cases where females showed better discriminative abilities between male calls recorded in areas of sympatry versus allopatry (Littlejohn 1960, 1965; Littlejohn and Loftus Hills 1968), these differences were associated with character displacement in temporal components of the male's mating calls. In birds, where learning plays a greater role in call discrimination, responses may be more flexible, and individuals sharpening their discrimination through associative learning should benefit, even in cases where there are only minor disadvantages to hybrid matings. Such initial disadvantages could relate to behavioral as well as genetic incompatibilities. (As a possible example, members of a mixed pair, while attempting to feed young, may experience difficulties in choosing a depth of water optimal for both birds.) In cases where there is no disadvantage to hybridization between individuals of two populations, "response convergence" to signal differences should occur and may result in rapid introgression. Where calls serve multiple functions (e.g. territorial advertisement and mate attraction), male and female need not show parallel changes in response. In cases of interspecific territoriality, for example, males may learn to react equally to both call-types, while females learn to discriminate the two calls. The meadowlarks provide a possible example (see Szijj 1966, Rowher 1972).

Reproductive isolation.—Observational data, film analysis, and playback experiments suggest that, in most cases, the later visual courtship displays of Western Grebes may have little to do with reproductive isolation, for species isolation is largely complete before they begin. Instead, such displays may be involved in mate evaluation at a more subtle level (Nuechterlein in prep.). Advertising is the only display commonly preceding such interactions between unmated birds. This provides strong circumstantial evidence of the central role of the Advertising call in isolating the two phases.

Within sympatric populations of the two color phases in California, Oregon, and Utah, reproductive isolation appears to be nearly complete, confirming reports by Storer (1965), Lindvall (1976), and Ratti (1979). Intermediates were frequent, however, within several Mexican populations examined by Feerer (1977). Although sample sizes are limited, he reports a frequency of 33% ($n = 54$) for birds with intermediate plumage counted at Laguna Tuxpan (population size: 105 individuals), and 30% ($n = 15$) for Laguna Cuitzeo (population size: 50 individuals). Plumage, but not bill color, intermediacy also appears to be more common in museum specimens (Robert W. Storer pers. comm.), and the possibility that there are seasonal plumage differences (Ratti 1979) should be investigated. Plumage differences between dark- and light-phase birds may be striking only for adult birds that are in full breeding plumage. This would mean that the plumage classification "intermediate" is a heterogeneous group comprised of hybrids, juveniles, and adults in winter plumage.

Within populations of breeding birds at Tule Lake and Upper Klamath, intermediates were very rare and showed no intermediacy in bill color or Advertising call characteristics. The hybrids of Blue-winged/Golden-winged Warbler crosses, "Brewster's" and "Lawrence's" warblers, similarly possess intermediate plumage, but not song (Gill and Murray 1972b). Ficken and Ficken (1968a, b) indicated that these hybrids also have difficulties in finding mates. Short (1963), Ficken and Ficken (1967), and Gill and Murray (1972a) all report rare instances of males having songs of the inappropriate species.

Systematic considerations.—Whether or not the two color phases should be recognized as separate species remains an open question. In a practical sense, Short (1969) recommends that populations capable of forming a zone of overlap and hybridization, where both parental and hybrid types coexist, be considered semispecies having separate binomial names. He warns that it is critical, however, to consider all reactions between two forms before undertaking a full taxonomic evaluation, for forms coexisting in one area of contact may interbreed in other areas (e.g. Sibley and West 1958), and "evidence of the stabilization of a single hybrid swarm warrants conspecific status for the parental forms" (Short 1969). In this regard, it seems important to investigate reproductive isolation and behavioral interactions within Western Grebe populations of Mexico.

If dark- and light-phase Western Grebes remain classified as morphs, they may represent a unique case, for "no other broadly sympatric avian polymorphic species is known to exhibit such a low incidence of interbreeding" (Ratti 1979: 584). If, however, they are classified as distinct species, they may still be unique, for I know of no other instance in which males of two separate species regularly engage in *mutual* display to attract females. This dilemma underscores the futility of attempting to impose static classifications on populations undergoing the continuous process of speciation via mechanisms still poorly understood.

Perhaps a more interesting and meaningfully phrased question is to ask instead whether isolating mechanisms are being diminished or strengthened, and whether the two morphs are genetically diverging or converging through time. Unfortunately, these are historical questions difficult to address except indirectly, for example through evidence of character displacement in areas of recent sympatry. The phenomenon of reproductive "response displacement" (i.e. the sharpening of discrimination responses to mating call or song differences within areas of sympatry), as found in this study, is similarly suggestive. It seems imperative that future studies examine more closely the actual mechanisms involved, the degree to which the phenomenon is general to birds, and the importance of such learned responses to the speciation process.

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PREY DROPPED BY HERRING GULLS (*LARUS ARGENTATUS*) ON SOFT SEDIMENTS

BRETTON W. KENT

Department of Zoology, University of Maryland, College Park, Maryland 20742 USA

ABSTRACT.—The prey dropped by Herring Gulls (*Larus argentatus*) on soft sediment substrates in northwest Florida were examined between January and April 1979. Bivalves were the dominant prey, with the scallop (*Argopecten irradians*) accounting for over half of the prey dropped. Only the largest available prey were dropped. Gastropods were abundant but were not dropped due to greater resistence to breakage than bivalves. *Received 10 June 1980, accepted 2 December 1980.*

GULLS are well known for their ability to open shelled invertebrates by dropping them on hard substrates (Tinbergen 1953, Harris 1965, Barash et al. 1975). In this paper I examine the prey dropped by wintering Herring Gulls (*Larus argentatus*) on soft substrates in the Turkey Point region of Franklin County, Florida. This area has a diverse fauna of large, hard-shelled invertebrates that potentially could be utilized by gulls, but hard substrates for drop sites are absent. Most of the intertidal zone consists of grassflats of muddy sand interrupted by occasional bars of firmly packed sand. The objectives of this study were to examine the diet of Herring Gulls using sandbar drop sites and to correlate this diet with the relative vulnerability of different prey to being opened on sandbars.

METHODS

Gull drop sites were examined on three sandbars near the Florida State University Marine Laboratory at Turkey Point between January and April 1979. All three sandbars are bordered by seagrass beds composed of shoal grass (*Halodule wrightii*) and turtle grass (*Thalassia testudinum*). Gulls forage on these grass flats during low tides and take prey to the nearest sandbar for dropping. When the gulls reach the bar, they make a vertical ascent to about 10–15 m, hover briefly before releasing the prey, and then, following the release, make a short spiral descent to the sandbar to examine the prey.

Gulls were observed dropping prey items during low tides. In order to examine the prey eaten during each observation period, I walked along sandbars just before they were covered by the incoming tide. The species and size of each prey item was recorded. The maximum anteior-posterior dimension of bivalves and gastropods, the carapace width of crabs, and the test diameter of urchins were recorded. Some prey were too badly broken to be measured. The size distributions of the major prey species available to gulls were obtained by systematically searching the grass beds exposed at low tide where the gulls normally foraged. These prey were replaced after being measured.

The vulnerability of prey was examined by dropping prey from known heights onto firmly packed sandy soil. This substrate was similar to, but slightly softer than, the sandbars normally used by gulls. Prey were dropped initially from 10.0 m, and the number of each species stunned or broken was recorded. Unopened prey were then dropped from 12.5 m, and the procedure repeated at 2.5-m intervals to a height of 22.5 m.

RESULTS

The prey dropped by Herring Gulls are listed in Table 1. Because no systematic differences occurred between the three sites, the data were pooled. Bivalves were the major prey, with the scallop (*Argopecten irradians*) accounting for over half of the observed feedings. Three species, the cockle (*Trachycardium egmontianum*), the spider crab (*Libinia dubia*), and the urchin (*Lytechinus variegatus*), were moderately important. The remaining species were only infrequently eaten. No gastropods were

TABLE 1. Prey dropped on sandbars by Herring Gulls between January and April 1979.

Prey species	Size range eaten (mm)	Number eaten	Percentage of diet	Percentage broken
Bivalves				
Argopecten irradians	41–87	186	56.0	24.0
Dinocardium robustum	55–85	8	2.4	87.5
Trachycardium egmontianum	32–53	52	15.7	78.8
Lucina floridana	36	1	0.3	100.0
Macrocallista nimbosa	87–148	6	1.8	66.7
Mercenaria campechensis	67–95	3	0.9	100.0
Decapod crustaceans				
Libinia dubia	23–87	44	13.3	100.0
Callinectes sapidus	87–90	2	0.6	100.0
Echinoids				
Lytechinus variegatus	49–58	30	9.0	100.0

dropped and eaten. Several times during the study I observed gulls turning over gastropods (*Busycon spiratum, B. contrarium,* and *Fasciolaria lilium*), but they were not carried to sandbars and dropped. The gulls did peck at the foot of each overturned snail. These snails were collected and held in a tank of circulating seawater, and all survived, with only minor damage to the opercula.

Not all prey had to be broken to be eaten (Table 1). *Argopecten* when dropped were frequently only stunned, but not broken. Gulls inserted their beaks between the gaping valves and removed the soft parts. All other prey usually had to be broken in order to be eaten. Observations with binoculars during the drops showed that bivalves broke most readily when one valve received the full impact of being dropped. Bivalves that landed on the commissure between the valves rarely broke. Crabs broke most readily when they landed upside down so that the carapace was smashed. Urchins broke at all points of impact and were usually broken further by short drops made while the gull was standing.

Comparisons of the size distributions in the grass beds and at drop sites of *Argopecten, Libinia,* and *Trachycardium* all show a consistent pattern (Fig. 1). Within a prey species, Herring Gulls show a decided preference for the largest available prey. For all three species, gulls were able to find and eat prey larger than those I could find living in grass beds. This absence of large *Argopecten, Libinia,* and *Trachycardium* in grass beds suggests that these individuals are rapidly located and consumed by gulls.

No comparison between living and dropped *Lytechinus* was possible because most urchins dropped by gulls were too badly broken to be measured. The other prey items were eaten too infrequently to allow any definitive conclusions about size selection, although several qualitative comparisons can be made. The largest *Lucina floridana* and *Macrocallista nimbosa* eaten are very similar to the maximum sizes I have observed in the grass beds. For *Dinocardium robustum, Mercenaria campechensis,* and *Callinectes sapidus,* the largest size eaten (Table 1) is considerably smaller than the largest available (106, 153, and 151 mm respectively). Despite the small sample sizes for these species, it can be concluded that the largest individuals eaten are probably very close to the largest the gulls are capable of handling, because they closely approximate the sizes of the largest prey of a similar type eaten (Table

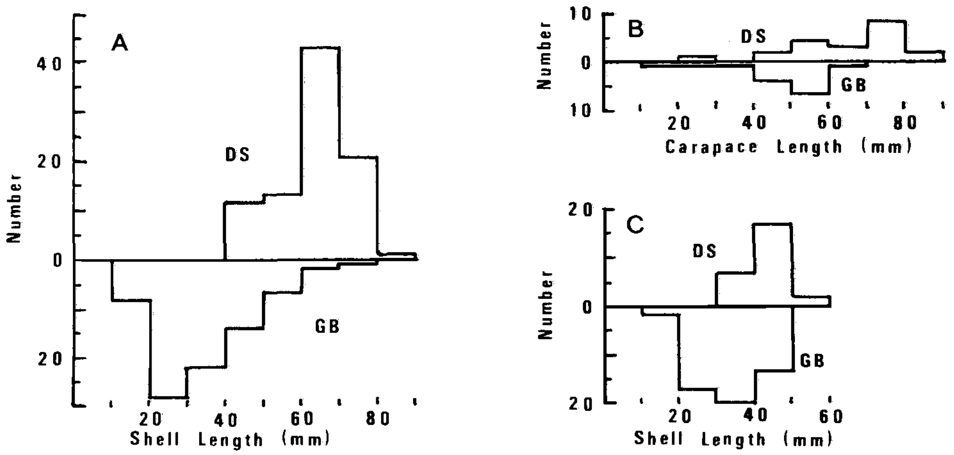

Fig. 1. Size distributions for Herring Gull prey from drop sites (DS) and grass beds (GB). A = *Argopecten irradians,* B = *Libina dubia,* and C = *Trachycardium egmontianum.*

1). The only apparent exception is *Macrocallista,* but, because of its elongate, flattened shape, it is comparatively light for its length.

Gastropods, which are very common in the grass beds but are not dropped by gulls, are much more resistant to being opened by dropping than bivalves (Table 2). The two most frequently eaten bivalves, *Argopecten* and *Trachycardium,* were readily stunned or broken, while the gastropods, *Busycon spiratum, B. contrarium,* and *Fasciolaria lilium,* were not. Stunned bivalves gaped widely and did not respond when touched. Such prey could be readily eaten by gulls.

None of the gastropods sustained any shell damage or showed a response analogous to gaping in bivalves. Snails remained deeply withdrawn into their shells throughout the experiment. After the experiment the snails were placed in a tank of circulating seawater to see if any had been stunned or killed. After 24 h, 2 *Fasciolaria,* 2 *B. spiratum,* and 3 *B. contrarium* were dead. All of the dead snails were so deeply withdrawn into their shells that they would have been unavailable to gulls. The surviving snails showed no ill effects from having been dropped.

TABLE 2. Number of prey stunned or broken when dropped on firm, sandy soil. Each prey item was dropped from progressively greater heights (10.0–22.5 m by 2.5-m increments) until it was either stunned or broken.

Prey species	*n*	Size range (mm)	Number stunned	Number broken	Percentage opened	Mean height when opened (m)
Bivalves						
Argopecten irradians	5	64–68	5	0	100.0	10.5
Trachycardium egmontianum	4[a]	44–49	2	2	100.0	16.8
Gastropods						
Busycon spiratum	5	85–93	0	0	0.0	—
Busycon contrarium	5	88–112	0	0	0.0	—
Fasciolaria lilium	5	65–78	0	0	0.0	—

[a] A fifth *Trachycardium* was broken when a *B. spiratum* was inadvertently dropped on it from 17.5 m. The *B. spiratum* was not damaged.

DISCUSSION

In order to be profitable, prey selected for dropping must be easily broken or stunned and large enough to offset the energy required to find, carry off, and drop them. Such constraints must be particularly important for gulls in areas lacking hard substrates, because prey break less readily on soft substrates than on hard ones (Barash et al. 1975). The absence of gastropods as dropped prey and the selection of the largest prey that could be handled reflect these constraints.

Gastropods, either alive or as the abode of hermit crabs, have been dropped successfully by gulls in other areas (Colton 1916, Oldham 1930, Magalhaes 1948, Harris 1965, Spight 1976). In almost all these cases snails were dropped on hard substrates. Where only soft substrate drop sites are available, snails are much less desirable prey items than bivalves because of their greater resistance to breakage (Table 2). Furthermore, bivalves need only be dropped until either stunned or broken, while gastropods may need to be dropped and broken more than once in order to extract the tissues completely (Zach 1978).

The greater durability of gastropods is not caused by differences in shell thickness. Thick-shelled *Trachycardium* (valves 1.4–1.9 mm thick) could be readily broken, while the thinner-shelled gastropods *B. spiratum* and *Fasciolaria* (0.6–1.0 mm) could not (Table 2). This difference was particularly obvious when a *B. spiratum* was accidentally dropped on a *Trachycardium* from 17.5 m. The *Trachycardium* was badly fractured, while the *B. spiratum* was undamaged.

One important difference between bivalve and gastropod shells is the internal reinforcement of the shell spire caused by the helical growth form in gastropods. Because snails deeply withdraw into their shells when handled and dropped, they tend to land on the strengthened spire, which should increase durability. Differences in the crystalline structure of the shell can also affect shell strength (Vermeij and Curry 1980), but I have not investigated this possibility.

Selection for the largest prey that can be handled for dropping has been observed previously in gulls (Siegfried 1977) and crows (Zach 1978). Large prey not only yield a larger reward than that obtained from small prey but also break more readily (Siegfried 1977, Zach 1979). Selection for the largest prey should be particularly important when prey is dropped over soft substrates. The mean number of drops needed to open a prey is greater on soft substrates than it is on hard substrates (Barash et al. 1975), causing a concomitantly higher energetic investment in each prey. The selection of the largest and most easily broken prey by the gulls in this study (Fig. 1) therefore is not surprising. Although it appears that energetic and structural constraints prevent the effective use of small prey by dropping, the data should not be construed to show that small prey are not eaten. Small prey may be swallowed whole and the empty shell later regurgitated (Colton 1916, Harris 1965). This tactic reduces the energetic investment in each prey item and allows gulls to consume small prey profitably.

Soft substrate dropping sites impose severe constraints on the prey items selected for dropping. Some prey, such as gastropods, cannot be readily broken and must be ignored. More susceptible prey can apparently only be dropped in the larger, more energetically profitable, and more easily broken sizes.

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APPENDIX. Prey species delivered to Thick-billed Murre chicks at Coburg Island and Cape Hay.

Prey species	Coburg	Cape Hay
FISH		
Arctic cod, *Boreogadus saida* (Lepechin) 1774	+	+
Arctic staghorn sculpin, *Gymnocanthus tricuspis* (Reinhardt) 1841	+	
Twohorn sculpin, *Icelus bicornis* (Reinhardt) 1841	+	
Arctic sculpin, *Myoxocephalus scorpioides* (Fabricius)	+	
Nybelin's sculpin, *Triglops nybelini* Jensen 1944		+
Sand lance, *Ammodytes* spp.[a]		+
Polar eelpout, *Lycodes truneri* Bean 1978	+	
INVERTEBRATES		
Parathemisto libellula (Lichtenstein)	+	+
Parapasiphae sulcatifrons Smith		+
Gammarus wilkitzi Birula	+	
Harmothoe spp.[a]	+	

[a] All specimens were picked up from murre breeding ledges, except *Ammodytes* spp. and *Harmothoe* spp., which were visual identifications only of prey fed to chicks. All others or very similar species were seen fed to chicks by adults.

The fifth annual meeting of the **Colonial Waterbird Group** will be held **22–25 October 1981.** A symposium on the factors affecting reproductive success in colonial birds is planned. Those interested in contributing to the symposium should submit an abstract by **1 August 1981;** abstracts for contributed papers must be received by **1 September 1981.** For information on either, contact **J. Burger, Department of Biology, Livingston College, Rutgers University, New Brunswick, New Jersey 08903.** For information on registration, contact **Brian Chapman, Department of Biology, Corpus Christi State University, Corpus Christi, Texas 78412.**

A **Conference-Workshop on Southeastern Coastal and Estuarine Birds** will be held at the field laboratory of the Belle W. Baruch Institute for Marine Biology and Coastal Research of the University of South Carolina, near Georgetown, South Carolina, **11–13 September 1981.** Those working on coastal or estuarine species in the southeast are invited to present the results of their research; presentations by graduate students are especially welcome. A limited number of graduate student awards, covering room and registration fees, are available. Contact **Keith L. Bildstein, Program Chairman, Department of Biology, Winthrop College, Rock Hill, South Carolina 29733** for information on the program or student awards; contact **Bobbie Christy, Local Chairman, Baruch Field Laboratory, P.O. Box 1630, Georgetown, South Carolina 29440** for information on registration and housing (this information will be mailed to AOU, COS, and WOS members in the southeast automatically).

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The Working Group on Granivorous Birds-INTECOL is organizing a symposium on **"The role of granivorous birds (especially Corvidae and Columbidae) in ecosystems"** in association with the Third International Congress of Ecology, to be held in Warsaw, Poland, **5–11 September 1982.** Topical areas will include population dynamics, biomass and production rates, energetics, impacts of granivorous birds in ecosystems, and management of pest situations. Inquiries regarding presentation of a paper or poster should be directed to **Prof. Dr. Jan Pinowski, Institute of Ecology PAS, Dziekanów Leśny, 05-150 Łomianki, Poland (telex 817378 IEPANPL).**

The **Meandarra Ornithological Field Study Unit** (MOFSU) was formally established as a research group of the University of Queensland, Australia, in December 1980. MOFSU is active in field research in the area of Meandarra, 300 km west of Brisbane. Major emphasis is on the behavior and ecology of communally breeding species. MOFSU welcomes visitors and volunteer field assistants in its program. MOFSU is not in a position to provide financial support for students pursuing degrees, but may accept them for work on field projects. For further information contact **Dr. Douglas D. Dow, Director, MOFSU, Department of Zoology, University of Queensland, Brisbane, Australia 4067.**

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REVIEWERS FOR *THE AUK*, 1979–1980

The Auk is fortunate to benefit from the services of many individuals who act as reviewers of manuscripts that are submitted. Their efforts are considerable, and their care and constructiveness continues to impress me an an Editor and as a sometimes author. The individuals listed below helped make publication of a journal with high scientific and scholarly standards possible; my thanks to all of them.

Individuals who have contributed reviews of two or more manuscripts are indicated by an asterisk.

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