the cause of the delay is unknown in our case, it is perhaps noteworthy that M49 was a yearling; most yearling males are not territorial and therefore do not breed.

Adoption of crouched positions by M49 may also have contributed to the reverse mountings, for the crouched position with raised tail resembles the posture typically assumed by females prior to copulation. Males that mount females, however, engage in no behavior similar to F62's treading. She did not appear to be attempting to maintain balance, and she did not beat her wings as males do. Instead, her movements suggested those of a female shaping a nest's cup. Ficken (1963) reported three reverse mountings by American Redstarts (*Setophaga ruticilla*) and suggested that the crouched position of the male stimulated the female's pseudomale behavior. A male Prairie Warbler nest-shaped prior to being mounted by his mate (Nolan 1978: 109).

To summarize, the circumstances associated with the reverse mountings by F62, i.e. delay in renesting and adoption by the male of a position resembling the female's pre-copulatory posture, are consistent with two of the factors Morris (1955) identified as leading to pseudomale and pseudofemale behavior.

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Foraging Behavior of Male and Female Nuttall Woodpeckers

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Woodpeckers have been the focus of attention in examining the ecological significance of intersexual niche divergence (Kilham 1965, 1970; Selander 1965; Ligon 1968, 1973; Jackson 1970; Kisiel 1972). Many of the North American species of the genus *Picoides* exhibit intersexual niche divergence (Austin 1976). This study was undertaken to quantify the foraging behavior of males and females of *P. nuttallii* and to determine if and to what extent subdivision of the foraging niche occurs.

Two selective advantages have been proposed to explain the observed tendency of the sexes to occupy separate subniches. The first assumes a limited food supply, with selection favoring those individuals most efficient in utilizing the available food resources (Selander 1966). Second, Kilham (1965) suggests that friction arising from repeated competition may tend to weaken the pair bond. Thus, selection would promote differences in feeding, roosting, and other habits where competitive friction might arise.

All field observations on Nuttall Woodpeckers were collected on the 800-ha Hastings Natural History Reservation, Monterey County, California, which is operated by the Museum of Vertebrate Zoology, University of California, Berkeley (Linsdale 1947, Griffin 1974). Live oaks (*Quercus agrifolia*) dominate on lower hillsides and are co-dominant with valley oaks (*Q. lobata*) on broad valley bottoms. Live and valley oaks also occur in riparian areas, together with willow (*Salix* spp.) and California sycamore (*Platanus*

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TABLE 1. Differential frequencies of use of trees, diameter and angle of foraging sites, and foraging techniques by male and female Nuttall Woodpeckers on the Hastings Natural History Reservation during 1976.

	Percent use		Percent difference[b]
	Male	Female	
Species of tree	(186)[a]	(141)[a]	
Live oak	38.7	47.5	NS
Valley oak	26.9	23.4	NS
Blue oak	13.4	13.5	NS
Miscellaneous	21.0	15.6	NS
Diameter of foraging site	(426)	(312)	
0–2.5 cm	24.4	53.2	28.8**
5.0–10.1 cm	45.3	34.0	11.3**
≥12.6 cm	30.3	12.8	17.5**
Angle of foraging site	(230)	(144)	
Vertical	33.0	23.6	NS
Oblique	48.7	60.4	11.7*
Horizontal	18.3	16.0	NS
Foraging technique	(229)	(177)	
Tapping	40.2	29.9	10.3*
Probing	32.2	30.5	NS
Gleaning	27.5	39.6	12.1*

[a] Sample size.
[b] NS = not significant, * = $P < 0.05$, ** = $P < 0.01$.

racemosa). *Picoides nuttallii* were found regularly in these areas, foraging primarily in the oaks. Miller and Bock (1972) examined the use of oaks by *P. nuttallii* in relation to the relative abundance of these plant species at Hastings. Strong seasonal shifts occurred in the use of live, blue (*Q. douglasii*), and valley oaks, although these three oaks were all used extensively throughout the year.

I observed woodpeckers each morning and in the late afternoon from June to October 1976; midday observations were infrequent due to reduced foraging activity during these hours. I recorded frequency of use of species of tree or shrub for foraging, diameter and angle of foraging perch, and foraging technique employed by the bird. Height of the occupied tree and height of the woodpecker above ground were also estimated at the first sighting of each foraging individual. General weather condition and the sex and age (young vs. adult) of the foraging individual were also noted.

I distinguished three general foraging techniques: tapping, probing, and gleaning. Tapping behavior of *P. nuttallii*, unlike that of many other *Picoides* species, was most often associated with surface feeding. Woodpeckers often delivered soft, tangential blows, apparently to widen crevices in branches and bark. Persistent drilling perpendicular to the bark, indicating subsurface feeding, was rarely observed. Probing behavior referred to stationary or slow-moving woodpeckers that poked their bills into crevices and bifurcations of branches. Probing behavior often was accompanied by turning the head side to side and peering into crevices. Gleaning behavior involved rapid movements of woodpeckers on trunks and branches within each tree; food items were obtained as they occurred on the surface.

For the first 2 months of the study, birds could be aged on the basis of plumage characters (Ridgway 1914, Bent 1939). Data were collected only on juvenile birds that foraged unaccompanied by adults. Following the postjuvenal molt in August, all birds were classified only as "adult" male or female.

I used Chi-square contingency tests to evaluate the frequency of use of tree species, diameter and angle of foraging sites, and feeding technique. Student's *t*-test was used to establish 95% confidence interval estimates of mean height of trees used by the sexes and mean heights at which the sexes foraged in the trees. Chi-square tests for homogeneity indicated no significant differences in frequencies of occurrence of any of the foraging categories (diameter and angle of foraging site, tree species, or foraging technique) between adult and juvenile males, or between adult and juvenile females. Accordingly, the age classes were combined, and the data are summarized in Table 1.

The greatest difference in foraging behavior between sexes of *P. nuttallii* in any of the features measured was in the diameter of the foraging perch. Females used smaller branches and twigs more frequently than did males. Differences in frequencies of use of species of trees and shrubs by males and females were not statistically significant.

Females used obliquely-oriented positions significantly more often than did males, while males foraged primarily by tapping and females foraged primarily by gleaning (Table 1). Males foraged significantly lower in trees (5.8 ± 0.19 m) than did females (7.28 ± 0.25 m). No difference existed in the mean height of trees used by males and females.

There are several obstacles to clear interpretation of the differential foraging behaviors of the sexes of *P. nuttallii*. For example, gleaning behavior is obligatory for woodpeckers foraging on twigs and foliage, because these substrates are too small or fragile for tapping or probing. As females foraged on twigs and foliage more often than did males, it is not surprising that the foraging technique used by females was primarily gleaning. Similarly, females used more obliquely-oriented branches than did males, probably because oblique branches were more prevalent in areas of the tree with branches of relatively smaller diameters. Branches with large diameters, used most often by males, tended to be lower in trees, while branches with smaller diameters, used most often by females, were higher in the trees, thereby influencing the mean height at which the sexes foraged.

I interpreted differences between the sexes in foraging technique, angle of foraging substrate, and height of foraging position to be consequences of differential use of diameter of foraging site. Three indications support this interpretation: 1) differential use of diameter of foraging site by males and females was by far the greatest difference of any of the foraging categories; 2) diameter of foraging site, in the 0–2.5-cm range, was the only category in which the frequency of use differed significantly between the sexes of juvenile woodpeckers; and 3) this interpretation is consistent with Short's (1971) conclusions for differential foraging of the sexes of *P. nuttallii* in Kern County, California.

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