SEXUAL DIFFERENCES IN FORAGING BEHAVIOR IN TWO SPECIES OF *DENDROCOPOS* WOODPECKERS

J. DAVID LIGON

Two recent studies on woodpeckers (Kilham, 1965; Selander, 1966) support the hypothesis of Rand (1952), which states that within a species sexual dimorphism may aid in reduction of competition for food. In an extensive discussion of intraspecific differences in foraging, Selander (1966: 143–145) diagrams the solutions open to birds faced with de-creased availability of food, and Kilham (1965) discusses possible causes, other than those directly related to food supply, for the evolution of traits that reduce intersexual competition for foraging sites. Neither author discusses in detail the problem of origin of stereotyped behavioral differ-ences between the sexes.

Sexual differences in foraging behavior of two species of *Dendrocopos*, the Red-cockaded Woodpecker (*D. borealis*) and the Arizona woodpecker (*D. arizonae*), are described in this report, and a discussion of the pos-sible origin of this phenomenon in woodpeckers is presented. These two species differ greatly in the degree of sexual dimorphism of body size and bill length, to which much importance has been attached (Selander and Giller, 1963; Selander, 1965, 1966).

The Red-cockaded Woodpecker inhabits open pine forests of the south-eastern United States. It is found only in areas where pines predominate and is probably most common on the Atlantic coastal plain. The range of this species extends northward to Virginia and Kentucky, and west-ward to Oklahoma and Texas (A.O.U., 1957).

The range of the Arizona Woodpecker extends from extreme southern Arizona and New Mexico, where it is associated with oak woodland, south into Michoacan (Davis, 1965: 537).

METHODS

The methods employed in studying the feeding habits of each species were similar. I observed individuals of each sex for extended periods of time and made notes on their feeding behavior. I timed the birds with a stopwatch as they fed in various sections of the trees. Neither species was common enough in the study areas to note the foraging techniques of an individual and then to move on to locate another, as Selander (1966: 122) did.

As time units were not independent (the feeding activities of a woodpecker in one unit, such as a minute, might influence its activities in the following minute), the length of time that a bird fed in a particular region was not tested statistically. Random single observations were tested with the chi-square, and in addition the data on *D. borealis* were tested using the Watson U-squared test. I used the Friedmann test and chi-square on the *D. arizonae* data, making the assumption (not always

Figure 1. Pine flatwoods near Gainesville, Alachua County, Florida. Photographed in August 1963.

strictly true) that where a bird fed in one tree did not influence its choice of feeding sites in the next tree visited.

Statements describing the foraging behavior of each species apply only to the populations studied. Both Kilham (1965) and Selander (1966) emphasize that intraspecific regional differences may be great due to a variety of factors. D. H. Morse (in litt.) has data suggesting that individuals of *D. borealis* forage differently in Louisiana than those I observed in Florida. Also, there may be seasonal variations in foraging patterns, as illustrated by the work of Davis (1965).

Unlike both Davis (1965) and Selander (1966), I recorded foraging behavior of adults only. I found that immature woodpeckers of both species were more labile in their foraging behavior than were adults.

D. borealis.—Observations on this species were made near Gainesville, Florida, from May 1962 to August 1963, in pine flatwoods consisting primarily of second-growth longleaf pine, *Pinus australis* (Figure 1). All detailed observations reported here were made of birds in pines. I located ten groups of *D. borealis,* each consisting of a pair or a pair plus one or more additional birds. As the sexes are indistinguishable in the field, 16 individuals were marked with colored leg bands or airplane dope in order to make individual recognition possible. I recorded foraging sites of nine individuals on repeated occasions, noting in which of three regions of the tree the bird was feeding (Figure 3).

I also obtained stopwatch timings for three different females and a single male. The male was timed for two periods exactly one month apart. All stopwatch recordings were made in February and March.

D. arizonae.—This species was studied near Portal and Apache, Cochise County, Arizona, from 20 May to 20 July 1964. In Cave Creek Canyon (Figure 2), near Portal, oaks (*Quercus*) were the most common trees and were the trees most visited

Figure 2.   Oak woodland in Cave Creek Canyon, Cochise County, Arizona. Photographed in May 1967.

by these woodpeckers. Other trees utilized in this area were sycamores (*Platanus racemosa*), walnuts (*Juglans*), pines (*Pinus*), willows (*Salix*), and Arizona cypress (*Cupressus arizonica*). Agaves (*Agave palmeri*) also were visited.

I found this species difficult to study before the young fledged, as have other workers (Brandt, 1951: 660; Swarth, 1904). Territories are large and the birds are silent and rather secretive at this time. Often when an individual was located, it soon made a long flight and became lost to view. This was especially true on the steep, oak-covered hillsides of Cave Creek Canyon. Detailed foraging observations and stopwatch timings of four males and three females were obtained. The trees were divided into trunk, limbs and branches, and twigs, in a manner similar to that described for the pines. I made stopwatch timings for females on 159 trees and for males on 63 trees. Most of the trees used were medium-sized oaks.

TABLE 1
USE OF FORAGING SITES BY *Dendrocopos borealis*

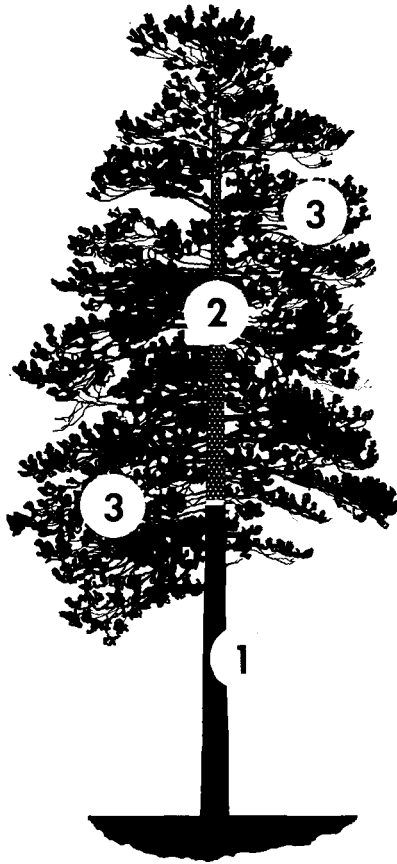|	Male		Females	
Location	Time in seconds	Per cent	Time in seconds	Per cent
Trunk below 15 feet	225	4.2	6,091	77.5
Trunk above 15 feet	2,665	50.4	1,703	22.5
Limbs and branches	2,416	45.4	0	0
Totals	5,306	100.0	7,794	100.0

Figure 3. Longleaf pine, showing the subdivisions of foraging sites of *D. borealis*. 1. Trunk from ground level up to about 15 feet. 2. Remainder of trunk. 3. Limbs, branches, and needles.

RESULTS

Differences in foraging sites of males and females of each species are statistically significant at the 0.01 probability level.

D. borealis.—Males of this species forage primarily high in the pines and to a large extent on the branches, whereas females forage almost entirely on the trunk (Table 1). This distinct difference was seen at all seasons, but both sexes fed on pine cones in fall and winter.

A bird foraging on the trunk may remove the shingle-like bark by flaking it off with the bill, or it may grasp pieces of bark with the bill or insert the bill under the bark and pry it off. The feet are also important tools in trunk foraging, especially in females. The woodpecker

TABLE 2

USE OF FORAGING SITES BY *Dendrocopos arizonae*

	Males		Females	
Location	Time in seconds	Per cent	Time in seconds	Per cent
Trunk	4,421	73.5	5,646	39.4
Limbs and branches	1,558	25.9	6,094	42.5
Twigs	37	0.6	2,590	18.1
Totals	6,016	100.0	14,330	100.0

may grasp a piece of bark with its feet and pull it free by flying a few inches away from the tree. It then returns to the spot from which the bark was removed. Bark is often scratched away by both feet simultaneously. A common technique is for the woodpecker to back down the tree, flaking bark away with the feet and picking up exposed prey with the bill. Occasionally a bird pulls away bark with one foot while grasping the tree with the other.

Males often peck directly on small limbs, rather than with glancing or

TABLE 3

MEASUREMENTS OF *Dendrocopos borealis* AND *Dendrocopos arizonae*[1]

Item	Sex	N	Mean	Standard deviation	Coefficient of variation
Dendrocopos borealis[2]					
Culmen	♂	29	16.93	0.69	4.10
	♀	20	16.51	0.57	3.45
Tarsus	♂	31	17.98	0.85	4.74
	♀	21	17.70	0.76	4.32
Wing	♂	31	115.30	3.95	3.42
	♀	23	116.01	2.01	1.73
Weight[3] (g)	♂	5	42.4		
	♀	4	45.3		
Dendrocopos arizonae[4]					
Culmen	♂	126	22.43	1.16	5.17
	♀	79	19.25	0.89	4.62
Tarsus	♂	121	19.48	0.65	3.34
	♀	74	18.43	0.61	3.31
Wing	♂	107	115.04	1.90	1.65
	♀	77	111.75	1.98	1.77
Weight[5] (g)	♂	11	49.4	2.32	4.68
	♀	5	44.1	1.31	2.97

[1] Measurements in mm.

[2] All specimens adult and all from Florida.

[3] From Hartman (1955). The standard error for males is 3.5 and for females is 3.2.

[4] From Davis (1965). His "Arizona combined" values were used.

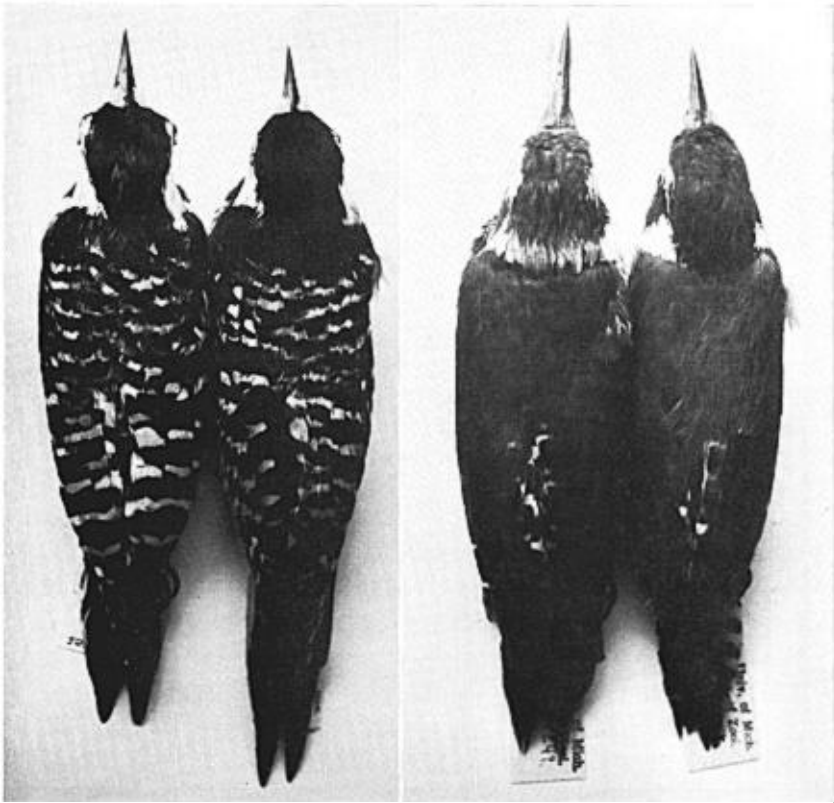[5] Data provided in part by J. Davis.

Figure 4. Dorsal view of a pair of *D. borealis* on the left and *D. arizonae* on the right. Males are to the left. The different degree of sexual dimorphism in bill length in the two species shows clearly.

flaking blows. They frequently move along the underside of limbs, hanging upside down as they progress, sometimes dropping to a lower limb without returning to the trunk.

Adults were never observed on long-dead trees. However, trees that have recently died and which still bear needles are apparently rich sources of food. Red-cockadeds were attracted to recently burned areas where the needles on the trees had been killed by heat. They were never seen to feed on the ground.

No statistically significant differences were found between the sexes either in bill length or body size in Florida populations of *D. borealis* (Table 3; Figure 4). Unlike the situation in some species, e.g. *Centurus striatus* (Selander and Giller, 1963; Selander, 1966), the striking sexual

TABLE 4
RATE OF TREE[1] VISITATION BY *Dendrocopos arizonae*

Sex	Time[2]	No. trees	No. trees/hr.
Female	0800–0900	47	47[3]
Female	0700–0735	29	50
Female	0735–0755	23	69
Male	1433–1443	10	60

[1] All oaks of medium height (12–15 feet).

[2] Mountain Standard Time.

[3] In one tree for 14 minutes.

differences in foraging behavior observed in this species could not have been predicted from an examination of preserved specimens.

D. arizonae.—This species also shows some segregation of foraging sites, but there is a large amount of overlap (Table 2). Behavioral differences are apparently correlated with morphological ones (Table 3; Figure 4) that probably result in differences in foods taken. Selander (1966: 124) found foraging differences to be quantitative rather than qualitative in the strongly dimorphic species, *Centurus striatus,* and this also appears to be the situation in *D. arizonae.* Individuals of both sexes peer into and examine crevices in the rough oak bark, but males, with their longer beaks, appear to probe into holes and cracks more than do the females. No females were seen making deep excavations in search of prey, whereas males engaged in such activities on several occasions. In one instance I watched a male work on an excavation in the trunk of a living sycamore for more than 14 minutes before he extracted a large grub. The hole from which he removed the larva extended 1½ inches into the living tree. Females are more likely to flake off superficial bark than are males, and a female was once seen to remove bark with her feet by scratching the way *D. borealis* females do.

Members of both sexes often cover much tree surface rapidly (Table 4), flying or jumping from tree to tree. One female visited 46 trees in a 1-hour period. She remained in a single oak for 14 minutes of the hour gleaning insects from the outer twigs and leaves. This tree was one of the few in the vicinity with lush foliage.

ADAPTIVE SIGNIFICANCE

In *D. borealis* the advantages of intraspecific specialization seem obvious. Males and females of *D. borealis* stay together and utilize the same large area throughout the year (Ligon, MS). They are sometimes gregarious and several individuals may be seen foraging on the same tree simultaneously. Segregation of foraging areas reduces possible intersexual

competition. By utilizing only a portion of the tree, members of each sex can specialize to a greater degree in foraging techniques. Use of the feet by females may be an example of this.

D. arizonae typically does not forage in groups, but both members of the pair feed in the same territory and often maintain contact vocally. The use of different foraging stations or techniques by each member of the pair presumably increases efficiency in food gathering.

In some woodpeckers incubation begins before the clutch is complete, often resulting in starvation of the last-hatched young (Skutch, 1956). Such starvation occurred in both species considered here (Ligon, MS) and further suggests that food may sometimes be a limiting factor in these woodpeckers.

Another explanation of sexual differences in foraging, first presented by Kilham (1965), is not directly related to food supply. In all woodpeckers thus far studied, both sexes cooperate to a large degree in all phases of the breeding cycle. The pair is together for some time prior to nesting, "building up social bonds which will enable the members of a pair to meet the hazards of raising young in effective cooperation" (Kilham, 1965: 143). Other authors also have mentioned the importance of "teamwork" (Lawrence, 1967: 57) or "harmony" (Skutch, 1948: 254) between mated woodpeckers. Antagonistic and sexual drives of woodpecker pairs are delicately balanced. On occasion antagonism predominates after nesting has commenced (Kilham, 1966), in at least one known instance resulting in breeding failure (Skutch, 1948: 252). By foraging at different sites or in different manners chances of hostile interactions between mates are decreased. A secondary result is more efficient utilization of the habitat, further increasing reproductive success.

Variation in Bill Size

The lack of significant sexual dimorphism in beak length in D. borealis (coefficient of difference 0.33, see Mayr et al., 1953) despite the pronounced differences in foraging sites utilized may be a result of several factors. (1) Both sexes of D. borealis feed on superficial layers of the trees and do not make deep excavations for prey with their bills. (2) Females, which feed almost entirely on the trunk, frequently use their feet to remove heavy layers of bark. (3) The sexual differences in foraging behavior in the Florida populations may be of recent origin, resulting from the utilization of smaller second-growth timber, which possibly is poorer in food resources than mature trees.

The habitat of D. arizonae is fragmented at its northern end (see Davis, 1965: 538, Figure 1), producing an island-like situation. Like many of the insular species discussed by Selander (1966: 129), the sexes have

little overlap in culmen length (coefficient of difference 1.55, indicating a 94 per cent nonoverlap). The rarity of other species of woodpeckers of a similar adaptive type apparently has allowed this species to expand its foraging potential through increased sexual differentiation.

The high degree of intrasexual variability of bill length in *D. arizonae* (Table 3) may be a result of a somewhat restricted gene flow between populations in which slightly different selective forces operate on bill size. Beak size appears to be rapidly and strongly influenced by natural selection in some woodpeckers, as both absolute and relative differences in bill length between the sexes may vary widely from subspecies to subspecies (see the Ladder-backed Woodpecker, *D. scalaris*, Davis, 1965: 567, Figure 7).

Evolution of Sexual Dimorphism in Foraging

In attempting to explain the origin of sexual dimorphism in foraging tools or behavior in the woodpeckers considered here, I have assumed that several aspects of general woodpecker biology preceded sexual differentiation of foraging. One of these is dominance of the male. The male is dominant in *D. borealis* and *D. arizonae*, as well as in the Hairy, *D. villosus* (Kilham, 1965) and Downy, *D. pubescens* (Staebler, 1949: 120) woodpeckers. Secondly, males are larger than females in most species of woodpeckers. These traits can be considered as preadaptations for sexual dimorphism of foraging.

The male utilizes its dominance to forage in the most productive portions of the trees, with the female giving way and feeding in less desirable areas. Selander (1966: 118) suggests that female woodpeckers of the species that he studied may have changed more than the males, indicating that the females have adjusted to the dominance of their mates. By the nature of their anatomical specializations woodpeckers seem to be primarily adapted to foraging on tree trunks and large limbs; thus the trunk is here assumed to be the original or basic foraging station. Pecking and excavating on trunks is done more by males than by females of *Centurus striatus, C. aurifrons* (Selander, 1966: 124, 127), and *Dendrocopos villosus* (Kilham, 1965). Males of *D. stricklandi* (Ligon, 1968) and *D. arizonae* (present study) forage on the trunk more than do the females. In these species the tendency for larger size and longer bills in the males may have been accentuated by selection for sexual differences in foraging sites or manner.

In *D. borealis*, on the other hand, the males forage largely on the branches and the sexes are alike in size and bill length (Table 3). Because of the dominance of males to females, the assumption is maintained that the most productive foraging sites are utilized by males. The trunks of

the small second-growth pines might be poorer in food resources than the limbs and branches; however, this has not been studied. I suggest that males may have become somewhat reduced in size as a result of selection for efficient branch foraging. Why have they not become even smaller? In contrast to many species of woodpeckers in which the nest cavity is excavated by both members of the pair, *D. borealis* makes no new excavation for the nest site. The female instead lays the eggs in the permanent roost cavity of the male (Ligon, MS). Thus the males cannot be much smaller than females. In the males selection may be balanced for small size for feeding on small branches and large enough size to excavate cavities that will readily admit females. Loss of dominance by the males is another possible consequence of smaller size and is perhaps of even greater importance.

ONTOGENY OF FORAGING BEHAVIOR

Kilham (1965) observed that males of *D. villosus* appeared by habit or innate behavior to be unable to work in the manner of females. Selander (1966: 128) states that the morphological differences in bill and tongue structure could alone account for differences in foraging behavior in the species that he studied, by each sex's learning where its foraging apparatus was most effective. This is probably also true of the strongly dimorphic *D. arizonae*.

The problem is possibly more complex in *D. borealis* where, although the sexes have conspicuous differences in foraging behavior, no corresponding morphological ones are manifest. Dependence of the juveniles on their parents for food is unusually long in this species. Immature birds are fed to some degree by the adults for five or more months after fledging (Ligon, MS).

The long period of juvenile dependency may be connected to the specialized foraging behavior of adults. If specialized foraging requires a long learning period, premature independence would be disadvantageous. A possible example of such specialized behavior is the removal of bark with the feet by females. I never saw this in males of *D. borealis*.

RELATIONS WITH OTHER SPECIES

D. borealis.—I could detect no differences in either feeding sites or methods between male *D. borealis* and *D. pubescens*. It is perhaps significant in this regard that *D. borealis* was often antagonistic to *D. pubescens*, driving it away from trees in which both species foraged. In contrast, *D. borealis* and Red-bellied Woodpeckers (*Centurus carolinensis*) often fed in close proximity, apparently without antagonism.

D. arizonae.—I observed no interspecific interactions related to foraging

in which this species was involved, although *D. arizonae* overlaps some-
what with its congeners *D. scalaris* and *D. villosus* during the breeding
season (cf. Davis, 1965: 549). Near Apache, Arizona, the oaks are in low
areas following a broad valley. The surrounding hillsides are almost tree-
less but are dotted with agaves. Here *D. scalaris* forages primarily on
the hillsides, but also comes downhill into the oaks and thus into the
territories of *D. arizonae*. In Cave Creek Canyon a pair of *D. villosus*
nested near the Southwestern Research Station in 1965 and 1967, within
the altitudinal belt given by Davis (1965: 549) for *D. arizonae*. On 14
May 1965 I saw a male of *D. arizonae* come from his nest near the station
and drive away an individual of *D. villosus* that had drummed near his
nest.

Trunk Foraging

Exaggerated sexual dimorphism in bill size, with correlated differences
in foraging behavior, have thus far been demonstrated most convincingly
in trunk-foraging species. The Huia (*Neomorpha acutirostris*) of New
Zealand is the classic example of this (Oliver, 1955: 518). This species
and the woodpeckers that have been studied share several features that
may accentuate these sexual differences. (1) In *D. borealis, Neomorpha,*
and to some extent *D. arizonae,* the members of a pair move through
their territory together, maintaining contact. This in itself might lead
to friction if competition for the same foraging sites were strong. The pair
bonds are long or permanent in these species, thus compatibility is of
great importance. (2) Food may be less accessible on the trunk, with
trunk foragers expending a greater amount of energy in foraging activities
than birds feeding elsewhere. Davis (1965: 559, 561) discusses the ap-
parent correlation between the types of trees used in foraging and bill
size, which suggests that food may be difficult to obtain on the trunk.
(3) Sexual differences in feeding behavior may exist in many bird species,
as suggested by Selander (1966: 141), but might be more subtle in non-
trunk foragers. Differences in beak proportions or sizes are perhaps
usually more important in trunk foragers, although behavioral and loca-
tional differences can be the most apparent factors, as in *D. borealis* and
apparently also in the Brown-headed Nuthatch, *Sitta pusilla* (Norris,
1958: 253).

SUMMARY

The Red-cockaded (*Dendrocopos borealis*) and Arizona (*D. arizonae*) woodpeckers demonstrate sexual differences in foraging behavior. In the former species there is little morphological correlation with the behavioral differences, whereas in the latter a pronounced sexual difference in bill length exists.

Males of *D. borealis* forage to a large degree on the branches and twigs of pines, while the females forage almost exclusively on the trunk, often at low elevations. The two sexes of *D. arizonae* also forage in different parts of the trees but overlap much more than in *D. borealis*. In *D. arizonae* the differences in beak size can be correlated with differences in foraging techniques, thus the sexes may utilize the same portions of the trees in somewhat different ways.

Two possible mechanisms for the evolution of sexual foraging differences are discussed. The first assumes a limited food supply, with selection favoring those individuals that are most efficient in utilizing the food resources of their habitat. Dominance of one sex (male) is suggested as an important factor in stabilizing sexual differences in feeding behavior. Secondly, differences in foraging could have arisen primarily by selection for those birds that cooperate best with their mates. A secondary result of selection for increased compatibility is a more efficient utilization of the habitat.

Possible reasons that some trunk foragers appear to demonstrate sexual differences more conspicuously than do birds that do not forage on trunks include: (1) the long-term nature of the pair bond in some species requiring compatibility between members of the pair; and (2) a reduced accessibility or quantity of foods on tree trunks as compared with other foraging sites.

LITERATURE CITED

AMERICAN ORNITHOLOGISTS' UNION. 1957. Check-list of North American birds. Fifth edit. Baltimore, Amer. Orn. Union.

BRANDT, H. 1951. Arizona and its bird life. Cleveland, Bird Research Foundation.

DAVIS, J. 1965. Natural history, variation, and distribution of the Strickland's Woodpecker. Auk, **82:** 537–590.

HARTMAN, F. A. 1955. Heart weight in birds. Condor, **57:** 221–238.

KILHAM, L. 1965. Differences in feeding behavior of male and female Hairy Woodpeckers. Wilson Bull., **77:** 134–145.

KILHAM, L. 1966. Nesting activities of Black-backed Woodpeckers. Condor, **68:** 308–310.

LAWRENCE, L. DE K. 1967. A comparative life-history of four species of wood-peckers. Orn. Monographs, **5**: 1–156.

LIGON, J. D. 1968. Observations on Strickland's Woodpecker, *Dendrocopos strick-landi*. Condor, **70**: 83–84.

MAYR, E., E. G. LINSLEY, AND R. L. USINGER. 1953. Methods and principles of systematic zoology. New York, McGraw-Hill.

NORRIS, R. A. 1958. Comparative biosystematics and life history of the nuthatches *Sitta pygmaea* and *Sitta pusilla*. Univ. California Publs. Zool., **56**: 119–300.

OLIVER, W. R. B. 1955. New Zealand birds. Wellington, A. H. and A. W. Reed.

RAND, A. L. 1952. Secondary sexual characters and ecological competition. Fieldiana-Zoology, **34**: 65–70.

SELANDER, R. K. 1965. Sexual dimorphism in relation to foraging behavior in the Hairy Woodpecker. Wilson Bull., **77**: 416.

SELANDER, R. K. 1966. Sexual dimorphism and differential niche utilization in birds. Condor, **68**: 113–151.

SELANDER, R. K., AND D. R. GILLER. 1963. Species limits in the woodpecker genus *Centurus* (Aves). Bull. Amer. Mus. Nat. Hist., **124**: 213–274.

SKUTCH, A. 1948. Life history of the Golden-naped Woodpecker. Auk, **65**: 225–260.

SKUTCH, A. 1956. Roosting and nesting of the Golden-olive Woodpecker. Wilson Bull. **68**: 118–128.

STAEBLER, A. E. 1949. A comparative life history study of the Downy and Hairy woodpeckers (*Dendrocopos pubescens* and *Dendrocopos villosus*). Ph.D. thesis, unpublished, Ann Arbor, Univ. of Michigan.

SWARTH, H. S. 1904. Birds of the Huachuca Mountains, Arizona. Pacific Coast Avif., **4**: 1–70.

Department of Biology, Idaho State University, Pocatello, Idaho.