FORAGING ECOLOGY OF STRICKLAND'S WOODPECKER IN ARIZONA

HANS WINKLER

Davis (1965) was the first to shed light on many problems regarding the systematics, morphology, and ecology of Strickland's Woodpecker (*Picoides stricklandi*). Drawing arguments from all these fields he showed that the forms with plain backs and those with barred backs are similar enough to each other to be considered 1 species. The northern populations of the "*arizonae*" form of the species (those from Arizona, NW Mexico, N Sinaloa, S Sinaloa, Nayarit, W Michoacán, Tzitzio-Las Trojes), according to him, differ ecologically more from southern "*arizonae*" populations than all of these differ from "*stricklandi*" (México, Veracruz) populations. The woodpeckers of northern Mexico, Arizona, and New Mexico seem to prefer oaks as feeding stations whereas the other populations live in pine forests (Davis 1965). The birds of the Chiricahua Mountains belong to the populations which are believed to prefer oaks (see Davis 1965). Balda (1967) found only a few Strickland's Woodpeckers in his oak woodland study area in the Chiricahua Mountains. He recorded more in the oak-juniper woodland and in the riparian canyon both of which contain some pines (mainly Apache pine [*Pinus engelmannii*] and Chihuahua pine [*P. leiophylla*]). Ligon (1968 a,b) made observations both on "*stricklandi*" and "*arizonae*" and confirmed Davis' findings on ecology. He also found ecological differences between the sexes in these woodpeckers that parallel morphological differences. In "*stricklandi*" the sexes differed predominantly in the selection of different portions of the trees and in "*arizonae*" they differed mainly in methods of foraging (Ligon 1968a). However, the data (Ligon 1968b) seem to me not totally convincing in this respect. In both cases, males, which have the longer bills, appeared to prefer the lower regions of a tree, i.e., the trunk.

Various studies on other species of *Picoides* showed that marked differences in feeding behavior due to different ecological situations might occur (Austin 1976; Hogstad 1976; Jackson 1970; Skoczylas 1961; Travis 1977; Winkler 1972, 1973; for a general discussion of the problems involved see Curio 1975). Davis (1965) indicates that shifts can also be found in the Strickland's Woodpecker's feeding behavior. Because of the importance of such studies in ecological comparisons (Selander 1965), I provide here further evidence of variation in the behavioral ecology of this species.

METHODS

My studies were carried out in the Chiricahua Mountains, Cochise Co., Arizona, in some of the same areas where Ligon and Davis worked. The main habitat investigated was the riparian woodland along the South Fork of Cave Creek Canyon down to the Portal Ranger Station. Other observations were made in the woodland around the Southwestern Research Station of the American Museum of Natural History. I observed the woodpeckers from 12 March to 6 May 1974 (excepting 14–18 April). Ecological data were obtained by walking slowly and irregularly through the habitats. For the analysis of feeding techniques and feeding strata I included only what the bird was doing when I first encountered it. I followed a bird as long as the bird showed no signs of alarm, or until I lost contact with it. As in previous studies (Winkler 1973), I rejected from analyses foraging data obtained within 1 h before sunset, data from encounters that resulted from my having heard the bird pecking, and data on feeding activities occurring during or closely after interactions with other Strickland's Woodpeckers. Data edited in this way should be statistically reliable. In order to get estimates of the various activities of the woodpeckers for estimates of a time budget, I determined the relative frequencies of 5 min intervals in which a particular activity was recorded at least once. A total of 2907 intervals (practically the entire time spent in woodpecker occupied areas) served as a basis for these estimations, the assumption being that my method of observation (including observations at trees with holes) did not systematically influence the data (a safe assumption at least for the very far reaching signals).

At least 5 pairs of Strickland's Woodpeckers were observed. At first I analyzed data by 10-day periods, though statistical analysis justified lumping ecological data into 2 seasonal subunits: (1) the period between 12 March and 20 April, and (2) the period from 21 April to 6 May.

RESULTS

Fig. 1 gives the proportion of tree species used by male and female Strickland's Woodpeckers in the riparian canyon. Only those observations that showed the woodpeckers pecking were considered. Thus possible distortion resulting from the use of all feeding techniques was excluded. Considering Balda's (1967) data on the plant species composition and these findings, it is readily seen that both sexes preferred pines during the first seasonal segment. Through application of coefficients of selection (Jacobs 1974) it appears that during the nesting season (21 April to 6 May), males used pines roughly in proportion to their abundance (the same is true when comparing frequencies) and preferentially used Arizona sycamores (*Platanus wrightii*) in both seasonal subunits particularly the later one. Females used pines slightly more than males in both seasonal divisions. Neither sex preferentially used oaks as a pecking substrate, but rather, seemed to avoid them. Differences between the sexes ($\chi^2 = 5.560$, N = 79) were not significant during the first period. They are significant in the second of the 10-day periods ($\chi^2 = 10.965$, P < 0.05, N = 25). However, if the records of males on sycamores are lumped with the category "other trees,"

FIG. 1. Proportion (with 95% confidence limits) of tree species used by female (N = 32, 13) and male (N = 47, 12) Strickland's Woodpeckers. The relative density values of the corresponding tree species are shown in the bottom row based on data from Balda (1967).

P: Apache pine (*Pinus engelmannii*), Chihuahua pine (*P. leiophylla*), and ponderosa pine (*P. ponderosa*) combined. Q: three oak species (*Quercus arizonica, Q. rugosa,* and *Q. emoryi*) combined. h: Silverleaf oak (*Q. hypoleucoides*). w: Arizona sycamore (*Plantanus wrightii*). O: other trees including agave *Agave* sp. and alligator juniper (*Juniperus deppeana*). All data from the South Fork of Cave Creek Canyon, Chiricahua Mts., Arizona.
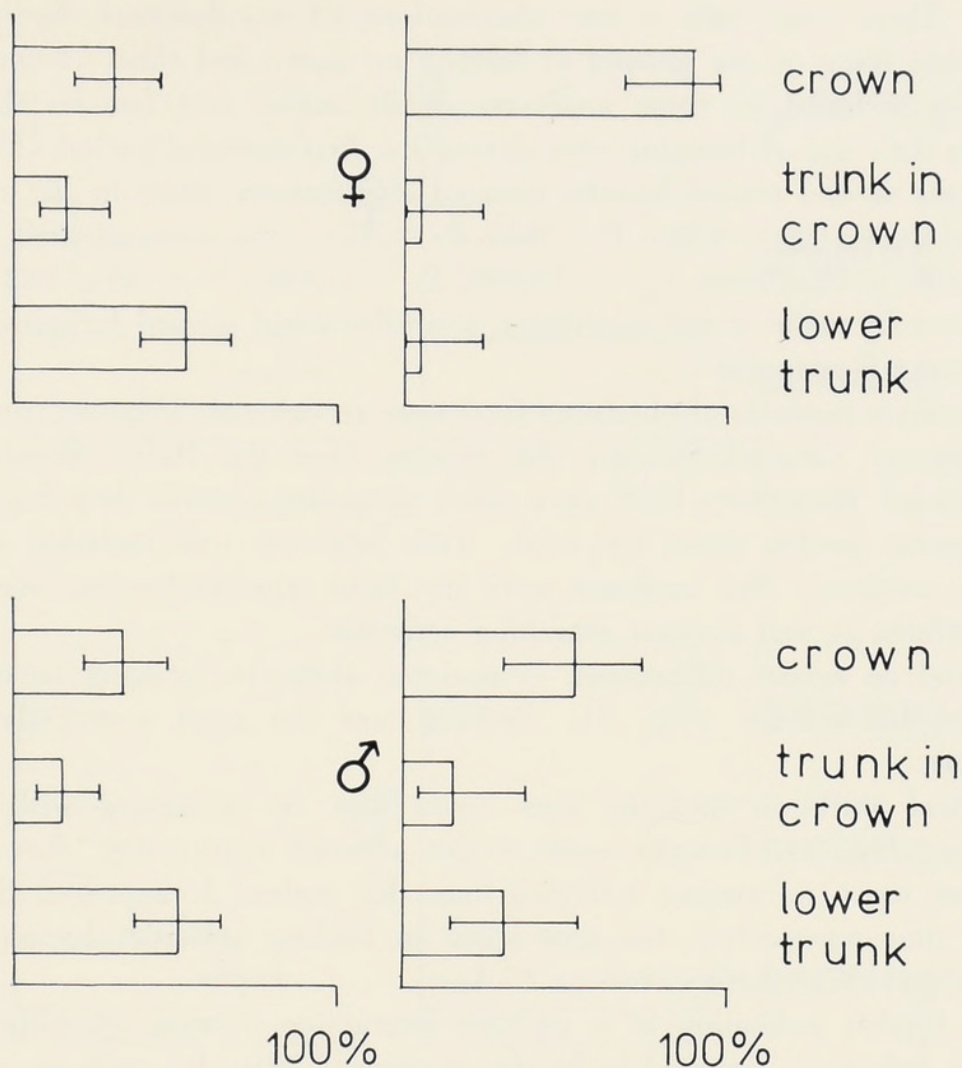
FIG. 2. Relative use (with 95% confidence limits) of the parts of a tree by female (N = 49, 16) and male (N = 59, 19) Strickland's Woodpeckers. Data from the first seasonal period (12 March–20 April) are given on the left and from the second one (21 April–6 May) on the right.

these differences disappear. In the last week 2 females were almost always found in 1 dead Douglas-fir (*Pseudotsuga menziesii*) and these might bias the data considerably (also those in the sections below). Differences between the seasons for females were significant ($\chi^2 = 24.995$, P < 0.005, N = 45) and for males ($\chi^2 = 19.995$, P < 0.001, N = 59).

Silverleaf oaks (*Quercus hypoleucoides*) have a smooth bark whereas the other oaks (*Q. arizonica, Q. rugosa, Q. emoryi*) have a rough furrowed bark and therefore were separated in the analysis. The woodpeckers only hammered vigorously on silverleaf oaks.

To facilitate further analysis of foraging (all activities) 3 subdivisions of a tree were recognized: trunk below crown, trunk within crown, and the

crown. There were only a few observations of woodpeckers feeding on dead limbs lying on the ground or feeding on agave and these observations were not included in these analyses. While males and females did not differ in their use of foraging sites during the first seasonal period (Fig. 2), during the second period females foraged significantly more in the crowns than did males ($\chi^2 = 5.018$, P $<$ 0.05, N $=$ 35). The seasonal shift shown by females is significant ($\chi^2 = 15.996$, P $<$ 0.0005, N $=$ 65), and while that shown by males is not significant, a similar trend toward foraging more in the crown is apparent.

Three main methods of obtaining food were recognized: gleaning, probing, and pecking. Characteristically this species (and the Hairy Woodpecker [*P. villosus*], Kingsbury 1932, pers. obs.) excavates narrow, deep holes and subsequently probes them for food. This behavior was included in the pecking category. Not analyzed were the light taps used when searching bark surfaces as well as other searching activities.

I found no sexual differences, or seasonal shifts in foraging techniques used by this species (Fig. 3). Pecking was the most commonly used technique.

Seasonal shifts in foraging sites could also be associated with other activities (Fig. 4). Females seem to be affected more; e.g., they spent 1.2 times more in nesting activities than did males. It appeared that as nesting time approached, the time spent in feeding activities became less. I first observed incubating birds on 27 April.

As a further indication of a possible interaction between signalling and foraging behavior, it should be briefly mentioned that also such an activity as acoustic behavior is "stratified." Both males and females gave 75% of their rattles (66 analyzed) and 60% of their call notes (70 analyzed) in the crown. I found that 74.3% of the drumming (40 analyzed) was also performed in the crown.

DISCUSSION

The data presented here show that the woodpeckers change their foraging habits in conjunction with internal and external changes. This relates to the problem of generalists vs. specialists. In short (Alcock 1975, Curio 1975, Morse 1971), "generalist" feeding should occur during food shortage and "specialist" feeding during high prey availability, but this seems to be in contrast to the findings of this as well as other studies (Curio 1975). The designations "specialist" or "generalist," respectively, indicate according to Morse (1971) whether an individual "concentrates the majority of its activities on one or a few categories" or whether it uses "several
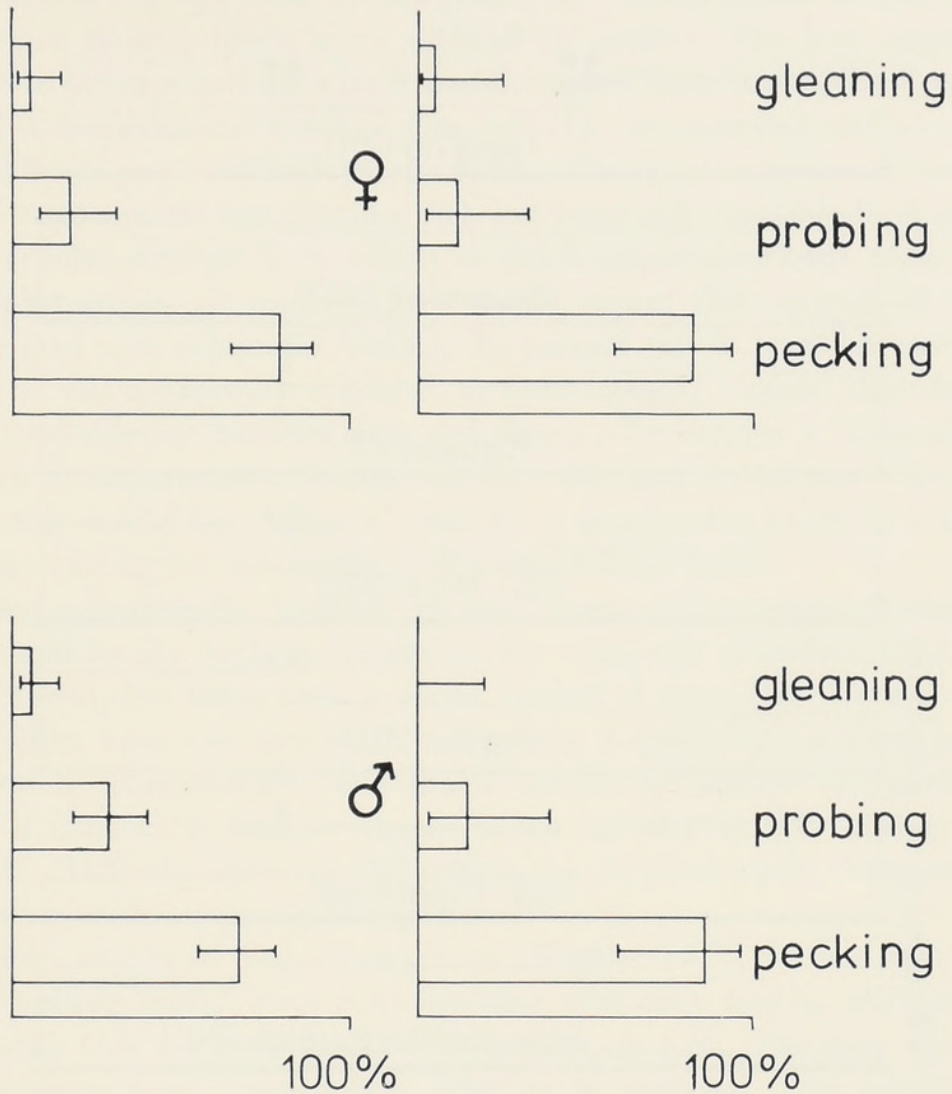
Fig. 3. Relative frequency (with 95% confidence limits) of the feeding techniques employed by female (N = 42, 17) and male (N = 72, 14) Strickland's Woodpeckers. Data from the first seasonal period (12 March–20 April) on the left and from the second one on the right (21 April–6 May).

categories with considerable frequency." One approach to this problem is to look at the possible behaviorial mechanisms and strategies underlying these categories. Two such strategies may be discerned. The first one I would call "schematic feeding," schematic because the behavioral elements exhibit low diversity, because they often are stereotyped (fixed action patterns), and because their interplay is quite fixed. Morphological features connected with this behavior are often regarded as highly specialized and well adapted. These traits, then, correspond to an environmental situation that provides predictable, though very often sparse, resources that have to be exploited efficiently.
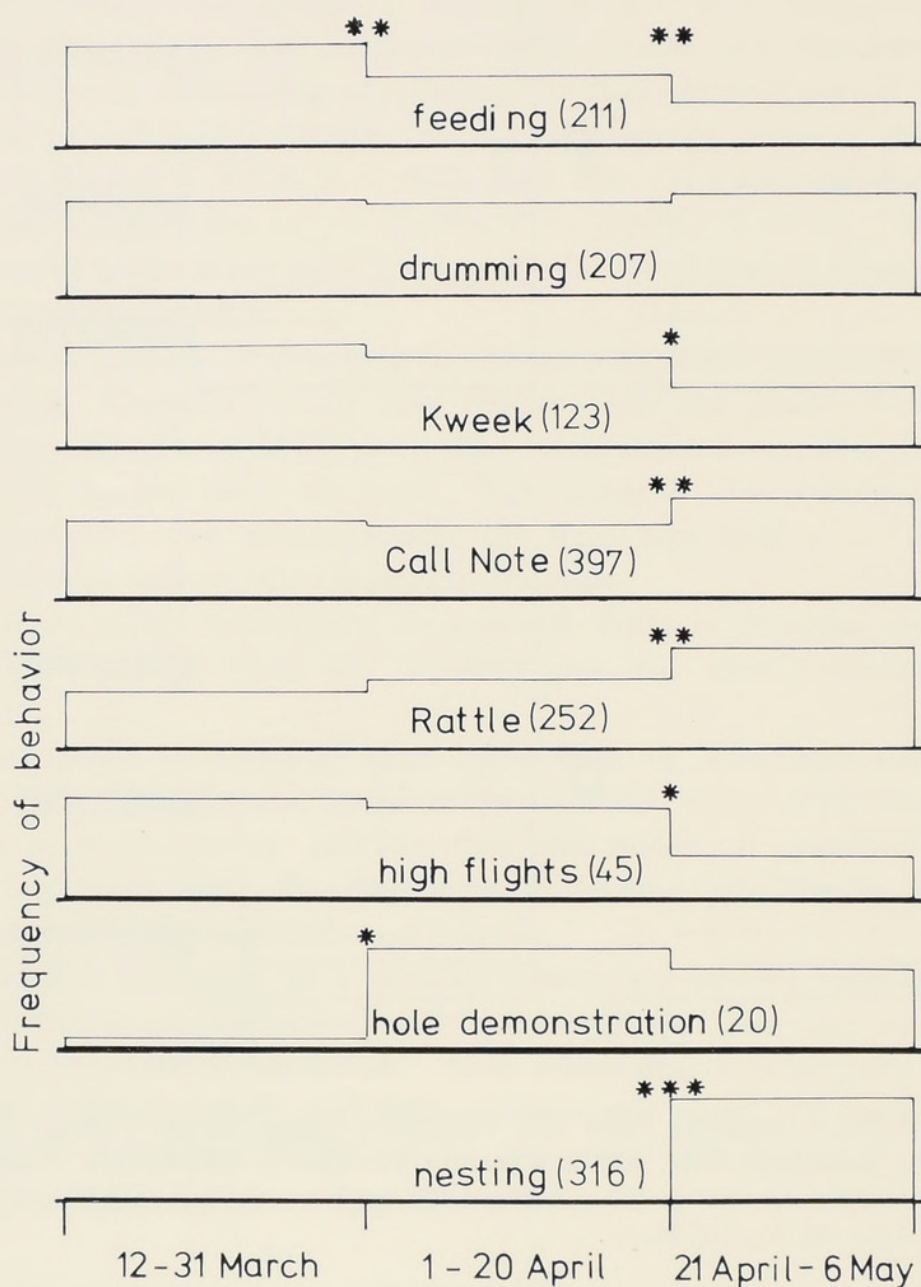
FIG. 4. Seasonal shifts in frequency of some behavior of Strickland's Woodpeckers. Drumming is a signal given by males; *kweek* is a call of females; call notes and rattles are vocalizations used by both sexes. "High flights" denotes long distance flights well above the tree tops. Hole demonstration behavior is a combination of visual and acoustical signals used by the birds for announcing prospective nesting holes. Asterisks denote the 0.05(*), 0.01(**), and 0.001(***) significance levels for the differences between adjoining periods (x^2, based on the frequency of 5 min intervals in which the respective activity was recorded, see text). For the sake of better illustration, data were scaled after the largest section of each category. Total frequencies are given in brackets.

The second strategy shall be designated as "opportunistic feeding." Here behavior is diverse, hence more difficult to predict. The low adaptiveness of some techniques and associated morphological structures (like flycatching in pied woodpeckers, *Picoides*) can only be compensated for by a high availability of prey with high energy yield. This set of responses is associated with an environment that provides rich but temporally variable food supplies.

The general strategy is to switch or grade opportunistically from one of these substrategies to another. One would expect that specialized feeding is associated with schematic feeding. In general this is true, but specialized feeding is not exclusively confined to that category, hence, the aforementioned contradiction between data and theory. To become a "generalist" or to switch to opportunistic feeding has its costs, and it does not always pay; it obviously would be a waste of time for a woodpecker to sit in a tree top in winter waiting for the chance to flycatch a large insect.

Within opportunistic feeding, in accordance with present theory, temporally and locally high specialization for one, very abundant food source can be found, but taken over a longer period of time (see Winkler 1972), over a wider area and over more individuals, a generalistic pattern emerges. Furthermore opportunistic individuals should generalize temporally and locally if demand is high or supply is low as long as this strategy yields a payoff. Thus the apparent difficulties can be resolved by acknowledging the duality in the meaning of "specialist."

Previous studies of pied woodpeckers (Winkler 1973) showed that during the pre-nesting season conditions favoring schematic feeding are prevalent. This seems true for Strickland's Woodpecker as well. The data also show that the increase of opportunistic behavior is stepwise. Tree selection was affected first; males and females showed equally marked shifts. Stratum selection changed less drastically and more in females, who seemed to be under more stress, than in males. Therefore one can conclude that stratum selection is more conservative than tree species selection. Finally, the feeding techniques were unaffected. They may become affected, however, when the nesting season proceeds and the necessity for opportunistic feeding further increases. Data from other woodpeckers and also the observations of Davis (1965) and Ligon (1968a) support this assumption for Strickland's Woodpecker. These concepts are illustrated in Fig. 5.

Differences between the sexes seem to arise in *P. stricklandi* (not, for instance, in the Downy Woodpecker [*P. pubescens*], pers. obs.) during the time of opportunistic feeding only. Conclusions are thus difficult to draw; the very nature of opportunistic feeding, as it is thought of here, may give rise to a strong bias resulting from the feeding habits of individual birds in particular situations. Both Davis (1965) and Ligon (1968b) made
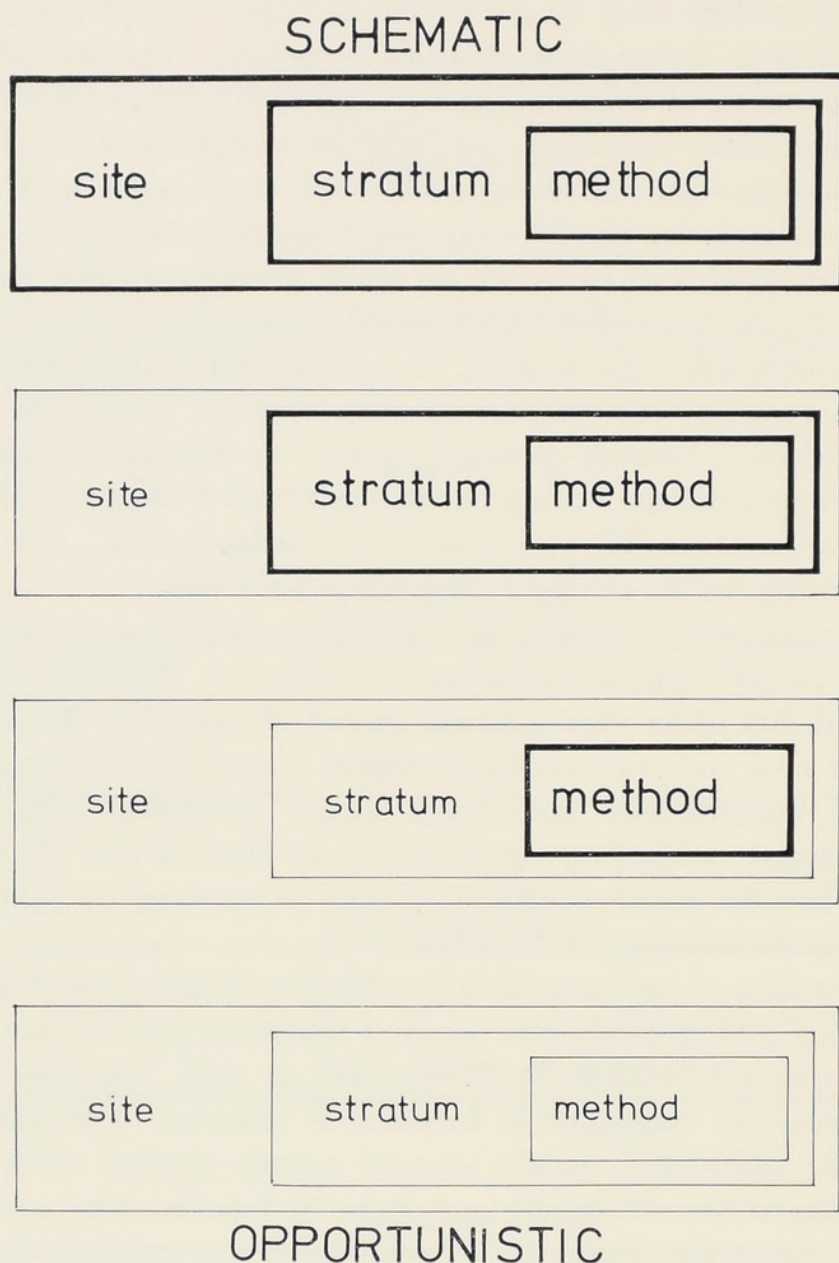
SCHEMATIC

FIG. 5. Schematic representation of the differential effects of increasing opportunistic feeding behavior on site (here: tree species) selection, stratum selection, and feeding techniques. Dark lines and large letters indicate that the corresponding aspect of foraging behavior is fixed and restricted in variability.

their observations in Arizona in a season when opportunistic feeding should be prevalent (June and July, and May to July, respectively).

The characteristics of conservative schematic feedings are useful for many comparative studies and might even clarify evolutionary relationships. The previously unknown strong predilection for pines of even the northern populations of Strickland's Woodpecker fits well with the data for other populations (Davis 1965, Ligon 1968a). It also suggests that this species

has evolved in a Mexican, pine-dominated, Pleistocene arboreal center. As the range of the Red-cockaded Woodpecker (*Picoides borealis*) is associated with that of loblolly pine (*Pinus taeda*) and longleaf pine (*P. palustris*) (Jackson 1971), so the range of the Strickland's Woodpecker is strikingly well associated with that of the Chihuahua pine (*P. leiophylla*) and Apache pine (*P. engelmannii*) (Mirov 1967). Hairy Woodpeckers also have some preference for pines in many areas (see Jackson 1971) and select them even in almost pure deciduous woodland (pers. obs.). The Mexican Chickadee (*Parus sclateri*) and the Mexican Junco (*Junco phaeonotus*) similarly seem to be confined to areas in which Apache and Chihuahua pines occur (Balda 1967). Grace's Warbler (*Dendroica graciae*) and the Yellow-throated Warbler (*D. dominica*), which can be found at the same localities as Strickland's Woodpecker and Red-cockaded Woodpecker, respectively (pers. obs.), may have had a similar speciation history (Mengel 1964) as these woodpeckers. The ecological data presented here are consistent with the hypothesis that Strickland's Woodpecker (and maybe the Red-cockaded Woodpecker, Jackson 1971) may have split off from an ancestral Hairy Woodpecker stock.

SUMMARY

Strickland's Woodpeckers were studied in the pre-nesting and early nesting periods in the Chiricahua Mountains of Arizona. This woodpecker prefers to feed upon pines in the pre-nesting season, but is less selective during the nesting season. In contrast to earlier reports, an avoidance of, rather than a preference for oaks was found. During the pre-nesting season, trunk feeding prevails; a preference for crown feeding emerges later. The relative frequency of use of various feeding techniques did not change during the period investigated. Changes in feeding behavior were associated with changes in other behavior. Differences between the sexes appeared only in the nesting season. Also, females differed from males with regard to patterns of seasonal change in behavior other than feeding. The changes in feeding behavior are discussed and the concept of schematic and opportunistic feeding is introduced.

LITERATURE CITED

ALCOCK, J. 1975. Animal behavior. An evolutionary approach. Sinauer, Sunderland.
AUSTIN, G. T. 1976. Sexual and seasonal differences in foraging of Ladder-backed Woodpeckers. Condor 78:317–323.

BALDA, R. P. 1967. Ecological relationships of the breeding-birds of the Chiricahua Mountains, Arizona. Ph.D. thesis, Univ. Illinois, Urbana, Illinois.

CURIO, E. 1975. Experimentelle Untersuchungen zur Öko-Ethologie von Räuber-Beute-Beziehungen. Verh. Dtsch. Zool. Ges. 1975:81–89.

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

HOGSTAD, O. 1976. Sexual dimorphism and divergence in winter foraging behaviour of Three-toed Woodpeckers *Picoides tridactylus*. Ibis 118:41–50.

JACKSON, J. A. 1970. A quantitative study of the foraging ecology of Downy Woodpeckers. Ecology 51:318–323.

———. 1971. The evolution, taxonomy, distribution, past populations, and current status of the Red-cockaded Woodpecker. Pp. 4–29 *in* The ecology and management of the Red-cockaded Woodpecker (R. L. Thompson, ed.), Tallahassee, Florida, Bur. Sport Fish. Wildlf., U.S. Dept. Int., and Tallahassee Timbers Res. Stat.

JACOBS, J. 1974. Quantitative measurements of food selection. A modification of the foraging ratio and Ivlev's electivity index. Oecologia 14:413–417.

KINGSBURY, E. W. 1932. A study of the Hairy Woodpecker. Master's Thesis. Cornell University, Ithaca, New York.

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

———. 1968b. Sexual differences in foraging behavior in two species of *Dendrocopos* woodpeckers. Auk 85:203–215.

MENGEL, R. M. 1964. The probable history of species formation in some northern wood warblers (Parulidae). Living Bird 3:9–43.

MIROV, N. T. 1967. The genus *Pinus*. Ronald Press Co., New York.

MORSE, D. H. 1971. The insectivorous bird as an adaptive strategy. Ann. Rev. Ecol. Syst. 2:177–200.

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

SKOCZYLAS, R. 1961. Zahlendynamik, Vertikalverteilung und Territorialverhalten des Großen Buntspechtes (*Dryobates major* L.) in einer Kiefernheide. Polish with German summary. Ekol. polska Ser. A9:229–243.

TRAVIS, J. 1977. Seasonal foraging in a Downy Woodpecker population. Condor 79:371–375.

WINKLER, H. 1972. Beiträge zur Ethologie des Blutspechts (*Dendrocopos syriacus*). Das nicht-reproduktive Verhalten. Z. Tierpsychol. 31:300–325.

———. 1973. Nahrungserwerb und Konkurrenz des Blutspechts, *Picoides* (*Dendrocopos*) *syriacus*. Oecologia 12:193–208.

INSTITUT FÜR LIMNOLOGIE, BERGGASSE 18/19, A-1090 WIEN, AUSTRIA. ACCEPTED 21 FEB. 1978.