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WITHIN-SEASON TRENDS IN THE FORAGING BEHAVIOR OF THE MOUNTAIN CHICKADEE

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ABSTRACT.—We compared foraging behaviors of adult Mountain Chickadees (*Parus gambeli*) within and among breeding seasons. Foraging behaviors differed little between nestling and fledgling "feeding" periods of the breeding cycle with the exception of substrate use and foraging distance from the bole. During the nestling period birds spent the majority of foraging time searching for prey on the needles in the outer crown whereas during the fledgling period the birds spent significantly less time in the outer crown yet more time on new shoots. Among year variation was significant for the majority of foraging variables and data pooled for the entire breeding season masked within season trends. Our results indicate that within season comparisons of foraging behavior are important for revealing significant trends in behavior. They also suggest that Mountain Chickadees are opportunistic feeders and may time their breeding season with the growth of white fir so that older nestlings or fledglings are present when new shoots are expanded and thus contain a greater availability of prey to meet the demands of the older offspring. *Received 27 Jan. 1995, accepted 12 May 1995.*

Pooling foraging observations across the breeding season (Airola and Barrett 1985, Hill and Lein 1988, Grundel 1990) or into specific calendar months (Brennan 1989, Wagner 1981, Miles 1990) could fail to recognize minor, yet significant shifts in behavior associated with either the stages of the breeding cycle, nestling age, plant phenology or insect availability (Root 1967, Hejl and Verner 1990, Sakai and Noon 1990). In addition, among year comparisons are important because behavior may be influenced by annual weather patterns which affect plant phenology and insect availability and abundance as well as the onset and duration of the breeding season (Szaro et al. 1990, Dahlsten et al. 1992). The goal of our study was to observe whether the foraging behavior of Mountain Chickadees (*Parus gambeli*) differed between the nestling and fledgling "feeding" stages of the breeding cycle among years. Our specific objectives were to (1) determine the proportion of time Mountain Chickadees spend on each foraging location, substrate and tactic in white fir (*Abies concolor*) within the breeding season; (2) compare proportion of time spent on various locations, substrates and tactics within and between the two stages of feeding young (nestling, fledgling) during the breeding season each year and; (3) compare proportion of time spent on various locations, substrates and tactics during each stage among years.

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STUDY AREA AND METHODS

Our study area was in Modoc County in northeastern California (Dahlsten and Copper 1979, Dahlsten et al. 1992). The area is composed of white fir (60%) while the remaining 40% consists of ponderosa pine (*Pinus ponderosa*), Jeffrey pine (*P. jeffreyi*), a naturally occurring Jeffrey X ponderosa pine hybrid, incense cedar (*Calocedrus decurrens*) and western juniper (*Juniperus occidentalis*) (Kleintjes 1993). Two 50 ha study plots, located 11.3 km apart, contain a total of 175 artificial nestboxes. There are 50 boxes at Toms' Creek (elev. 1675 m) and 125 at Yellowjacket Springs (elev. 1825 m). We used a color-banded population of breeding Mountain Chickadees that has been continuously monitored since 1965 (Dahlsten et al. 1992).

During the breeding seasons of 1990–1992, the breeding biology of the Mountain Chickadees was monitored from commencement of nestbuilding to the last day of fledging of second broods. Boxes were monitored 1–3 times a week in both plots. All data on nest condition, egg and nestling development and adult presence were also recorded. Breeding phenology was categorized according to calendar dates of egglaying/incubation, brooding and fledging of first broods, renests and second broods. We used a sequential observation technique with binoculars to record the foraging behaviors of adult Mountain Chickadees (Brennan and Morrison 1990). Each foraging observation ($N = 1$) consisted of a timed series of sequential records. At first sighting of a bird, a minimum of 10 seconds was allowed to pass (to avoid recording conspicuous behaviors). A series of sequential records was then recorded for a minimum of 20 to a maximum of 60 sec. Each record was equivalent to a set of variables which corresponded to the individual bird's foraging location, substrate and prey capturing maneuver (tactic). A new record (line of data) was made each time a bird changed foraging location, substrate or maneuver. New records were added to the observation until either the bird was lost from sight or the minimum time was reached. Each observation sequence was recorded on a tape recorder. The tape was rewound and each record timed according to a stopwatch and transcribed onto a data sheet. A minimum distance of 50 meters was moved between each observation to increase the likelihood of independence between observations made on the same day.

We used foraging variables modified from Remsen and Robinson (1990) to describe behaviors: tree species (white fir, Ponderosa pine, other); tree height (estimated to the nearest meter with a clinometer); bird height (in both meters and one-third crown intervals); horizontal location in tree (bole, inner, middle and outer one-third); foraging substrates on which activity occurred (needles, shoots, buds, air, small twigs, lichen, bark and other); time (for each record and total observation time); date; sex (if color band is visible). In addition, we recorded the tactic used to procure or attempt to procure prey. These included (1) searching (looking for prey-no predatory action); (2) perch gleaning (to pick food from a nearby substrate when in a perched position); (3) hang gleaning (to pick food from a nearby substrate while hanging upside down); (4) hover gleaning (to pick food from a nearby substrate while hovering in the air); (5) pecking (to drive bill against substrate to remove food); (6) probing (to insert bill into substrate to remove hidden food); (7) flycatching (to leave perch and aerially catch prey); (8) flaking (to pry bark and remove it to reach prey underneath); and (9) other. Foraging observations were collected during 1 June–15 July, 1990, 17 June–27 August, 1991 and 1 June–8 August, 1992. Foraging observations were recorded from both plots between 06:00–20:00 hr PST, 3–5 times per week while walking nestbox transect lines.

Raw data from each foraging observation were transformed from frequency of occurrence per observation to percentages of total observation time a bird used a specific location, substrate or tactic (Brennan and Morrison 1990). Conversion of the data to percent of total observation time per individual transformed the data from discrete to continuous variables and assured independence of samples. Percentages were modified with a square root of the arcsin transformation because the range of percentages (for proportional data) did not lie between 30–70% (Sokal and Rohlf 1981).

A graphical procedure suggested by Morrison (1984) was used to determine the minimum number of observations needed to obtain appropriate estimates (stable means and variances) of behavior. We conducted the analysis on 1991 data for four variables that represented common use of substrate, tactic and location.

Means and variances for each variable of activity, location and tactic within the entire season for each year were compared using a standard one-way analysis of variance for equal sample sizes (Zar 1984). Pairwise comparisons of percent mean values were made with Tukeys HSD method (Zar 1984). Data were grouped into the two within breeding season stages that corresponded with feeding of young; nestling (brooding in cavity) and fledgling (post-brooding; outside of cavity). Since nestling development was not synchronous among nests (earliest and latest first broods varied by approximately 15 days), stage one ended during the week that first broods began to fledge. Therefore, stage two contained mostly fledglings with a few older first broods, renests and second broods in boxes. Means and variances for each variable of activity, location and tactic within and between breeding stages for each year were compared using a two-way factorial analysis of variance for proportional sample sizes (Zar 1984). We used Bonferroni-adjusted probability values (0.05/3 levels = $P < 0.016$) to adjust for the factorial design and variable degrees of freedom within each test. Separate ANOVA's were conducted on location level within crown, location distance from bole, foraging substrate and tactic. If significant interaction occurred between either period × level, period × substrate or period × tactic multiple comparison testing was used to seek significant differences between cell means (User-defined contrasts (UDC), Systat 1992).

Between year comparisons were made between equivalent breeding stages using a two-way factorial analysis of variance for proportional sample sizes ($P < 0.016$, Zar 1984). Separate tests were conducted on the same grouping of variables listed above. User-defined contrasts (UDC) were used for multiple comparison testing when the interaction between year × levels were significant. All statistical analyses were performed with Systat © 1992.

RESULTS

The breeding phenology of the Mountain Chickadee was nearly synchronous with the development of white fir shoots during all three years of the study despite the significant difference in phenologies among years (Table 1). Each year, white fir bud expansion occurred approximately one month after date of first egg and at this time in 1991 and 1992, the majority of nests contained nestlings 1–6 days old (Table 1). Of the three years, date of first laid egg was latest in 1991 (1 June) yet the latest date on record in 27 years at this site was 13 June (Dahlsten et al. 1992). Results of the sample size analysis indicated that the estimated means of various samples appeared to converge with the mean value for samples of a size N > 40. The standard deviations of the estimates stabilized within 50–60 observations so we chose a minimum sample size of fifty for appropriate estimates of behavior. Results were similar to those found by Brennan and Morrison (1990) for Mountain and Chestnut-backed

TABLE 1
BREEDING PHENOLOGY OF THE MOUNTAIN CHICKADEE, MAY–JULY 1990–1992, IN MODOC CO., CALIFORNIA

Measurement	1990	1991	1992
Date of first laid egg (DFE) of first broods	6 May	1 June	1 May
Date one month after DFE	10 June	1 July	1 June
Total number of first brood nests (N)	59	33	38
Percent of nests containing eggs	23%	6%	23%
Percent of nests containing nestlings 1–6 d old	35%	84%	68%
Percent of nests containing nestlings 7–12 d old	41%	9%	9%
Dates when >70% of first broods had fledged	18–25 June	13–18 July	10–17 June
Number of renests	4	2	4
Number of second broods	2	3	3
Dates of white fir bud expansion	15–22 June	25 June–2 July	3–10 June

chickadees in the Central Sierra Nevada. Birds were observed foraging on substrates other than white fir during all three years of the study. However, between 75–92% of the observations were recorded from white fir, therefore only these data were used for analysis.

The results indicated that during all three years, Mountain Chickadees spent a significantly greater proportion of their time foraging in the outer third of the crown (1990, $F = 7.87$; 1991, $F = 73.0$; 1992, $F = 78.9$; $P < 0.05$) (Fig. 1A). They also spent a significantly greater proportion (between 54–78%) of their foraging time searching for prey (1990, $F = 73.59$; 1991, $F = 199.58$; 1992, $F = 509.43$; $P < 0.05$) while perch gleaning and hang gleaning were the most common tactics used for obtaining prey (Fig. 1B). Only in 1991, did the birds spend significantly more time hang gleaning (18%) ($F = 199.58$, $P < 0.05$) (Fig. 1B). In 1990, the birds also spent a significantly greater proportion of time in the mid height crown level (47%) ($F = 7.87$, $P < 0.05$), whereas in 1991, they spent significantly more time on the middle (36%) and upper (40%) thirds of the crown ($F = 7.4$, $P < 0.05$) (Fig. 1C). Foraging on needles comprised the significantly greatest proportion of time spent on any given substrate in 1990 (57%) ($F = 61.68$, $P < 0.05$) and in 1991(45%) ($F = 65.6$, $P < 0.05$) (Fig. 1D). However, in 1992 birds spent nearly equal amounts of time on needles (36%) and shoots (33%) with both substrates being used significantly more than any others ($F = 62.81$, $P < 0.05$) (Fig. 1D).

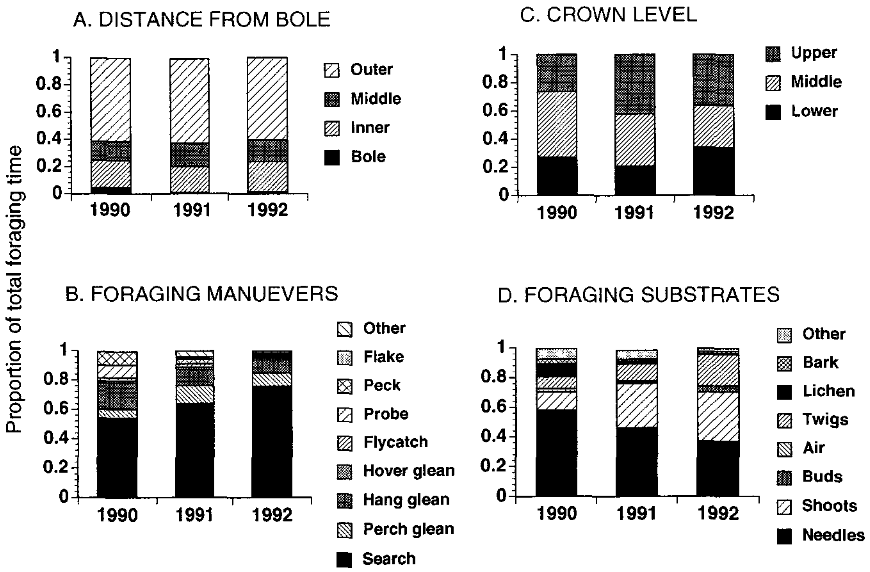

FIG. 1. Proportion of total observation time Mountain Chickadees spent on each foraging location, substrate and maneuver in white fir during the entire breeding season in Modoc Co., California, 1990–1992 (N = 120).

Within breeding season periods corresponded with 6–23 June (1st broods, stage 1) and 24 June–8 July (post-brooding, stage 2) in 1990, 18 June–13 July (stage 1) and 14 July–27 August (stage 2) in 1991 and 25 May–11 June (stage 1) and 15 June–8 August (stage 2) in 1992. Although statistical comparisons of behaviors produced variable results each year, two significant trends within the breeding season existed: an increased use of available shoots and an avoidance of the outer crown during the fledgling period. There were no significant differences in use of crown levels or foraging maneuvers between periods each year (Table 2).

Each year, the birds spent over 50% of their foraging time on older needles while feeding first broods. However, during period 2 (the stage of feeding older nestlings and fledglings) the birds significantly decreased their use of needles in exchange for more foraging time on new shoots (Table 2) (Fig. 2A–C). In 1992, use of shoots increased up to 57% during the fledgling period which was greater than any other substrate use (Table 2) (Fig. 2A–C). During the fledgling period of 1991 use of shoots only increased to (40%) and did not significantly differ from use of needles (30%), however, both needles and shoots were used significantly more than any other substrate ($P < 0.05$, UDC) (Fig. 2A–C).

During two of the three breeding seasons chickadees tended to avoid

TABLE 2

F VALUES AND SIGNIFICANCE LEVELS FROM TWO-FACTOR ANOVA'S USED TO TEST FOR SIGNIFICANT DIFFERENCES BETWEEN MOUNTAIN CHICKADEE FORAGING VARIABLES, PERIODS AND THEIR INTERACTION WITHIN EACH YEAR

	df	1990 *F* value	1991 *F* value	1992 *F* value
Crown height level				
Level	2	7.87[a]	7.40[a]	0.81
Period	1	0.00	0.02	0.00
Level × period	2	2.15	1.50	0.33
Distance from bole				
Distance	3	60.29[a]	73.00[a]	78.90[a]
Period	1	0.00	0.38	0.15
Distance × period	3	10.40[a]	6.10[a]	0.84
Substrate				
Substrate	7	61.68[a]	65.60[a]	62.81[a]
Period	1	0.04	0.01	0.09
Substrate × period	7	4.44[a]	10.37[a]	31.11[a]
Maneuver				
Maneuver	8	73.59[a]	199.58[a]	509.43[a]
Period	1	0.01	0.00	0.17
Maneuver × period	7	1.14	1.52	2.32

[a] $P < 0.016$ (Bonferroni-adjusted probability of $P < 0.05/3$), two-way ANOVA for proportional sample sizes.

foraging in the outer crown during the fledgling season and instead significantly increased their use of the bole and inner layers during 1990 and the middle layer in 1991 (Table 2, Fig. 3A–C).

The interaction between foraging variables and year within the nestling and fledgling period of the breeding season was significant for all groups of variables in both periods with the exception of crown height level during the fledgling period (Table 3). Each year birds spent the majority of their foraging time in the middle and upper crown levels. In contrast, during the 1990 nestling period, chickadees spent significantly more time (52%) in the midcrown than they did in 1992 (24%) (Table 3). Birds also spent significantly less time in the inner crown during 1990 than in either 1991 or 1992 (Table 3, Fig. 3A–C). Because bird height level significantly differed between years and not seasons we used a two sample *t*-test ($P < 0.05$) to compare between year differences (1991 and 1992) of the mean height (m) of birds and white fir. Data from 1990 was excluded due to measurement errors. The mean tree height (±SD) of white fir used by the birds was 15.8 m (±5.2) (N = 100) in 1991 and 16.3 m (±6.6)

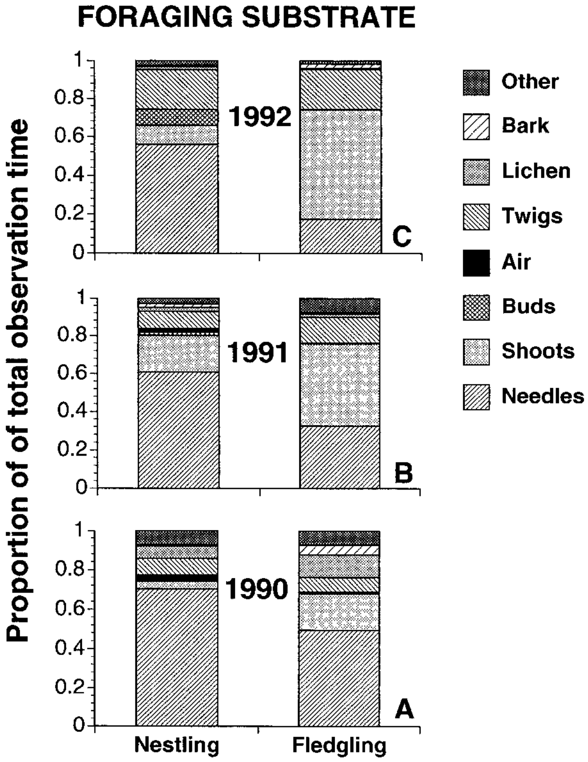

FIG. 2. Proportion of total observation time Mountain Chickadees used a foraging substrate of white fir during the nestling and fledgling "feeding" periods of the breeding season in Modoc Co., California, 1990–1992 (for each stage; N = 60, 1991–1992 and N = 54, 1990).

(N = 100) in 1992. Mean foraging height for birds was 10.0 m (±4.6) (N = 100) in 1991, and 9.8 m (±5.4) (N = 100) in 1992. Neither mean tree height nor foraging height significantly differed between years.

For the proportion of time spent on various foraging substrates, chickadees used shoots and twigs significantly more and needles significantly less during the 1992 fledgling period than they did in 1990 (Table 3, Fig. 2A–C). During the nestling period use of buds (8%) and small twigs (20%) was significantly greater in 1992 (Table 3, Fig. 2A–C). The most consistent, and not surprising trends in behavior across years for both feeding stages, was in chickadee foraging maneuvers. Birds spent the greatest percentage (50–70%) of time searching for prey, with hang gleaning and perch gleaning the most commonly used maneuvers for procuring

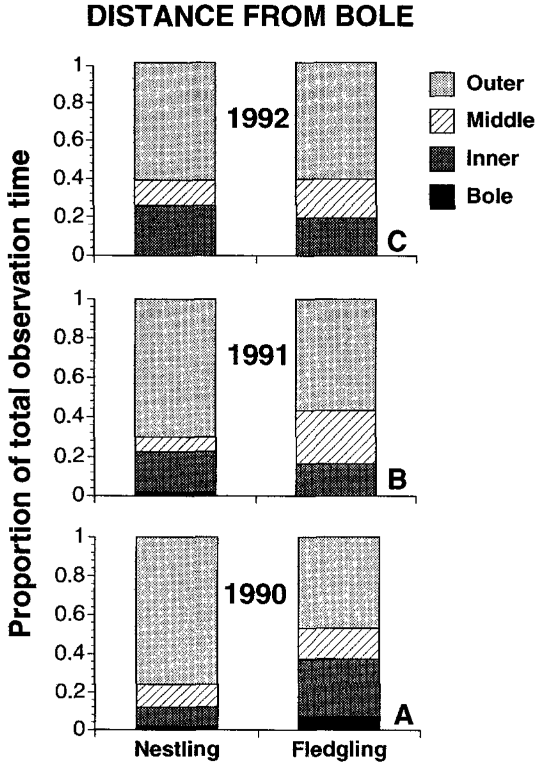

FIG. 3. Proportion of total observation time Mountain Chickadees spent foraging in the crown of white fir as a distance from the bole during the nestling and fledgling "feeding" periods of the breeding season in Modoc Co., California, 1990–1992 (for each stage; N = 60, 1991–1992 and N = 54, 1990).

prey. However, in 1990 the birds spent significantly less time perch gleaning compared to hang-gleaning (Table 3).

DISCUSSION

Our results found that Mountain Chickadees vary their foraging behavior both among and within breeding seasons. Among year variation was significant for the majority of variables whereas within breeding season behaviors varied little between the nestling and fledgling "feeding" periods with the exception of substrate use and foraging distance from the bole. This suggests that Mountain Chickadees may time their breeding season with the growth of white fir so that either older nestlings or fledglings are present when new shoots are expanded and thus contain a greater availability of prey to meet the demands of the older offspring. Brennan

TABLE 3

F VALUES AND SIGNIFICANCE LEVELS FROM ANOVA'S USED TO TEST FOR SIGNIFICANT DIFFERENCES BETWEEN MOUNTAIN CHICKADEE FORAGING VARIABLES, YEARS AND THEIR INTERACTION WITHIN "FEEDING" PERIODS

	df	Nestling period F value	Fledgling period F value
Crown height level			
Level	2	1.8	5.30[a]
Year	2	0.01	0.03
Level × year	4	4.34[a]	2.19
Distance from bole			
Distance	3	174.80[a]	68.79[a]
Year	2	0.63	0.26
Distance × year	6	2.81[a]	2.61[a]
Substrate			
Substrate	7	85.50[a]	67.3[a]
Year	2	73.90[a]	68.2[a]
Substrate × year	14	22.50[a]	19.1[a]
Maneuver			
Maneuver	7	249.05[a]	339.4[a]
Year	2	182.03[a]	207.5[a]
Maneuver × year	14	61.60[a]	83.87[a]

[a] $P < 0.016$ (Bonferroni-adjusted probability of $P < 0.05/3$), two-way ANOVA for proportional sample sizes.

(1989) also found within breeding season and among year variations in Mountain Chickadee foraging behavior, but these were in calendar month comparisons. In our study, we attributed within and among seasonal variation to annual differences in weather which in turn influenced plant phenology, breeding bird phenology and prey availability (see Kleintjes 1993). In addition, our significant within-season differences confirmed the importance of comparing stages of the breeding cycle, particularly since dates of the breeding season greatly differed among years.

Similar to Grundel and Dahlsten (1991) and Brennan (1989), we found that Mountain Chickadees spent the majority of their foraging time on white fir. In addition, the birds spent the majority of time on the outer crown. This was expected as the majority of prey found in the nestling diet were also found on the outer foliage (Grundel and Dahlsten 1991, Kleintjes 1993). Moreover, we examined differences in type of foliage used, i.e., needles, buds, and shoots. When data were pooled for the entire breeding season we found the birds spent the majority of their time on needles. In contrast, when data were compared between the "feeding" stages, we found the birds spent a significantly greater amount of time on new shoots within the fledgling period. We attributed these differences to the availability of prey associated with the flush of new growth rather than a function of the fledgling stage. For example, insects such as *Acantholyda* sp. (Hymenoptera: Pamphiliidae) and *Choristoneura retiniana* (Lepidoptera: Tortricidae) were found both on the new growth of white fir and in the diet of nestling Mountain Chickadees (Grundel and Dahlsten 1991, Kleintjes 1993). The results are not surprising as Perrins (1991) found the breeding season of European *Parus* spp. to also coincide with the flush of new growth and availability of associated insect larvae.

The proportion of time the birds foraged in locations away from the bole also significantly differed between the nestling and fledgling stages of the breeding season. Although the birds still spent the greatest percentage (45–62%) of their time in the outer foliage compared to the inner canopy, they increased their use of the inner foliage during the fledgling periods of 1990 and 1991. Reasons for this change were likely a function of insect availability and more importantly, nestling age. It is known that after fledging birds often forage in family flocks and adults no longer need to watch for nest predators. Instead, adults spend more time attending fledglings in the protection of the inner canopy (Royama 1966). We often observed adult Mountain Chickadees feeding prey directly to fledglings resting on the inner branches. In 1990, birds spent a greater amount of time on the bole and inner canopy during the fledgling period than any other year which may have been due to the greater number of nests that fledged early in the breeding season.

Adult birds spent nearly equal amounts of time foraging in all three crown levels of white fir. This makes sense as proportions of selected prey differed little among the three crown levels (Kleintjes 1993). In contrast, Grundel (1984) found the birds spent the majority of their time in the upper crown, probably due to differences in insect availability and observation methods. Grundel repeatedly observed a limited number of specific breeding pairs for 30s intervals for extended periods of time whereas we collected 60s sequential observations on as many birds as possible throughout the season.

The percent of observation time spent on various foraging maneuvers was significantly different among years. The greatest amount of foraging time was spent searching whereas foliage gleaning maneuvers, typical of the Paridae, were the second most common use of time. Minor annual differences in proportions of various maneuvers were most likely due to changes in availability and abundance of different prey items, i.e., gleaning Lepidoptera and Hymenoptera larvae from shoots vs. flycatching adult moths from the air.

Our data indicate that Mountain Chickadees will vary their foraging behavior both within and among breeding seasons. Such plasticity in behavior allows adult Mountain Chickadees to exploit prey availability on white fir throughout the breeding season for feeding both nestlings and fledglings. This work also illustrates that within season comparisons of foraging behavior associated with feeding stages of the breeding cycle avoid masking differences in behavior that may result from pooling data into calendar months, an entire breeding season or years.

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LITERATURE CITED

AIROLA, D. A. AND R. H. BARRETT. 1985. Foraging and habitat relationships of insect gleaning birds in a Sierra Nevada mixed-conifer forest. Condor 87:205–216.

BRENNAN, L. A. 1989. Comparative use of forest resources by Chestnut-backed and Mountain chickadees in the Western Sierra Nevada. Ph.D. diss., Univ. of California, Berkeley, California.

——— AND M. L. MORRISON. 1990. Influence of sample size on interpretations of foraging patterns by Chestnut-backed Chickadees. Stud. Avian Biol. No. 13:187–192.

DAHLSTEN, D. L. AND W. A. COPPER. 1979. The use of nestboxes to study the biology of the Mountain chickadee (*Parus gambeli*) and its impact on selected forest arthropods. Pp. 217–260 *in* The role of insectivorous birds in forest ecosystems (J. G. Dickson, R. N. Conner, R. R. Fleet, J. C. Kroll and J. A. Jackson, eds.). Academic Press, New York, New York.

———, D. L. ROWNEY, AND P. K. KLEINTJES. 1992. Population dynamics of the Mountain Chickadee in Northeastern California, Pp. 502–510 *in* Wildlife 2001: populations (D. McCullough and R. Barrett, eds.). Elsevier Applied Science Publ., New York, New York.

GRUNDEL, R. 1984. The foraging behavior of parent Mountain Chickadees *Parus gambeli:* factors influencing prey selection and notes on the bird's role in regulating insect populations. Ph.D. diss., Univ. of Texas, Austin, Texas.

———. 1990. The role of dietary diversity, prey capture sequence and individuality in prey selection by parent Mountain Chickadees (*Parus gambeli*). J. Animal Ecol. 59: 959–976.

——— AND D. L. DAHLSTEN. 1991. Feeding ecology of Mountain Chickadees (*Parus gambeli*): patterns of arthropod prey delivery to nesting birds. Can. J. Zool. 69:1793–1804.

HEJL, S. J. AND J. VERNER. 1990. Within-season and yearly variations in avian foraging locations. Stud. Avian Biol. No. 13:202–209.

HILL, B. G. AND M. R. LEIN. 1988. Ecological relationships of sympatric Black-capped and Mountain chickadees in southwestern Alberta. Condor 90:875–884.

KLEINTJES, P. K. 1993. Relationship of insect availability to the foraging behavior and nestling diet of Mountain Chickadees. Ph.D. diss. Univ. of California, Berkeley, California.

MILES, D. B. 1990. The importance and consequences of temporal variation in avian foraging behavior. Stud. Avian Biol. No. 13:210–217.

MORRISON, M. L. 1984. Influence of sample size and sampling design on analysis of foraging behavior. Condor 86:146–150.

PERRINS, C. 1991. Tits and their caterpillar food supply. Ibis 133, suppl. 1:49–54.

REMSEN, J. V. AND S. K. ROBINSON. 1990. A classification scheme for foraging behavior of birds in terrestrial habitats. Stud. Avian Biol. No. 13:144–160.

ROOT, R. B. 1967. The niche exploitation pattern of the Blue-gray gnatcatcher. Ecol. Monogr. 37:317–350.

ROYAMA, T. 1966. Factors governing the hunting behavior and selection of food by the Great Tit, *Parus major.* J. Anim. Ecol. 39:619–660.

SAKAI, H. F. AND B. R. NOON. 1990. Variation in the foraging behaviors of two flycatchers: associations with stage of the breeding cycle. Stud. Avian Biol. No. 13:237–244.

SOKAL, R. R. AND F. J. ROHLF. 1981. Biometry. 2nd ed. W. H. Freeman, San Francisco, California.

SYSTAT. 1992. Systat for the Macintosh, Version 5.2. Systat Inc., Evanston, Illinois.

SZARO, R. C., J. D. BRAWN, AND R. P. BALDA. 1990. Yearly variation in resource use behavior by ponderosa pine forest birds. Stud. Avian Biol. No. 13:226–236.

WAGNER, J. 1981. Seasonal change in guild structure: oak woodland insectivorous birds. Ecology 62:973–981.

ZAR, J. L. 1984. Biostatistical analysis. 2nd ed. Prentice-Hall, New Jersey.