

# FLOCK FORMATION OF TWO PARIDS IN RELATION TO CYCLICAL SEED PRODUCTION IN A PINYON-JUNIPER WOODLAND

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**ABSTRACT.**—Cyclical production of seeds in a pinyon-juniper (*Pinus edulis*-*Juniperus monosperma*) woodland enabled us to assess the effects of resource abundance on the winter foraging ecology and flock formation of two avian seed predators, the Mountain Chickadee (*Parus gambeli*) and the Plain Titmouse (*P. inornatus*). During the winter of low seed abundance (1986/1987), chickadees and titmice converged in microhabitat use. Chickadees exhibited a coarse-grained response by selectively foraging in areas with greater ponderosa pine (*Pinus ponderosa*) density during the winter of high seed production, but shifted to a fine-grained use of microhabitat during the following year by randomly foraging in different tree species. Titmice displayed a fine-grained response in microhabitat use irrespective of seed abundance, but foraged significantly more in ponderosa pine during the winter of low seed production (becoming more like chickadees in use of tree species). Conversely, foraging behavior was consistent between years, and the two species were separable based upon the use of juniper substrates (e.g. chickadees foraged more on juniper needles than titmice, titmice foraged more on the ground beneath juniper).

The convergence in microhabitat use by chickadees and titmice during the winter of low seed abundance may be attributed to the prevalence of mixed-species flocks. During the year of a mast seed crop, chickadees and titmice foraged singly or in pairs 80% of the time and were never observed together. Half of all individuals were observed in flocks the following year, and two thirds of flocking chickadees and nearly all (88%) gregarious titmice participated in mixed flocks. Monospecific flocks of chickadees used less juniper and foraged distinctly from titmice (e.g. probed more, pecked less, gleaned from an inverted position), but converged in these characteristics in the presence of titmice. Only two titmice ever occurred in mixed-species flocks, yet up to six chickadees formed these mixed-species flocks. Chickadees apparently join titmice, as substantiated by the observed shifts in foraging ecology by chickadees in the presence of titmice, and perhaps gain knowledge of resource locations from resident titmice (chickadees are potentially altitudinal migrants within our study area). We observed an increase in sociality during periods of low seed abundance, which supports the proximate role of resource levels in promoting flock formation, but does not preclude the possibility that other factors that are a consequence of low resource abundance (e.g. decreased time available for vigilance) provide the primary impetus for flocking behavior. Received 18 July 1989, accepted 18 January 1990.

PINYON-JUNIPER woodlands exhibit marked cycles in the production of seeds and berries. Mass production of seeds occurs every 5–6 years in pinyon pine (*Pinus edulis*) and every 2–3 years in juniper (*Juniperus monosperma*), such that in some years no seeds or berries are produced (Balda and Masters 1980). This local synchrony in seed production may be related to escaping

depletion by overwhelming birds and mammals that feed upon seeds ("flooding the system" [e.g. Balda 1987]).

Two avian seed predators that winter in the pinyon-juniper woodlands of northern Arizona are the Mountain Chickadee (*Parus gambeli*) and the Plain Titmouse (*P. inornatus*) (Shrout 1977, Balda and Masters 1980). Given the extreme annual variation in resource production, we were interested in the responses of these two seed predators in terms of flock formation and foraging ecology (microhabitat use, foraging be-

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havior) during a winter (1985/1986) with a mast crop of both pinyon seeds and juniper berries, and during a winter (1986/1987) with almost no seed and berry production. Specifically, we examined the flocking behavior of chickadees and titmice in relation to seed production during each winter, to determine whether differences in foraging ecology existed between these congeners, and to ascertain whether foraging ecology changed between winters in response to differences in food abundance.

If one subscribes to the "increased foraging efficiency" hypothesis as the primary consequence of flock formation (Krebs et al. 1972; Caraco 1979a, b), then it is expected that Mountain Chickadees and Plain Titmice will form flocks during the winter of low seed abundance to increase the likelihood of locating scarce and patchily distributed resources. Formation of flocks will bring individuals and species into closer contact, and competitive interactions may counter potential benefits due to increased foraging efficiency. Species that flock during times of low resource levels ("ecological crunches," *sensu* Wiens 1977) therefore should forage more distinctly in mixed-species flocks than when flocking with conspecifics. Species within flocks of oak woodland birds in Arizona were spatially segregated in microhabitat use. For example, Bridled Titmice (*P. wollweberi*) altered their foraging ecology (foraging stance, substrate use, and position in canopy) when in the presence of Bushtits (*Psaltriparus minimus*) (Austin and Smith 1972). Willow Tits (*Parus montanus*) avoided trees in which Crested Tits (*P. cristatus*) foraged, and shifted their position within the canopy of the tree in the presence of either Crested or Great (*P. major*) tits (Alatalo 1981).

Conversely, social facilitation or "copying behavior" predicts increased similarities between species when foraging in mixed flocks. Morse (1978) observed several unambiguous cases of copying behavior in Blue Tits (*P. caeruleus*) attracted to sites previously or concurrently occupied by other foraging individuals (conspecifics as well as other species). Krebs (1973) experimented with mixed-species flocks of Black-capped (*P. atricapillus*) and Chestnut-backed (*P. rufescens*) chickadees in an aviary to demonstrate that flock members (of both species) converged in foraging behavior in response to successful individuals (of either species). This led Krebs to propose that social learning played an important role in flock behavior and con-

tributed to the increased advantage of heterospecific over monospecific flocks because total scanning range of the flock could be increased because of the presence of different species that foraged in different locations.

Thus, we made several predictions in regard to flock formation and foraging ecology of Mountain Chickadees and Plain Titmice in response to changes in annual productivity of seeds: (1) chickadees and titmice will alter their foraging ecology in response to differences in food abundance between winters; (2) both species will exhibit increased sociality during the winter of low seed abundance; and (3) consequently, each species would be expected to diverge in foraging characteristics, particularly when participating in mixed-species flocks as compared with when foraging in monospecific flocks or alone. Alternatively, if sociality facilitates resource acquisition, then convergence in foraging ecology would be expected of species in mixed-species flocks. It should be possible, therefore, to distinguish between the contrasting predictions of the "competition" hypothesis and "social facilitation" hypothesis regarding mixed-species flock formation.

#### METHODS

Our study was conducted during the winters (November–March) of 1985/1986 and 1986/1987 in a 20-ha area ca. 26 km north of Flagstaff, Coconino County, Arizona. Vegetation on the study area was representative of a transition between pinyon-juniper woodlands characteristic of lower elevations (1,670 m; upper sonoran life zone) and ponderosa pine (*Pinus ponderosa*) forests characteristic of higher elevations (2,100 m; transition life zone) in the southwest.

#### MICROHABITAT ABUNDANCE

We quantified vegetation abundance and structure (microhabitat) to characterize the habitat and to compare bird species use relative to vegetation within this pinyon-juniper habitat. Thirty-five 20-m-radius (0.13 ha) plots were established 50 m apart from an arbitrary starting point in the study area in 1987. In each plot we counted all trees <2 m, 2–7 m, and >7 m in height (estimated visually). These categories were selected to separate young (reproductively immature) trees (<2 m) and pinyon and juniper trees (generally <7 m in height) from ponderosa pines. A 30-m transect bisected each plot in a randomly selected direction from which we estimated the height of live foliage that intercepted an imaginary vertical line extending up from the ground at 3-m intervals along the transect. Height categories for foliage cover were

0–1 m, 1.1–3 m, 3.1–5 m, 5.1–7 m, 7.1–10 m, and >10 m. Variables related to undergrowth were not recorded because shrubs were rare, and grass and forb cover was sparse or covered by snow during our study.

#### MICROHABITAT USE

The location of foraging birds (explained below) served as the center of a 20-m-radius plot. Microhabitat use was quantified as described for quantification of microhabitat abundance.

*Comparisons between species and years.*—Two-tailed *t*-tests were used to evaluate differences in microhabitat use between species within and between winters as well as for both years combined (overall species comparison). The assumption of homogeneity of variance between samples was evaluated by Levene's test; few comparisons departed from this assumption and a pooled variance estimate subsequently was used. Comparisons were considered significantly different if  $P < 0.05$ .

We performed discriminant analysis with forward stepwise inclusion of variables to characterize microhabitat use of the two species. Variables were entered initially into the equation if the variable significantly ( $P < 0.1$ , *F*-test) improved the discrimination between groups. We accepted a significance level of  $P < 0.1$  for entry of variables into discriminant analysis so as not to exclude variables that were nonsignificant ( $P > 0.05$ ) between species in the univariate tests (i.e. *t*-tests), but that may have provided significant contributions in this multivariate analysis at later steps in the procedure. Multicollinearity between variables was reduced by eliminating one of any pair of variables with an *r*-value of  $>0.7$ . The variable retained for possible inclusion in discriminant analysis was the one with the highest *F*-value for separation between groups.

Discriminant function equations were developed for each of the two winters of study and for both winters combined. To determine the temporal validity of these equations, we examined the ability of equations developed from one winter to correctly classify data (as to one of the two species) collected during the other winter. We validated the discriminant functions for each winter by randomly dividing the data set for each winter (and the overall data set for both winters combined), and using this random subset to develop the discriminant function and the remaining data to determine the accuracy of classification. The assumption underlying discriminant analysis of equal variance-covariance matrices between groups was evaluated with Box's-*M* statistic.

*Use versus abundance of microhabitat.*—A three-group discriminant analysis was run to determine whether each species used microhabitat in proportion to microhabitat abundance. Because a classification accuracy of 33% is expected by chance for each group in a three-group discriminant analysis, percentages  $>33\%$

represent increasing levels of success by the model in distinguishing between the groups. A high percentage of species-centered points (microhabitat use) classified incorrectly as randomly centered points (microhabitat abundance) would indicate that the species is using microhabitat in proportion to abundance (fine-grained response). The concept of "grain" is used to describe species responses to environmental heterogeneity to provide an understanding of how different species "perceive" their environment (Adicott et al. 1987).

#### FORAGING BEHAVIOR

Foraging activity increased after 0800, peaked between 1000–1300 (85% of all observations), and decreased sharply after 1400. Admittedly, this pattern of diurnal variation in foraging intensity was amplified further within our data set by the concentration of our efforts during the periods of the day when birds apparently were most active. We systematically traversed the study area, and when a foraging bird was encountered, we waited 10 s (to reduce bias due to observer disturbance and towards individuals foraging in conspicuous locations) and then recorded activity for 10–60 s. To describe the foraging activities and locations of these two species, we recorded foraging substrate (where foraging motions were directed; e.g. twig, small branch, medium branch, large branch, and trunk); foraging activity (e.g. glean, probe); distance (m) moved by flying or hovering; distance (m) moved by hopping, using wings only for balance; vertical foraging height (m); tree height (m); and horizontal location of bird in canopy measured as percent distance from tree bole (all heights and distances were visually estimated as we were trained to make visual estimates; Block et al. 1987). Data for substrate use and foraging mode were converted to percent use for each individual to standardize observation periods of different lengths.

Once we recorded data on an individual, the bird was not followed. We recorded data on only one individual per flock to minimize bias due to potentially correlated activities of flocking individuals. The observer resumed traversing the study area in the direction opposite to that in which the bird or flock disappeared. This minimized encountering the same individual or flock again. Encounter rates of birds by observers were calculated for each species, and statistical comparisons (*t*-tests; comparisons significantly different if  $P < 0.05$ ) were made between species for each winter and between winters for each species to assess the distribution and abundance of individuals (or flocks, because data on only one individual per flock were recorded) throughout the study area.

*Comparisons between species and years.*—Differences between species in foraging behavior within each winter and for both winters combined (overall species comparison) were evaluated using two-tailed *t*-tests

as for analysis of microhabitat use. Similarly, differences between years in foraging behavior for each species was assessed with a two-tailed *t*-test. Discriminant analysis was employed to characterize foraging behavior of the species with the same criteria and validation procedures as described previously for analysis of microhabitat use.

FLOCKING BEHAVIOR

When we encountered a foraging bird, we recorded whether the bird was foraging singly, as a pair, or in a flock ( $\geq 3$  birds), and the species composition and number of individuals if foraging in a flock. Percentage of time observed foraging singly, in pairs, or in monospecific or heterospecific flocks was assessed for each species and between winters. We used *t*-tests to test for differences in mean flock size between species and between years (comparisons significantly different if  $P < 0.05$ ). Differences in microhabitat use and foraging behavior between the two species were assessed separately for monospecific and heterospecific flocks using Mann-Whitney tests. To examine whether chickadees and titmice foraged differently in mixed-species flocks than when in the presence of conspecifics, the foraging ecology of each species was contrasted between these different assemblages.

RESULTS

MICROHABITAT ABUNDANCE

The understory comprised mostly (95%) small (<2 m) junipers and pinyons, each of which occurred in densities of approximately 86 stems/ha (Appendix 1). The study area was predominated (63%) by trees 2-7 m in height. Pinyon pine (45%, 163 stems/ha) and juniper (40%, 146 stems/ha) occurred in roughly equal numbers. Ponderosa pine represented 13% (72 stems/ha) of this woodland overall, and 83% of the trees >7-m tall were ponderosa pines (10 stems/ha). Live foliage was concentrated mainly (63%) below 3 m.

MICROHABITAT USE

*Comparisons between species and years.*—Mountain Chickadees foraged in areas of significantly ( $P < 0.05$ ) denser ponderosa pine than Plain Titmice, and in areas with greater foliage cover between 3 and 7 m in height during winter 1985/1986 (Appendix 1). During winter 1986/1987, chickadees used significantly denser juniper in the midcanopy (2-7 m) than titmice. Chickadees differed between years only by for-

TABLE 1. Discriminant analysis of Mountain Chickadees (MOCH) and Plain Titmice (PLTI) microhabitat use, and use of microhabitat by species (MOCH and PLTI) vs. microhabitat abundance, during two winters in northern Arizona. Variables retained for discriminant analysis resulted from the stepwise inclusion of variables that significantly ( $P < 0.1$ , *F*-test) improved the discrimination between groups (see text for details).

	Winter 1985/1986		Winter 1986/1987	
	MOCH vs. PLTI	Species vs. abundance	MOCH vs. PLTI	Species vs. abundance
Eigenvalue	0.464	0.815	0.130	0.539
Canonical correlation	0.563	0.670	0.343	0.592
Chi-square (df)	22.504 (4)	69.086 (10)	7.003 (2)	47.183 (10)
<i>P</i>	<0.001	<0.001	<0.05	<0.001
Variables* and correlation	HT3 HT4 PPHT2 PIHT2	HT3 HT4 PIHT2 JUHT1	JUHT2	PIHT2 HT1 HT5
Box's-M ( <i>P</i> )	<0.001	<0.001	>0.3	>0.3

\* Abbreviations for variables: JUHT1 (Juniper <2 m); JUHT2 (Juniper), PIHT2 (Pinyon), PPHT2 (Ponderosa) (all 2-7 m); HT1 (0-1 m), HT3 (3.1-5 m), HT4 (5.1-7 m), HT5 (7.1-10).

TABLE 2. Percent success, as classified from discriminant analysis of Mountain Chickadees (MOCH) and Plain Titmice (PLTI) microhabitat use, and use of microhabitat vs. abundance, during winters 1985/1986 and 1986/1987 in northern Arizona. Values in parentheses are results of subgroup classification (validation) using a random subset of 50% of that year's observations; NA = not applicable.

Year/actual group	Predicted group					
	Winter 1985/1986			Winter 1986/1987		
	MOCH	PLTI	Abundance	MOCH	PLTI	Abundance
1985/1986						
MOCH	69 (82)	22 (0)	9 (18)			
PLTI	32 (53)	26 (12)	42 (35)		NA	
Abundance	3 (0)	11 (6)	86 (94)			
MOCH	72 (91)	28 (9)		37	63	
PLTI	23 (53)	77 (47)		48	52	
1986/1987						
MOCH				23 (36)	40 (0)	37 (64)
PLTI		NA		28 (47)	52 (13)	21 (40)
Abundance				11 (50)	3 (0)	86 (50)
MOCH	70	30		56 (64)	44 (36)	
PLTI	24	76		81 (73)	19 (27)	

aging in areas with less dense foliage cover between 3 and 5 m during the second winter. Titmice significantly reduced use of juniper (but juniper was still used in proportion to its abundance) and increased use of 2- to 7-m tall ponderosa pines between years.

Discriminant analysis identified four variables that significantly separated microhabitat use between species during the first winter (Table 1); three variables related to use of ponderosa pine and areas with foliage cover between 3 and 7 m in height were previously identified by univariate tests and were discussed above. The discriminant function classified correctly ca. 75% of individuals based upon microhabitat use data from the first winter (Table 2). Validation of the discriminant function using a subset of the data resulted in 50% of the titmice being incorrectly classified as chickadees with respect to microhabitat use. The model derived from the second winter and applied to habitat use data from the first winter correctly identified many (70–76%) of the chickadees and titmice.

Discriminant analysis separated species by use of 2- to 7-m tall juniper during the second winter (Table 1). Classification was poor, however, as 81% of titmice and 44% of chickadees were misclassified. The discriminant function from the first year misclassified 60% of chickadees and approximately 50% of titmice (Table 2).

*Use versus abundance of microhabitat.*—Moun-

tain Chickadees were more specific in their use of microhabitat than Plain Titmice during the first winter. The discriminant function distinguished between chickadee microhabitat use and microhabitat abundance data, but was unable to successfully classify titmice (Table 2). Validation procedures using a subset of the data from the first winter resulted in about three quarters of the chickadees (70%) and titmice (76%) being identified correctly.

During the second winter, the discriminant function was less successful in discriminating the species and randomly centered points, although microhabitat abundance data remained a distinct group (86% classification success; Table 2). These relationships were considerably weakened when a subset of data was used to validate the model as species microhabitat use and microhabitat abundance data became inseparable.

#### FORAGING BEHAVIOR

*Comparisons between species and years.*—We encountered individuals of either species at 35-min intervals ( $SD = 18.9$ ) over both winters (1985/1986:  $\bar{x} = 34 \pm 18.9$  min; 1986/1987:  $\bar{x} = 36 \pm 19.0$  min;  $P > 0.05$ ,  $t$ -test). No significant differences in encounter rates were found between species for either winter (1985/1986: Mountain Chickadee  $\bar{x} = 36 \pm 28.2$  min, Plain Titmouse  $\bar{x} = 41 \pm 14.7$  min; 1986/1987: Moun-

TABLE 3. Discriminant analysis of Mountain Chickadee and Plain Titmouse foraging behavior during two winters in northern Arizona. Variables retained for discriminant analysis resulted from the stepwise inclusion of variables that significantly ( $P < 0.1$ ,  $F$ -test) improved the discrimination between groups (see text for details).

	Winter 1985/1986		Winter 1986/1987	
Eigenvalue		0.383		1.229
Canonical correlation		0.527		0.743
Chi-square (df)		19.328 (5)		47.702 (9)
$P$		0.002		<0.001
Variables <sup>a</sup> and correlation				
	JUTW	0.56	JUSE	0.38
	JUSE	0.49	JUTW	0.32
	JUHOP	0.43	JUGR	0.30
	JUNE	-0.36	PPFLY	-0.26
	JUSBMB	0.33	JUSBMB	0.25
Box's- $M$ ( $P$ )		<0.001		<0.05

<sup>a</sup> Abbreviations for variables: Juniper (JU) twigs (JUTW), search (JUSE), hopping rate (JUHOP), needles (JUNE), small and medium branches (JUSBMB), ground beneath tree (JUGR), foraging rate using wings in ponderosa pine (PPFLY); see also Appendix 2 for full descriptions of variables.

tain Chickadee  $\bar{x} = 53 \pm 34.1$  min, Plain Titmouse  $\bar{x} = 40 \pm 16.1$  min). Neither were there significant differences between winters for either species, despite the fact that chickadees were encountered less frequently (ca. 17 min more between encounters) during the second winter.

During the first winter, chickadees differed significantly from titmice in substate use. Chickadees foraged more upon ponderosa twigs of the outer canopy and less on juniper twigs (where titmice foraged 44% of the time, but which fell significantly to 18% during the second winter; Appendix 2). Chickadees foraged significantly more on juniper needles than did titmice, and chickadees gleaned from an inverted position, a behavior not employed by titmice. Chickadees used juniper needles significantly less during the second winter. Foraging behavior differed between these species during the second winter because titmice foraged in significantly smaller juniper and pinyon than did chickadees, and titmice spent more (22% vs. 4%) time on the ground. Overall, titmice spent significantly more time in and around juniper than chickadees did, and chickadees usually foraged more on needles and in taller trees.

Discriminant analyses corroborated the findings of the univariate tests. Foraging behavior was separable between chickadees and titmice during the first winter by variables related to juniper substrates and movement within juniper (Table 3). Classification success was high (chickadees = 77%, titmice = 76%), but was little better than 50% for titmice when the model was

validated on a subset of the data (Table 4). The discriminant function from the second winter correctly classified most (91%) of the titmice but only approximately 50% of the chickadees from the first winter. Three of the five variables of the discriminant analysis related to juniper substrates were the same between years (Table 3). The discriminant function for the second winter separated most chickadees and titmice (91% and 82%) into groups based upon their foraging behavior; this categorization held after validation procedures with half of the data set (Table 4). The model from the first winter correctly identified almost all (97%) chickadees, but correctly identified only approximately 50% of titmice.

#### FLOCKING BEHAVIOR

Mountain Chickadees and Plain Titmice foraged singly (78%) or in pairs (85%) during the first winter (Table 5). Mean flock size did not differ significantly between species (chickadee:  $\bar{x} = 1.91 \pm 0.995$  [SD],  $n = 32$ ; titmouse:  $\bar{x} = 1.91 \pm 1.04$ ,  $n = 33$ ). The two species were never observed together, although a chickadee foraged with 1-2 Golden-crowned Kinglets (*Regulus satrapa*) on three occasions. During the second winter, both species occurred in flocks (three or more birds) in ca. 60% of all observations. They occurred singly or in pairs in only 36% of the observations for chickadees and 38% for titmice (Table 5). About half of all foraging individuals (47.2% of chickadees and 42.5% of titmice) were observed in mixed flocks. Further, heterospecific flocks were more prevalent than

TABLE 4. Percent success, as classified from discriminant analysis of the foraging ecology of Mountain Chickadees (MOCH) and Plain Titmice (PLTI) during two winters in northern Arizona. Values in parentheses are results of subgroup classification (validation) using a random subset of 50% of that year's data.

Year/ actual group	Predicted group			
	Winter 1985/1986		Winter 1986/1987	
	MOCH	PLTI	MOCH	PLTI
Winter 1985/1986				
MOCH	77 (75)	23 (25)	97	3
PLTI	24 (50)	76 (50)	46	54
Winter 1986/1987				
MOCH	45	55	91 (69)	9 (31)
PLTI	9	91	18 (31)	82 (69)

monospecific flocks. Nearly two thirds (74%) of flocking chickadees and nearly all (88%) gregarious titmice participated in mixed-species flocks. The mixed flocks generally (60%) involved one or two titmice and one or two chickadees; Red-breasted Nuthatches (*Sitta canadensis*) and Brown Creepers (*Certhia americana*) participated on a few occasions (ca. 10% of all observations). Mean flock size did not differ between species (chickadee:  $\bar{x} = 3.33 \pm 1.67$  [SD],  $n = 36$  individuals; titmouse:  $\bar{x} = 3.28 \pm 1.65$ ,  $n = 40$ ), but flock sizes were significantly different between winters for both species ( $P < 0.001$ ,  $t$ -test).

Monospecific flocks of chickadees used significantly less juniper and foraged in a manner distinctive from titmice (e.g. chickadees probed more, pecked less, and gleaned from an inverted position; Table 6). A convergence in these characteristics was observed between species in heterospecific flocks. Chickadees significantly altered their foraging behavior in the presence of titmice (Table 6). Titmice foraged in significantly taller trees when in heterospecific flocks than when in monospecific flocks, although monospecific flocks of either species were not significantly different in selection of tree stature.

#### DISCUSSION

During the winter of low seed abundance in the pinyon-juniper woodland, Mountain Chickadees and Plain Titmice converged in microhabitat use. Chickadees had exhibited a

TABLE 5. Monospecific flock formation during two winters in a pinyon-juniper woodland of northern Arizona. Percentages represent frequency of foraging individuals observed either singly, in pairs, or in monospecific flocks.

Flock size	Mountain Chickadees		Plain Titmice	
	1985/1986 <sup>a</sup>	1986/1987 <sup>b</sup>	1985/1986 <sup>a</sup>	1986/1987 <sup>b</sup>
1	40.6	8.3	36.4	7.5
2	37.5	27.8	48.5	30.0
3	9.4	8.3	9.0	5.0
4	3.0	5.6	3.0	0.0
5	3.0	2.8	0.0	2.5
6	0.0	0.0	3.0	0.0

<sup>a</sup> Sample sizes are 32 observations for chickadees and 33 for titmice.

<sup>b</sup> Sample sizes are 36 observations for chickadees and 40 for titmice.

coarse-grained response in microhabitat use by selectively foraging in areas with greater density of ponderosa pine during the winter of mast seed abundance, yet they shifted to a fine-grained use by randomly foraging in different tree species during the following winter. Titmice exhibited a fine-grained response in microhabitat use irrespective of seed abundance. Yet titmice significantly increased use of ponderosa pine during the second winter and became more like chickadees in vegetation use. Chickadees, like titmice, foraged in the lower canopy of junipers during the second year, and the discriminant function developed from the first winter misclassified most (two thirds) of the chickadees as titmice. This supports our contention that species convergence in microhabitat use (especially by chickadees) occurred in a winter of low resource abundance.

Shifts in foraging ecology in response to changes in productivity are not unprecedented. Specifically, Wagner (1981) found that Plain Titmice significantly shifted tree-species use and foraged lower one winter relative to the other. Differences in the foraging ecologies of several parids between winters also have been related to resource abundance in an alpine larch forest (Laurent 1986). Production of larch seeds varied between winters and the primary seed consumer, the Willow Tit, increased use of other substrates (e.g. pine cones, branches, and ground) during years of low larch seed abundance. Microhabitat use (e.g. use of larch twigs or needles) also differed between winters for a number of other species and was correlated with the abun-

TABLE 6. Foraging ecology of Mountain Chickadees (MOCH) and Plain Titmice (PLTI) in monospecific and heterospecific flocks during winter 1986/1987 in northern Arizona. Microhabitat use and foraging behavior ( $\bar{x} \pm SD$ ) are compared between species within each assemblage (interspecies comparisons), as well as between monospecific and heterospecific flocks for each species (interflock comparisons;  $P_c$ : chickadees,  $P_t$ : titmice). Sample sizes are 17 chickadee and 19 titmouse monospecific flocks, and 13 chickadees and 7 titmice observed in heterospecific flocks.

Variable	Monospecific flocks		Heterospecific flocks		$P_c$	$P_t$
	MOCH	PLTI	MOCH	PLTI		
<b>Microhabitat use</b>						
Tree species (%)						
Ponderosa pine	30.5 $\pm$ 46.46	11.2 $\pm$ 28.01	18.5 $\pm$ 37.85	28.6 $\pm$ 48.80	NS	NS
Pinyon pine	48.3 $\pm$ 46.68	22.8 $\pm$ 32.96	40.7 $\pm$ 45.47	14.3 $\pm$ 37.80	NS	NS
Juniper	14.9 $\pm$ 34.21	64.3 $\pm$ 40.75***	33.6 $\pm$ 43.65	57.1 $\pm$ 53.45	NS	NS
Tree height (m)	6.0 $\pm$ 3.94	4.1 $\pm$ 2.52	4.3 $\pm$ 0.75	5.4 $\pm$ 2.50	NS	0.03
Foraging height (m)	3.3 $\pm$ 2.59	1.9 $\pm$ 1.42	2.4 $\pm$ 1.39	2.1 $\pm$ 1.54	NS	NS
Rel. foraging ht. <sup>b</sup> (%)	57.4 $\pm$ 22.86	48.2 $\pm$ 27.20	61.0 $\pm$ 23.07	40.0 $\pm$ 29.17	NS	NS
Substrate use (%)						
Needles	10.7 $\pm$ 27.33	7.0 $\pm$ 23.76	20.4 $\pm$ 31.64	5.9 $\pm$ 15.57	NS	NS
Twigs	49.5 $\pm$ 45.39	32.5 $\pm$ 43.16	21.4 $\pm$ 38.43	28.4 $\pm$ 46.60	NS	NS
Small branches	12.9 $\pm$ 29.10	22.4 $\pm$ 28.60	21.1 $\pm$ 37.04	29.4 $\pm$ 38.85	NS	NS
Ground	9.0 $\pm$ 22.20	28.5 $\pm$ 34.95	14.4 $\pm$ 31.86	36.3 $\pm$ 46.94	NS	NS
<b>Foraging behavior</b>						
Foraging activity (%)						
Probe	24.2 $\pm$ 36.25	5.6 $\pm$ 18.20*	8.4 $\pm$ 22.22	16.8 $\pm$ 26.97	NS	NS
Peck	00.0 $\pm$ 00.00	15.1 $\pm$ 32.92*	16.2 $\pm$ 31.21	00.0 $\pm$ 00.00	0.01	NS
Glean	25.9 $\pm$ 33.94	19.7 $\pm$ 32.01	21.4 $\pm$ 32.63	37.7 $\pm$ 47.70	NS	NS
Invert glean	3.8 $\pm$ 7.14	00.0 $\pm$ 00.00**	00.0 $\pm$ 00.00	1.0 $\pm$ 2.65	0.04	NS
Search	39.5 $\pm$ 41.63	59.6 $\pm$ 41.99	35.58 $\pm$ 38.13	52.89 $\pm$ 43.94	NS	NS
Foraging rate (perches/s)	0.29 $\pm$ 0.145	0.37 $\pm$ 0.356	0.28 $\pm$ 0.241	0.28 $\pm$ 0.204	NS	NS

\* Significance levels: \* =  $P < 0.05$ , \*\* =  $P < 0.01$ , \*\*\* =  $P < 0.001$ .

<sup>b</sup> % tree height/bird height.

dance of arthropod prey (e.g. caterpillars) on these substrates.

The foraging behavior of chickadees and titmice appeared to be consistent between years. The models developed for each of the two winters are similar, and species are separable based upon their use of juniper substrates. Morphological constraints imposed by body size and bill shape may restrict foraging behavior, and thus microhabitat use may represent a more plastic response to variations in resource abundance and distribution as evidenced by the shift from specific to random use of tree species between winters by Mountain Chickadees. Indeed, Alatalo (1982) found an inverse relationship between body size and versatility of feeding postures (a measure related to both foraging technique and use of vegetation structure) in tits during winter, leading him to assert that such versatility enabled birds to use scarce resources during winter.

The convergence in microhabitat use in

chickadees and titmice may be attributed to the prevalence of heterospecific flocks during the winter of low seed abundance. Half of all individuals were observed in flocks during the second winter (as opposed to none during the previous year of a mast seed crop), and nearly two thirds of flocking chickadees and almost all gregarious titmice were members of mixed flocks. Further, chickadees significantly increased their use of juniper and converged in foraging behavior in the presence of titmice.

This convergence in foraging ecology lends support to the social facilitation hypothesis. Both species may extend their visual field in the search for scarce and patchily distributed resources by forming flocks. The preponderance of mixed flocks implies a potential advantage of heterospecific flocks over monospecific flocks. Mixed-species flocks may generate a composite search pattern based on the assemblage of different species, which leads to an increased search efficiency (but see Hutto 1988 for an example



of a potential decrease in foraging efficiency for species within mixed flocks). Further, mixed flocks may accrue benefits from increased vigilance and decreased competition and aggression relative to flocks of conspecifics (Metcalfe 1989). We note that no more than two titmice were ever observed in a mixed-species flock, whereas up to six chickadees formed these heterospecific assemblages. We believe that the chickadees join titmice, especially because chickadees converged in foraging ecology in the presence of titmice. The gain to chickadees from titmice over conspecifics is not clear. Titmice are obligatory to the pinyon-juniper woodlands of northern Arizona and are permanent residents within this habitat (Balda and Masters 1980). Mountain Chickadees, in contrast, occur and breed in a variety of habitats in addition to pinyon-juniper. Given the proximity of the San Francisco Peaks (elevation = 3,950 m) to our study area and that chickadees selectively foraged in areas of greater ponderosa pine density within the pinyon-juniper woodland, and foraged significantly more in ponderosa pine than titmice, we hypothesize that many of the chickadees were altitudinal migrants that breed in the mountains and winter in the pinyon-juniper woodlands. These chickadees might benefit from learning the locations of seed-bearing trees (which are scarce during the year of almost no seed production) from resident titmice.

Increased sociality of chickadees and titmice during the winter of low seed abundance suggests that increased search efficiency may be the primary motivation for their flock formation. Morse (1967) documented decreased flock participation in another seed predator, the Brown-headed Nuthatch (*Sitta pusilla*), in response to decreased abundance of long-leaf pine seeds in Louisiana. Berner and Grubb (1985) supplemented food during the winter in deciduous woodlands, which resulted in reduced sociality in a number of bird species that included Carolina Chickadees (*Parus carolinensis*) and Tufted Titmice (*P. bicolor*).

The antithesis of the foraging efficiency explanation for the advantages of flock formation is the antipredation hypothesis, whereby increased detection of predators (e.g. Siegfried and Underhill 1975) or diffusion of predation risk (Hamilton 1971) is the primary impetus to flock. The antipredation and foraging efficiency hypotheses do not produce mutually exclusive predictions. The general supposition is that if

flocking is primarily to protect against predators, then flock formation should be independent of food abundance (e.g. Berner and Grubb 1985). As Hutto has suggested (pers. comm.), this assumption does not follow logically because there is ample evidence that foraging efficiency and vigilance are inversely related (e.g. Caraco 1979b, 1982; Sullivan 1984). Thus, the two hypotheses are inextricably linked. If predator protection served as the ultimate motivation for flocking behavior, then formation of flocks would not be independent of resource abundance because a reduction in vigilance is a direct consequence of the increase in search time for food, necessitated by scarce resources. Individuals that aggregate to compensate for reduction in vigilance should disperse once resource levels surpass some threshold that enables individuals to effectively scan for predators while foraging. This provides an alternative interpretation consistent with the reduction in flocking behavior observed in food supplementation experiments (e.g. Berner and Grubb 1985). Food abundance may provide a proximate mechanism for flock formation, yet other factors that are a consequence of reduced resource levels (such as decreased scan time) may provide the ultimate motivation for flocking. Thus, the occurrence of flocks we observed during periods of low resource levels does not necessarily support the food-mediated hypothesis as the primary impetus for flock formation in birds.

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APPENDIX 1. Microhabitat abundance and use of microhabitat by Mountain Chickadees (MOCH) and Plain Titmice (PLTI) during two winters in northern Arizona. Sample sizes are in parentheses; all values are  $\bar{x} \pm SD$ ; \* = significant ( $P < 0.05$ ) interspecific comparison, \*\* = significant ( $P < 0.01$ ) interspecific comparisons, and † = significant ( $P < 0.05$ ) interyear comparison for the species.

Variable	1985/1986		1986/1987		Overall		Micro-habitat abundance
	MOCH (32)	PLTI (31)	MOCH (30)	PLTI (29)	MOCH (62)	PLTI (60)	
<b>Trees &lt;2-m-tall per 20-m radius</b>							
Juniper (JUHT1)	17.8 ± 13.85	20.7 ± 9.91	13.4 ± 7.41	10.4 ± 7.06†	15.7 ± 11.34	15.7 ± 10.03	11.2 ± 5.02
Pinyon (PIHT1)	12.3 ± 7.64	12.4 ± 7.44	10.6 ± 6.20	9.3 ± 6.58	11.5 ± 6.98	10.9 ± 7.15	11.2 ± 4.74
Ponderosa (PPHT1)	1.3 ± 2.37	0.4 ± 0.80*	0.5 ± 1.11	1.4 ± 2.82	0.9 ± 1.89	0.9 ± 2.09	1.1 ± 1.90
<b>Trees 2-7-m-tall per 20-m radius</b>							
Juniper (JUHT2)	25.2 ± 15.52	29.6 ± 8.27	25.6 ± 11.29	19.4 ± 11.19*†	25.4 ± 13.53	24.7 ± 10.98	19.0 ± 8.28
Pinyon (PIHT2)	31.3 ± 19.28	25.2 ± 14.29	28.9 ± 12.59	31.4 ± 17.55	30.1 ± 16.30	28.2 ± 16.12	21.2 ± 9.74
Ponderosa (PPHT2)	8.8 ± 9.34	3.3 ± 4.43**	6.9 ± 7.52	10.4 ± 15.12†	7.9 ± 8.50	6.7 ± 11.46	6.9 ± 7.28
<b>Trees &gt;7-m-tall per 20-m radius</b>							
Juniper (JUHT3)	0.1 ± 0.18	0.1 ± 0.18	0.0 ± 0.00	0.0 ± 0.00	0.1 ± 0.13	0.1 ± 0.13	0.1 ± 0.68
Pinyon (PIHT3)	0.6 ± 1.37	0.1 ± 0.34	0.0 ± 0.00	0.0 ± 0.00	0.3 ± 1.01	0.1 ± 0.25	0.1 ± 0.51
Ponderosa (PPHT3)	3.7 ± 8.78	1.1 ± 1.39	1.2 ± 1.29	2.6 ± 3.92	2.5 ± 6.45	1.8 ± 2.98	1.3 ± 1.38
<b>Foliage height categories</b>							
0-1 m (HT1)	26.6 ± 14.50	31.0 ± 20.39	30.3 ± 26.19	21.4 ± 22.63	28.4 ± 20.90	26.3 ± 21.86	35.7 ± 21.73
1.1-3 m (HT2)	33.8 ± 19.30	28.7 ± 18.75	29.0 ± 21.71	25.5 ± 22.45	31.5 ± 20.47	27.7 ± 20.51	26.9 ± 1.45
3.1-5 m (HT3)	24.7 ± 19.67	9.4 ± 12.09**	9.3 ± 17.21†	12.1 ± 19.16	17.3 ± 19.93	10.7 ± 15.82*	6.3 ± 9.73
5.1-7 m (HT4)	8.8 ± 14.54	1.9 ± 5.43*	3.3 ± 8.44	5.9 ± 13.76	6.1 ± 12.19	3.8 ± 10.43	2.3 ± 5.47
7.1-10 m (HT5)	0.9 ± 2.96	0.0 ± 0.00	2.7 ± 6.40	3.1 ± 10.04	1.8 ± 4.97	1.5 ± 7.09	0.0 ± 0.00
>10 m (HT6)	0.0 ± 0.00	0.0 ± 0.00	0.7 ± 2.54	0.7 ± 3.71	0.3 ± 1.78	0.3 ± 2.58	0.0 ± 0.00

APPENDIX 2. Foraging ecology ( $\bar{x} \pm SD$ ) of Mountain Chickadees (MOCH) and Plain Titmouse (PLTI) during two winters in a pinyon-juniper woodland of northern Arizona. Asterisks denote significant interspecific comparisons: \* =  $P < 0.05$ , \*\* =  $P < 0.01$ , \*\*\* =  $P < 0.001$ ; † = significant ( $P < 0.05$ ) interyear comparison for the species.

Variable	Winter 1985/1986		Winter 1986/1987		Overall	
	MOCH	PLTI	MOCH	PLTI	MOCH	PLTI
<b>Tree height (m)</b>						
Juniper	4.4 ± 0.68	3.9 ± 1.12	3.9 ± 0.57	3.1 ± 1.10*†	4.2 ± 0.68	3.5 ± 1.18**
Pinyon	4.4 ± 1.92	3.6 ± 1.14	3.7 ± 0.96	3.0 ± 0.67*	3.9 ± 1.32	3.2 ± 0.86
Ponderosa	7.2 ± 1.79	0.0 ± 0.00	10.0 ± 3.63	8.9 ± 3.02	9.1 ± 3.38	8.9 ± 2.80
<b>Foraging height (m)</b>						
Juniper	2.4 ± 1.20	2.2 ± 1.22	2.3 ± 0.82	1.8 ± 1.18	2.3 ± 1.06	2.0 ± 1.21
Pinyon	2.5 ± 1.62	0.0 ± 0.00	2.4 ± 1.00	1.8 ± 0.46	2.5 ± 1.18	1.8 ± 0.41
Ponderosa	3.6 ± 1.52	0.0 ± 0.00	6.5 ± 4.23	4.6 ± 2.70	5.6 ± 3.81	4.5 ± 2.51
<b>Relative foraging height (% tree height/bird height)</b>						
Juniper	56 ± 31.4	56 ± 25.8	62 ± 27.7	60 ± 28.4	58 ± 29.6	57 ± 26.7
Pinyon	54 ± 23.4	0 ± 00.0	65 ± 18.6	61 ± 21.3	62 ± 20.2	60 ± 18.6
Ponderosa	51 ± 21.9	0 ± 00.0	65 ± 30.2	52 ± 19.9	60 ± 28.0	51 ± 18.6
<b>Location in canopy (% from tree bole)</b>						
Juniper	44 ± 40.7	50 ± 31.4	20 ± 35.4†	43 ± 37.0*	32 ± 39.7	46 ± 34.2*
Pinyon	11 ± 22.4	8 ± 19.3	29 ± 36.4†	25 ± 37.0†	20 ± 31.5	16 ± 30.5
Ponderosa	8 ± 20.6	1 ± 4.0*	21 ± 33.2	11 ± 25.9†	15 ± 28.3	6 ± 19.0*
<b>Foraging rate using wings (m/s)</b>						
Juniper	0.09 ± 0.06	0.08 ± 0.06	0.06 ± 0.08	0.03 ± 0.03†	0.07 ± 0.07	0.06 ± 0.05
Pinyon	0.04 ± 0.05	0.00 ± 0.00	0.05 ± 0.03	0.02 ± 0.02**	0.05 ± 0.04	0.02 ± 0.02*
Ponderosa	0.00 ± 0.00	0.00 ± 0.00	0.06 ± 0.04	0.03 ± 0.01*	0.06 ± 0.04	0.04 ± 0.03
<b>Foraging rate while hopping (m/s)</b>						
Juniper	0.06 ± 0.03	0.11 ± 0.10*	0.07 ± 0.05	0.09 ± 0.06	0.06 ± 0.04	0.10 ± 0.08*
Pinyon	0.08 ± 0.05	0.13 ± 0.08	0.07 ± 0.05	0.12 ± 0.08*	0.07 ± 0.05	0.12 ± 0.07*
Ponderosa	0.13 ± 0.05	0.00 ± 0.00	0.05 ± 0.05†	0.10 ± 0.08	0.08 ± 0.06	0.10 ± 0.07
<b>Needle use (%)</b>						
Juniper	25 ± 40.5	8 ± 22.9*	9 ± 23.5†	9 ± 25.4	17 ± 33.6	9 ± 24.0
Pinyon	6 ± 20.0	0 ± 00.0	14 ± 28.0	4 ± 12.7†	10 ± 24.6	2 ± 9.1*
Ponderosa	3 ± 11.8	0 ± 00.0	8 ± 23.5	1 ± 5.4	5 ± 18.8	<1 ± 3.8*
<b>Twig use (%)</b>						
Juniper	17 ± 34.9	44 ± 41.5**	0 ± 00.0†	18 ± 37.7†	8 ± 25.6	31 ± 41.3***
Pinyon	9 ± 24.7	11 ± 27.7	11 ± 29.5	3 ± 16.2	10 ± 27.1	7 ± 22.9
Ponderosa	12 ± 28.9	<1 ± 1.6*	5 ± 20.9	6 ± 21.2	8 ± 25.1	3 ± 15.2
<b>Small (&lt;5 cm) branch use (%)</b>						
Juniper	1 ± 6.1	3 ± 10.1	2 ± 7.9	10 ± 23.0*	2 ± 7.0	6 ± 18.0
Pinyon	1 ± 2.6	2 ± 9.0	<1 ± 2.1	3 ± 11.0	1 ± 2.3	3 ± 10.0
Ponderosa	2 ± 10.2	3 ± 15.8	3 ± 11.2	5 ± 21.3	3 ± 10.7	4 ± 18.7
<b>Ground use (%)</b>						
Juniper	17 ± 33.8	20 ± 32.7	4 ± 15.8†	22 ± 35.2*	10 ± 26.7	21 ± 33.7*
Pinyon	8 ± 22.5	3 ± 15.8	5 ± 17.1	9 ± 22.9	6 ± 19.8	6 ± 19.8
Ponderosa	0 ± 00.0	0 ± 00.0	3 ± 15.0	0 ± 00.0	1 ± 10.8	0 ± 00.0
<b>Glean (%)</b>						
Juniper	22 ± 37.9	15 ± 34.3	9 ± 19.9†	16 ± 31.2	15 ± 30.5	16 ± 32.5
Pinyon	8 ± 26.7	6 ± 23.3	9 ± 22.9	6 ± 20.4	9 ± 24.6	6 ± 21.7
Ponderosa	5 ± 20.2	3 ± 15.8	5 ± 16.8	3 ± 17.2	5 ± 18.4	3 ± 16.4
Ground	18 ± 34.1	19 ± 32.9	3 ± 13.8†	<1 ± 1.0	10 ± 26.7	9 ± 24.9
<b>Invert glean (%)</b>						
Juniper	3 ± 7.8	0 ± 00.0*	0 ± 00.0†	0 ± 00.0	1 ± 5.6	0 ± 00.0*
Pinyon	1 ± 3.8	0 ± 00.0	2 ± 4.7	2 ± 8.7	1 ± 4.3	1 ± 6.2
Ponderosa	0 ± 00.0	0 ± 00.0	1 ± 3.0	<1 ± 1.2	<1 ± 2.1	<1 ± 0.9
<b>Peck-probe (%)</b>						
Juniper	13 ± 29.5	18 ± 34.8	5 ± 18.5	12 ± 26.5	9 ± 24.8	15 ± 30.9
Pinyon	0 ± 00.0	1 ± 8.2	15 ± 33.1†	3 ± 10.3*	8 ± 24.8	2 ± 9.2
Ponderosa	0 ± 00.0	0 ± 00.0	12 ± 27.1†	3 ± 13.7*	6 ± 20.3	2 ± 9.7
<b>Search (%)</b>						
Juniper	13 ± 30.2	33 ± 41.2*	9 ± 21.0	36 ± 42.4**	11 ± 25.7	34 ± 41.5***
Pinyon	7 ± 22.1	5 ± 17.2	17 ± 33.9	9 ± 22.1	12 ± 29.0	7 ± 19.7
Ponderosa	9 ± 26.0	0 ± 00.0*	11 ± 28.3	10 ± 28.3†	10 ± 27.1	5 ± 20.5