TABLE 1. Measurements of *Quiscalus* from the Gibbstown-Bell City area, Louisiana.

		Measurements (mm)									
		Wing length		Tail length		Bill length		Bill depth		Tarsus length	
Species	*n*	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Adult male											
Q. major	13	174.4	3.80	175.3	6.34	30.76	1.111	11.68	0.400	47.38	1.344
Q. mexicanus	11	187.9	4.28	209.2	10.55	31.72	1.618	12.54	0.548	47.43	1.040
Adult female											
Q. major	43	136.9	2.64	131.0	4.47	25.22	0.919	9.56	0.197	39.08	0.881
Q. mexicanus	49	144.9	2.25	147.1	5.16	24.61	0.846	10.06	0.283	38.76	1.142

specimens were identifiable to species on the basis of eye color alone (see Selander and Giller, op. cit.: 43), and none showed evidence of mixed ancestry in any character. Measurements of adult male and female specimens, supplementing those presented graphically by Selander and Giller (op. cit.), are given in table 1.

The continuing eastward extension of the range of *Q. mexicanus* into that of *Q. major* provides an opportunity to study the ecological interactions of closely related species which overlap in niche requirements. We predict that *Q. mexicanus* will eventually reach the Atlantic coast states, becoming broadly sympatric with *Q. major*, and, in the process, replacing that species in upland habitats. This research was supported by the U. S. Public Health Service, Institute of General Medical Sciences (GM-15769).

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THE NUMERICAL RESPONSE OF WOODPECKERS TO INSECT PREY IN A SUBALPINE FOREST IN COLORADO

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Several field workers have reported concentrations of woodpeckers associated with insect prey attracted to trees killed by floods and fires (Yeager 1955; Blackford 1955) or with epidemics of forest insects (Massey and Wygant 1954; Baldwin 1960). Several other workers reported significant differences in numbers of woodpeckers inhabiting forests supporting endemic populations of forest insects and numbers of woodpeckers inhabiting similar forests supporting epidemic populations of forest insects (Amman and Baldwin 1960; Otvos 1965). None of these investigators observed the numerical response—the changes in densities of predators in response to changes in densities of prey (Holling 1959)—of woodpeckers to an increasing food supply, nor did they attempt to explain the differential response of each species in terms of foraging adaptations. The purpose of this paper is to present such a report.

METHODS

The study was conducted between July 1962 and August 1965 in a subalpine forest in the vicinity of Deadman Lookout in the Red Feather District of the Roosevelt National Forest, Larimer County, Colorado. The vegetation of the study area is dominated by Engelmann spruce (*Picea engelmanni*), subalpine fir (*Abies contorta*), and lodgepole pine (*Pinus contorta*). The woodpeckers studied included Northern Three-toed (*Picoides tridactylus*), Hairy (*Dendrocopos villosus*), and Downy (*D. pubescens*).

I censused woodpeckers by means of census plots (Amman and Baldwin 1960) and census strips (Davis 1963). Woodpeckers were so sparse that, to obtain a sufficient number of observations to adequately estimate densities, censusing was conducted during all daylight hours. To determine if birds were more active during a given time of day, I frequently censused a plot three times daily (early morning, around noon, and late afternoon) and statistically compared the results by means of contingency tests. I tested results only from those days that had consistent weather patterns throughout the whole day.

A small fire in October 1962 killed or damaged approximately 10 acres of trees within the study area. Censuses were conducted through portions of the burn, but no special effort was made to census the burned area until I realized in July 1964 that woodpeckers were feeding on bark beetles attracted to the fire-damaged trees. Although no attempt was made to census insects attracted to the trees, periodic examinations were made to identify the species of insects attracted to the trees and to gain an impression of their relative abundance.

I studied the foraging behavior of individual woodpeckers by noting the species and condition (living or dead) of each tree utilized, and the foraging site occupied by each bird in these trees. I timed each bird with a wrist watch as it foraged in different trees and in various sites.

RESULTS AND DISCUSSION

Prey populations. Even though bark beetles were not censused, their presence and high abundance during the fall of 1964 were readily apparent from entry holes in the bark, boring dust at the bases of fire-damaged trees, and larval galleries exposed by the flaking activities of woodpeckers. *Ips pilifrons* was the most abundant bark beetle in the trunks and larger branches, and *Pityophthorous* sp. the most abundant in the smaller branches and twigs of fire-damaged Engelmann spruce and lodgepole pine. Subalpine fir was not checked for insects because the trees were heavily laden with pitch and there was little woodpecker activity on them.

The decline in abundance of insect prey during the spring of 1965 was equally apparent. By June almost all of the bark on the fire-killed spruce and

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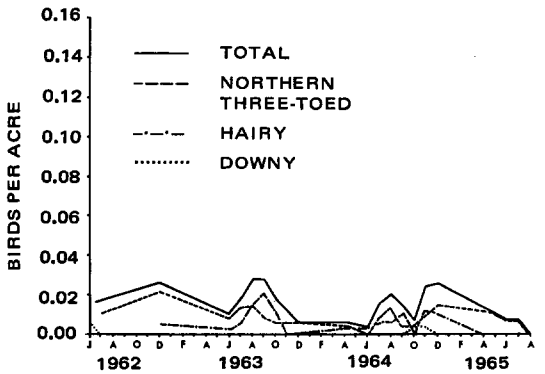

FIGURE 1. Densities of woodpeckers on the Deadman study area outside the 1962 burn.

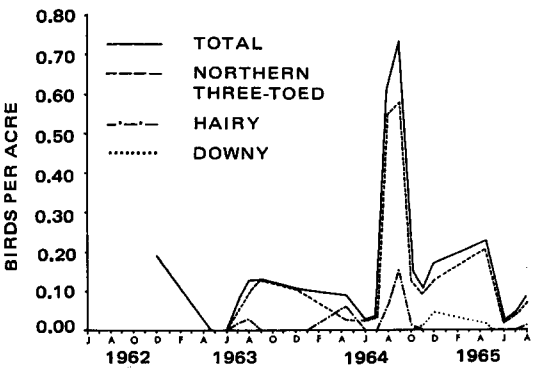

FIGURE 2. Densities of woodpeckers on the Deadman study area inside the 1962 burn.

lodgepole pine had been removed by woodpeckers in their search for bark beetles. I was able to locate very few insects in any of the remaining bark examined that spring.

Woodpecker populations. I conducted 14 triple censuses of the plot and observed 61 woodpeckers; 23 during the morning, 17 at noon, and 21 in the afternoon. This variation is not statistically significant and I concluded that woodpeckers were equally active during all hours of daylight.

I conducted a total of 178 censuses involving approximately 400 miles of walking and 500 hours of observation, and obtained 184 observations of woodpeckers. I censused mainly during the months of June through December. Deep, powdery snow prevented or impeded access to the study area each winter and spring, so I obtained no data for January, February, or March, and a limited amount of data for April and May. Census data were segregated into those obtained outside and those obtained inside the area of the 1962 burn; data for each month, or, in cases of limited data, series of months, have been combined. For example, a total of 200 acres was censused outside the burned area during the month of June 1962, and two Northern Three-toed Woodpeckers (an estimated 0.01 per acre) were observed.

Comparing estimates of densities outside the burned area (fig. 1) with those inside (fig. 2) shows that there was a fifty-fold increase in density of woodpeckers in response to insect prey in the fire-killed trees. Since nesting densities were comparable each spring (approximately one nest per 850 acres), I am certain that the numerical response was the result of drift and aggregation and not the result of increased reproduction.

Increase in density was most pronounced in the Northern Three-toed Woodpecker and least pronounced in the Downy Woodpecker. The Downy Woodpecker was observed only once prior to mid-October 1964, suggesting that the bird infrequently visits subalpine forests and that it remains during these visits only when there is a favorable food supply. Additional investigations may reveal that the Downy Woodpecker is a fugitive species (Hutchinson 1951) in subalpine forests.

Differences in intensity of the numerical response among the three species of woodpeckers may be attributed, in part at least, to adaptive differences in feeding behavior characteristic of each species. Table 1 strongly suggests that in subalpine forests the Hairy Woodpecker is the most generalized species, feeding primarily on insects in the trunks of both freshly killed and older snags of all three species of trees. The Northern Three-toed Woodpecker is specialized more for utilizing insects in the bark of trunks of

TABLE 1. Comparison of use by three species of woodpeckers of trees and foraging sites.[a]

	Northern Three-toed		*Hairy*		*Downy*	
	% of 288 occurrences	% of 4,440 min of utilization	% of 108 occurrences	% of 845 min of utilization	% of 17 occurrences	% of 161 min of utilization
Tree species						
Eng. spruce	72[a]	81	48[b]	36	93[c]	85
Lodgep. pine	17[a]	12	27[b]	46	0[a]	0
Subalp. fir	11[a]	7	25[b]	18	7[ab]	15
Tree condition						
Living	5[a]	2	1[a]	2	0[a]	0
Fire-killed	94[a]	97	65[b]	80	100[a]	100
Older snag	1[a]	1	34[b]	18	0[a]	0
Foraging site						
Trunk	92[a]	93	86[a]	81	0[b]	0
Branches ($>1''$ diam)	6[a]	6	11[a]	7	0[b]	0
Twigs ($\leq 1''$ diam)	2[a]	1	3[a]	12	100[b]	100

[a] Differences in frequency of utilization of trees and foraging sites by the three species of woodpeckers were compared statistically by means of the contingency test (χ^2). Those percentages of occurrence in a given row followed by the same letter are not significantly different; those followed by different letters are significantly different ($p \leq 0.05$). Temporal differences were not analyzed statistically because units of time are not independent events (Ligon 1968).

freshly killed spruce. The Downy Woodpecker is the most specialized species, feeding on insects in the bark of smaller branches and twigs of freshly killed spruce and, to a lesser extent, subalpine fir. Neither the Northern Three-toed nor the Hairy Woodpecker foraged to any extent on the trunks of freshly killed subalpine fir, presumably because of the high pitch content of fir.

Northern Three-toed and Downy Woodpeckers remained on the study area throughout the fall and winter of 1964–1965. Hairy Woodpeckers declined steadily after September 1964 and disappeared altogether between December 1964 and April 1965. The disappearance of the Hairy Woodpecker was probably related to a decline in available insect prey, conceivably as a result of its inability to compete effectively with the more specialized Northern Three-toed and Downy Woodpeckers for insect prey remaining in the fire-killed trees. The later disappearance of the Downy Woodpecker and the decrease in density of the Northern Three-toed Woodpecker during May and June 1965 were undoubtedly related to the decline in food supply and to the onset of breeding season.

SUMMARY

During the fall of 1964 resident populations of Northern Three-toed, Hairy, and Downy Woodpeckers concentrated upon bark beetles attracted to 10 acres of northern Colorado subalpine forest killed by a fire in 1962. The numerical response of the woodpeckers was graded; that of the Northern Three-toed Woodpecker was the most pronounced and that of the Downy Woodpecker least pronounced. Evidence is presented suggesting that the graded response was related to the foraging adaptations of each species of woodpecker.

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OBSERVATIONS OF THE NUTHATCH-LIKE WHITE-THROATED TREERUNNER (*PYGARRHICHAS ALBOGULARIS*) IN ARGENTINA

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The monotypic furnariid White-throated Treerunner (*Pygarrhichas albogularis*) of the southern Andean and Patagonian forests of Chile and Argentina is remarkable for its similarity in appearance and behavior to nuthatches (Sittidae) of the genus *Sitta* (A. W. Johnson, The Birds of Chile, Vol. II, p. 199, 1967). In view of this apparent case of convergence, the following information is offered concerning its habits. I observed this species briefly on several occasions during late November 1967 in southern or false beech (*Nothofagus*) forest in the lower Andes Mountains of western Neuquén and Río Negro, Argentina.

The White-throated Treerunner feeds by creeping over the bark of large to small trees (usually species of *Nothofagus*), generally moving up the trunk and out the branches. Its movements involve sidling, frequent abrupt, jerky shifts of the body, and changes in direction of movement. Actual feeding is by probing into all manner of crevices and under rough edges of the bark, and occasionally by light, woodpecker-like tapping. Individuals progress rapidly up the trunks of larger trees, and spend much of their time in smaller branches working around the bases of leaf petioles. North of San Martín de los Andes, Neuquén, I encountered pairs of White-throated Treerunners as commonly in second growth woodland (trees to 15 ft high and 6 inches in diameter) as in nearly mature forest. On one occasion (20 November, 4 km NE of San Martín de los Andes) I noted an