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ASPECTS OF THE BREEDING ECOLOGY OF THE PYGMY NUTHATCH (*SITTA PYGMAEA*) AND THE FORAGING ECOLOGY OF WINTERING MIXED-SPECIES FLOCKS IN WESTERN MONTANA

by

BARRY E. STORER

B.A., UNIVERSITY OF NEW HAMPSHIRE, 1973

Presented in partial fulfillment of the requirements

for the degree of

Master of Arts

University of Montana

1977

Approved by:

Chairman, Board of Examiners

Dean, Graduate School

Date June 13, 1977

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ABSTRACT

Storer, Barry E., M.A., June 1977 Zoology

Aspects of the Breeding Ecology of the Pygmy Nuthatch (Sitta pygmaea) and the Foraging Ecology of Wintering Mixed-species Flocks in Western Montana (114 pp.)

Director: Dr. Philip L. Wright PLW

Helpers at the nest were reported at 22 per cent of 36 Pygmy Nuthatch nests studied in California (Norris, 1958), however few quantitative data were given regarding the significance of these additional birds. One goal of the present study was to document the occurrence of this phenomenon in western Montana and make quantitative comparisons of the breeding ecology of nesting pairs with and without helpers.

Fifty-five birds were banded in February, 1976 on two study areas located near Missoula, Montana. Field work continued through June, 1976. Over 500 hours were spent in the field, with over 200 hours in direct observation of 12 active nest sites. Helpers were observed at two nests, but at only one did the helper persist throughout the breeding period.

The helper, probably a male, participated in excavation of nest cavities, delivery of nest material, feeding of the female during incubation, feeding of nestlings, and removal of fecal sacs. Participation by all three birds was roughly equal, although the helper was less active than the male in feeding the female. The pair with helper did not feed nestlings at a higher rate than pairs without a helper. Territories were mapped for three nest sites; the area for the pair with the helper was intermediate in size. Only two nests fledged successfully, including the one with the helper. The question of if, how, and whom a helper helps is discussed and helpers in the Pygmy Nuthatch are considered in relation to theories of their evolutionary origin.

During January, 1977 data were collected on foraging Pygmy Nuthatches, Black-capped Chickadees (Parus atricapillus), and Mountain Chickadees (P. gambeli) which occurred in flocks of varying composition. Ponderosa pines were divided into six foraging zones and the location of each bird was recorded as it was observed in scans of individual pines. Comparisons were made of the foraging niche when species were together in the same flock or alone. Although niches tended to broaden and become more alike when species foraged together, there were no significant differences between frequency distributions of observations in the six foraging zones, except that Black-capped Chickadees used upper zones more in the presence of Pygmy Nuthatches. The same comparisons were made when species were alone or together in the same tree, with the same results. Temperature had no effect on foraging zones, or on flock size.

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ACKNOWLEDGEMENTS

I wish to thank Dr. Philip Wright, my thesis advisor, for advice and encouragement throughout the study, and for first suggesting the Pygmy Nuthatch as a tractable species with potentially interesting biology. Dr. Andrew Sheldon and Dr. Arnold Bolle served on my thesis committee and were also helpful. The Zoology Department, University of Montana supported me with a teaching assistantship and provided a travel allowance.

Dr. Leroy Anderson and family kindly permitted me to band birds at their home, provided convenient access to one of my study areas, and showed more than casual interest in my activities.

Fellow graduate students also deserve appreciative note, with special thanks to Patricia Dolan for her encouragement during the study, helpful comments on the manuscript, and assistance with the figures. Also, the collective inhabitants of, and 707 Dickinson itself, provided a unique and much appreciated environment in which I could recharge my occasionally flagging spirits.

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CHAPTER I

INTRODUCTION

The Pygmy Nuthatch (Sitta pygmaea) is a sedentary, permanent resident of western Montana which is also widely distributed throughout the western United States in appropriate pine habitat. It is very similar in appearance, ecology, and behavior to the Brown-headed Nuthatch (Sitta pusilla) of the southeastern United States.

The only significant account of the breeding biology of the Pygmy Nuthatch has been given by Norris (1958), working in coastal Marin County, California, as part of a broad biosystematic and life history comparison of the Pygmy Nuthatch and the Brown-headed Nuthatch. Other, primarily anecdotal, accounts of the breeding habits are scattered throughout the literature of the past 80 years (Gignoux, 1924; Bleitz, 1951; Knorr, 1957; and others).

Two interesting aspects of Pygmy Nuthatch biology emerge from those accounts: (1) the Pygmy Nuthatch, unlike other nuthatches, occurs in small, highly gregarious flocks during the non-breeding season; (2) Norris reported that 22 per cent of 36 nest sites studied were attended by a third bird in addition to the two parents. This bird, a male, assisted in excavation of nest cavities and care and feeding of the young, but was probably not mated to the female. An additional bird also occurred at some nests of the Brown-headed Nuthatch.

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So-called "helpers at the nest" have been reported in over 130 species worldwide (Skutch, 1961). Most of these reports, however, record only single, atypical instances which probably occur in many species from time to time. Fry (1972) believed that the phenomenon may be of regular occurrence in perhaps 50 species, out of an estimated worldwide total of over 8,000. In North America, helpers have been well documented for only a few species in addition to the two nuthatches. These include the Florida Scrub Jay (though not the western subspecies) (Woolfenden, 1975), Mexican Jay (Brown, 1971, 1972), Pinyon Jay (Balda and Bateman, 1971), and Red-cockaded Woodpecker (Ligon, 1970). Brackbill (1971) has reported helpers at a nest of the Tufted Titmouse, but there is no indication of how regularly this occurs, although in another Parid, the Long-tailed Tit, it may be common (Gaston, 1973).

One goal of the present study was to give a general description of Pygmy Nuthatch breeding habits in western Montana, with particular emphasis on the documentation of the occurrence of helpers at the nest. Fry (1972) believed that helpers should not be expected at high latitudes, because high mortality caused by the severe winters would place a premium on the ability of a species to achieve a high reproduction rate, leaving no non-breeders to act as helpers. Although he seems to have erroneously generalized the Marin County area to the "hot southern parts of North America," western Montana should nevertheless represent a more severe climatic regime.

More importantly (assuming helpers occurred), I hoped to obtain comparative quantitative data sufficient to enable an assessment of the significance of helpers in the breeding ecology of individual nesting pairs.

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In a rather unrelated matter, I hoped to augment breeding data with information on the foraging ecology of the mixed-species flocks which occur in this area during the winter months. The Pygmy Nuthatch is an important component of these flocks, along with the Black-capped Chickadee (Parus atricapillus) and Mountain Chickadee (P. gambeli). Other flock members include the Red-breasted Nuthatch (Sitta canadensis), White-breasted Nuthatch (S. carolinensis), Downy Woodpecker (Picoides pubescens), Hairy Woodpecker (P. villosus), Brown Creeper (Certhia familiaris), and Golden-crowned Kinglet (Regulus satrapa).

Many ideas have been advanced in recent years concerning the advantages of flocking in birds, most authors believing that flocking must lower the risk of predation to, or increase the foraging efficiency of, participating birds (Moynihan, 1962; Morse, 1970; Cody, 1971; Murton, 1972; Lazarus, 1972; Krebs, 1973). Several theories dealing with the possibility of increased foraging efficiency have also dealt with the particular advantages which might be associated with foraging in mixed-species flocks.

Moynihan (1962) proposed that mixed-species flocks would reduce intraspecific competition by reducing the number of individuals of each species which would be necessary to achieve optimum flock size, whatever that might be and for whatever reason. A study by Morse (1970) indicated that some species might become more specialized in the presence of ecologically similar species. He theorized that with increased niche separation, each species would exploit its particular niche more extensively, resulting in an increase in the overall efficiency of exploitation of the food resource. Krebs (1973), on the other hand, working experimentally

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with Black-capped Chickadees and Cestnut-backed Chickadees (Parus rufescens), found that the two species diversified their foraging patterns when feeding together and lessened niche differences. He thus felt that the advantage of mixed-species flocks would occur in the ability of a number of not-too-different species to scan the overall food resource, and, through social learning, gain knowledge of the best foraging areas. This theory, besides the existence of experimental evidence for it, is also more appealing than Morse's in terms of individual selection.

With the knowledge both that chickadees and nuthatches occur in this area in both single- and mixed-species flocks, and that their foraging niches are reasonably similar (Bock, 1969), it was my intention to address the latter two hypotheses by looking for broadening or narrowing of the foraging niche when species foraged in each other's presence.

Although foraging niche segregation can occur along many different dimensions (spatial, temporal, food type), MacArthur and MacArthur (1961) argue that the spatial one is the most efficient for separating foraging birds. Temporal separation for birds foraging in the same flock would be nonexistent. Use of different food types, not themselves spatially separated, would require that each species forage over the entire spatial dimension; clearly more inefficient, for a generalist, than concentration of effort in one location. Fortunately, the most likely dimension to look at is also the easiest one to look at.

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CHAPTER II

METHODS

Field work began in early January of 1976, when I began investigating potential study sites, and continued until the end of June, after all young had fledged. During this time 110 trips were made to the study areas, with time in the field totaling 511 hours.

Description of the Study Areas

Both study sites were located along the southwestern edge of the Missoula valley (Fig. 1), adjacent to and including the lowermost elevations of a complex of ridges and low mountains, known as Blue Mountain, which reaches a maximum elevation of 1,970 meters.

One study site, located within the USFS Blue Mountain Recreation Area and henceforth referred to as the Blue Mountain study site, comprises open grassland of gentle relief, with patches of coniferous growth. This growth occurs fairly densely within the confines of several small, shallow ravines which drain the area; otherwise it is scattered and open. The upper edge of the study area terminates in more extensive coniferous growth which covers most of the mountainous area beyond. Elevation ranges from about 970 meters, 0.6 km from the Bitterroot River, to about 1,070 meters. Total area is about 200 hectares.

The other site was 1.5 km to the south of the Blue Mountain site. Access was from the property of Dr. Leroy Anderson, and henceforth this

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Figure 1: Location of the two study areas.

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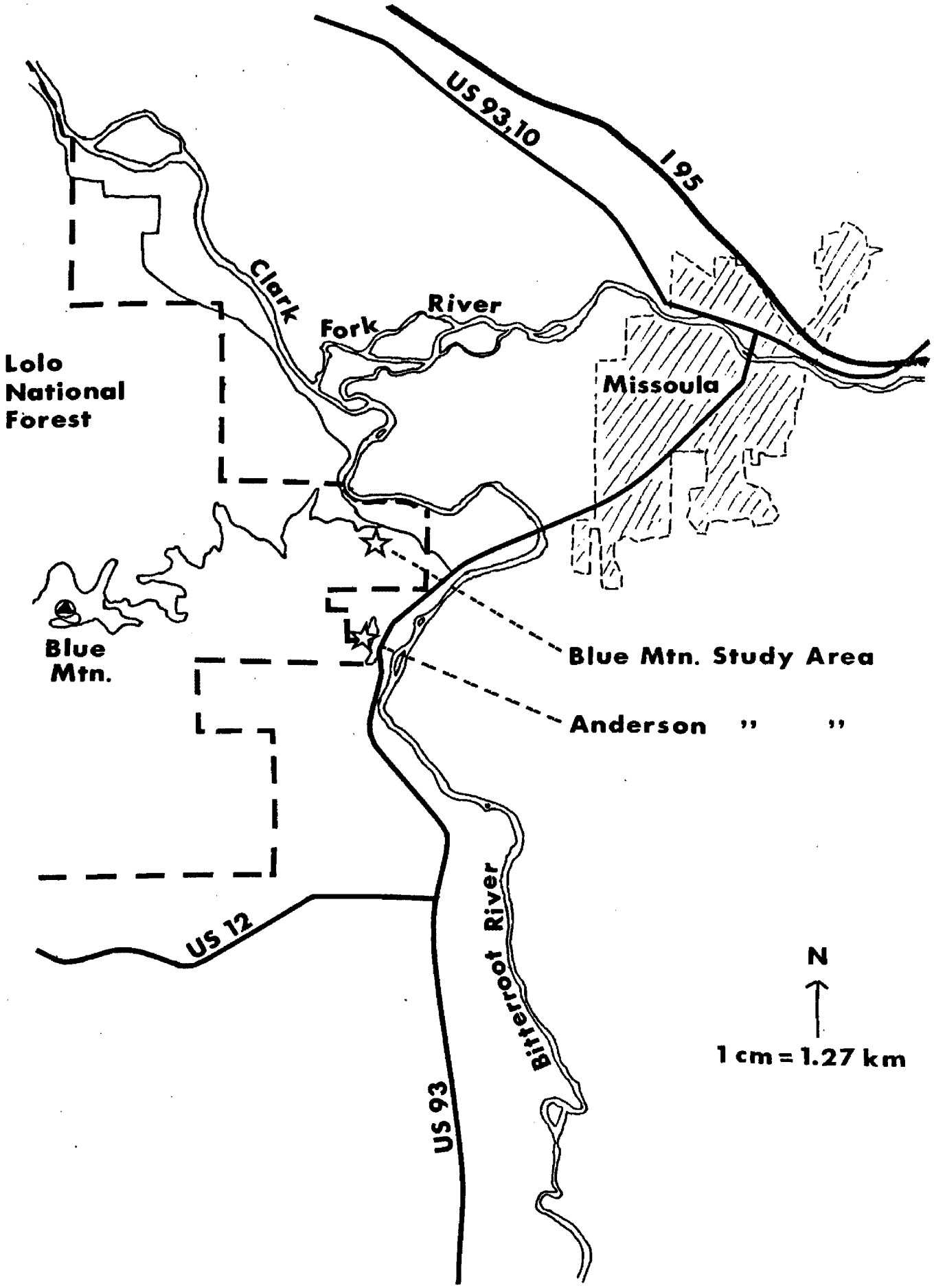

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site will be referred to as the Anderson study site. The character of this site is quite different from that of the Blue Mountain site: slope is about 40 per cent, the ground is strewn with overgrown talus, and trees are more uniformly distributed over the area. The study site faces to the southeast along the side of a ridge, ranging in elevation from 1,000 meters to 1,130 meters. Total area is about 50 hectares.

The predominant tree species on both sites is ponderosa pine (Pinus ponderosa), with a very occasional Douglas fir (Pseudotsuga menziesii). Small stand of quaking aspen (Populus tremuloides) occur on both sites. Both sites are generally devoid of deciduous undergrowth, except in the moister ravines of the Blue Mountain site.

The Anderson site was burned over several years ago, resulting in an abundance of snags and stubs in various stages of decay, as well as numerous fallen logs.

Trapping and Banding

In early February of 1976, feeding-trapping stations were established at two locations on the Blue Mountain study area. These consisted of simple hardward cloth enclosures, with funnel-shaped entrances at top and bottom and a door on the front, which were strapped to a tree with elastic cord. Suet was placed inside the enclosure and the door was left open for several days, during which time birds became accustomed to feeding at one of the locations.

A single trap was placed outside the Anderson's house. Birds quickly accepted this device, as there were other feeders present and they were accustomed to using them.

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From 13 February to 12 March, 55 birds were trapped and banded, 35 at the Anderson site and 20 at the Blue Mountain site. At times this was very easy to do, owing to the highly gregarious nature of the feeding flocks. As many as five birds were trapped at once at Anderson's, and it was the rule, rather than the exception, to take two or three at a time. Surprisingly, other species occurring with the Pygmy Nuthatches were trapped only infrequently, even though they fed regularly at the traps when the doors were open.

Birds were individually marked with a combination of from one to three celluloid color bands (red, white, yellow, blue, green, violet, orange, and black) on either leg. Some color combinations were used at both sites, however birds trapped at Blue Mountain were color-banded on the right let and those at Anderson's on the left leg, so that individuals from one site could still be distinguished on the other. An aluminum Fish and Wildlife Service band was placed on the opposite leg. For future studies, no more than two bands should be placed on a leg; three bands caused some birds to move awkwardly.

During the latter part of the banding period and in the weeks following, the study sites were traversed frequently and potential nest sites were located. I had hoped it would be possible at that time to follow the movements of marked birds on the study areas, but the manner and location in which these small birds foraged made this impossible.

Observations of Nesting Activity

During the time of excavation, incubation, and feeding of nestlings several observation periods from 1 to 4 hours long were conducted at active nest sites. All observations were made with a 20X spotting scope

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and a 9 X 36 binocular, at a distance of from 15 to 40 meters from the nest tree. No blind was used.

During these observation periods, note was made of activities such as excavation, bringing of nest material, entrance and exit of birds, feeding of the female, feeding of nestlings, and removal of fecal sacs. General note was made of other activity which occurred, such as interactions of pairs and threesomes with each other and with other species. Birds at the nest sites were usually, though not always, identifiable.

Although nest sites were approached as little as possible, at intervals nests were checked to determine clutch size or the condition of nestlings. Most nests required a stepladder or extension ladder to reach the nest cavity; dental mirror and flashlight were used to view the interior. Some nests were judged inaccessible with reasonable safety or without unreasonable disturbance of the nest site. Subsequent to death or fledging of the nestlings, most accessible nest sites were opened and measurements were taken of interior dimensions.

Territory

Boundaries of three territories were determined while birds were flying to and from the nest while feeding nestlings. Trees visited by foraging birds were marked with thumbtacks. After 16 hours of marking for a given territory, the trees farthest from the nest site were mapped with compass and tape measure.

Winter Flocking

Data on the foraging zones of foraging Pygmy Nuthatches, Black-capped Chichadees and Mountain Chickadees were gathered during 15 trips

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to the Blue Mountain study area made from 7 January to 9 February, 1977.

Ponderosa pines were divided into six foraging zones, as depicted in Figure 2. Zone 1L comprised the major tree branches in the lower half of the tree, zone 2L the secondary branches radiating from zone 1L, and zone 3L the smallest branches, foliage, and cones at the ends of the branches of zone 2L. Zones 1U, 2U, and 3U repeated this hierarchy in the upper half of the tree.

The intention was, once a flock had been encountered, to choose individuals randomly and record the zone in which they were foraging. This concept is easy to express but difficult to realize in the field. Obviously, birds which are not visible cannot be chosen, so it must be assumed that birds which are visible occur in the various zones in the same proportions as all birds. This may be a reasonable assumption for the relatively open growth habit of most ponderosa pines. Although one can select birds haphazardly, one can hardly select them randomly, and the possibility of unconscious observer bias is real. For this reason I chose a technique which, though not perfect, should have removed systematic observer bias. Upon encountering a flock, the method involved choosing a tree which was observed to have any birds at all in it, and then with a binocular systematically scanning the tree from top to bottom and recording the location of each bird the instant when it was first seen. No bird was deliberately observed twice, although this must have occurred on occasion. No tree was scanned more than once unless it was reasonably clear that it was occupied by a new group of birds. For each flock encountered the number of individuals of each species was also recorded.

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Figure 2: The six foraging zones in ponderosa pines.

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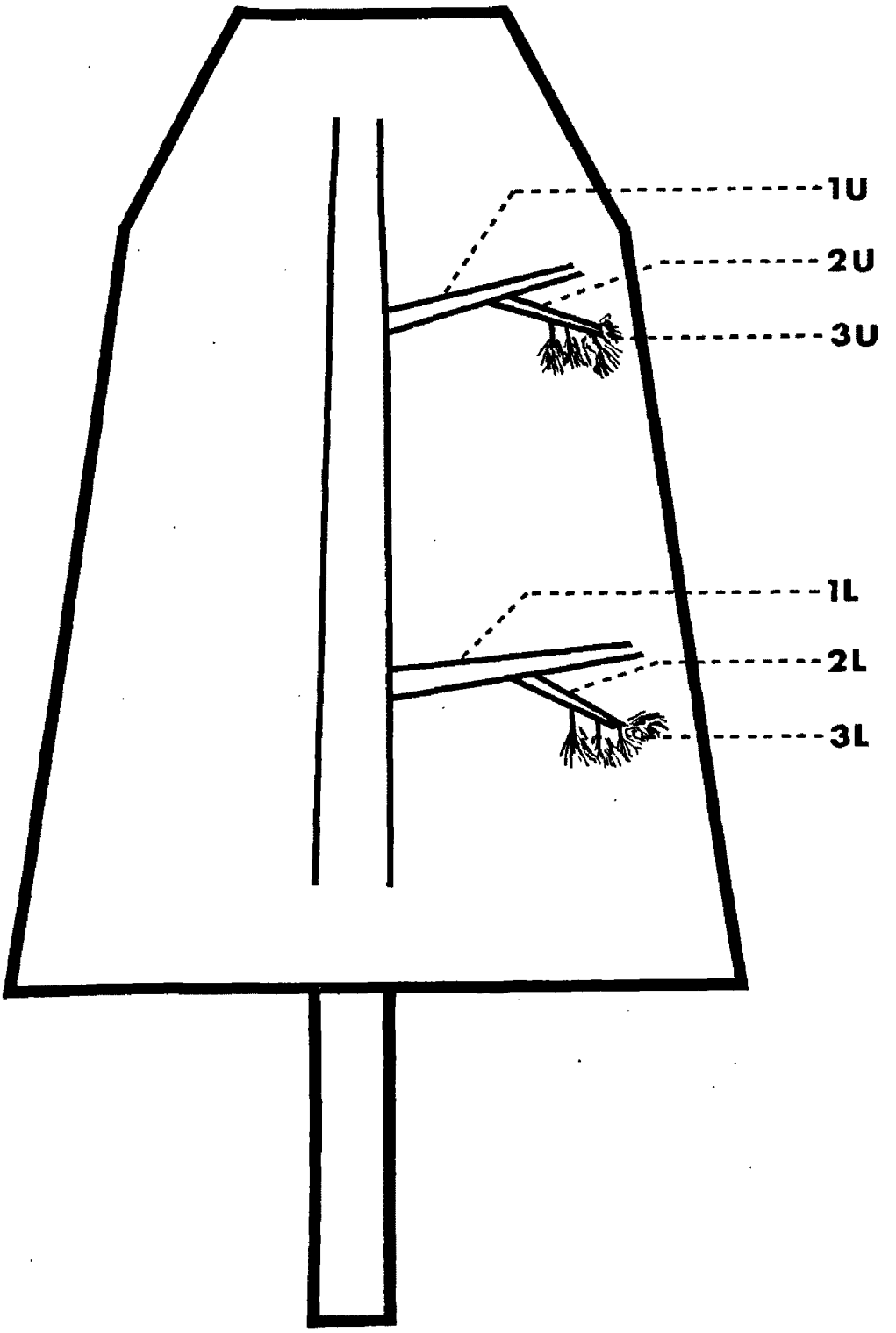

FORAGING ZONES

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These data were collected on and adjacent to the Blue Mountain study area, the area being traversed in a haphazard fashion among locations where flocks could be expected to occur. There was no way of knowing whether some flocks were encountered and observed more than once; undoubtedly they were, however I believe that this theoretical violation of independence of observations should not be of practical importance.

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CHAPTER IIIA

RESULTS: BREEDING

Nineteen sites were discovered on the two study areas which at some time had birds associated with them in a manner which suggested their potential as nest sites, ie., birds either frequenting existing cavities or excavating new ones. Unfortunately, birds persisted throughout the study at only 12 sites.

Early in the year there was a moderate amount of instability in the association of birds and nest sites. Some nest sites were associated with more than one pair of birds, some birds were associated with more than one nest site, and in a couple of instances new mates were acquired.

Birds associated with the 12 active nest sites accounted for only 19 of the 55 birds which had been banded (35%). A few additional banded birds were seen on the study area when nest sites were being investigated, but not during the actual breeding period. Although the other banded birds were undoubtedly present in the vicinity of the study areas, the potential area involved was too large and the available time was too small for a search to be practical. On the Anderson study area, the presence of a plentiful, stable food supply at the banding station (feeders present for several years) would seem to be involved in the low percentage of banded birds on the study area, but there is no indication as to whether birds habitually forage over a wide area or were specifically attracted to that location. It seems unlikely that the feeding

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station which I established at Blue Mountain could have achieved similar status.

Three birds were associated, at one time or another, with 3 of the active nest sites (A1, A5, A6). At A1, the third bird was observed on only one occasion and should hardly be categorized as a helper at the nest. At A5, a third bird participated in excavation over a period of 12 days, and then disappeared. I have no idea whether it left of its own accord, was driven out, or was killed. Only at A6 was a helper present throughout the entire course of breeding activity.

Most of the data taken on breeding activity and presented henceforth were obtained from observations on the threesome at A6 and five of the pairs. The remaining 6 of the 12 active nest sites were of limited use either because the birds were unbanded (B11, B13), the birds did not breed (A1, A5), or the sites were difficult to observe (A2, A4).

For future reference, Table 1 summarizes the active nest sites and associated birds; sexes were inferred from later breeding activity. Table 2 summarizes the physical characteristics of most of the active nest sites, and Figure 3 and 4 locate the sites on the Blue Mountain and Anderson study areas, respectively.

Excavation and Pre-incubation Activity

Excavation. The amount of excavation activity (defined as a bird pecking at or discarding debris from a cavity) occurring at the active nest sites varied greatly. Significant activity, involving excavation of a completely new nest cavity, occurred only at B1, B2, and A5, and possibly at A2. At the other extreme, no activity of any kind was observed at A1 and A6. Occasional activity was observed at A3 and B9.

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Table 1: Birds associated with the active nest sites.

Nest site	Date first discovered	Bird	Sex
A1	16 March	BR	?
		WO	?
		VR	?
A2	7 April	UB	M
		BV	F
A3	23 April	YG	M
		YR	F
A4	11 April	W	?
		VY	?
A5	11 April	RO	M
		KW	F
		BY	H
A6	7 April	BW	M
		UB	F
		WG	H
B1	22 March	Y	M
		WY	F
B2	5 April	RV	M
		UB	F
B9	24 April	RY	M
		UB	F
B11	7 May	UB	?
		UB	?
B12	8 May	YW	M
		YWR	F
B13	13 May	UB	?
		UB	?

M=male, F=female, H=helper, UB=unbanded bird

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Table 2: Characteristics of some of the active nest sites. All except B11 are *Pinus ponderosa*. B11 is *Populus tremuloides*.

Nest site	DBH (cm.)	Height (meters)	Cavity height (meters)	Condition of tree	General location
A2	21	2.9	1.8	Stub w/ bark intact, stubs of branches, extensive decay.	Among scattered pines on slope.
A3	28	6.5	5.0	Densely branched snag, no bark, some decay.	Within locally dense growth of smaller pines.
A6	39	6.7	6.5	Living pine w/ broken top, local decay on side where nest located.	Single tree in opening among scattered pines on slope.
B1	34	6.4	4.4	Densely branched snag, no bark, some decay.	At edge of fairly dense pine growth.
B2	32	1.7	1.3	Stub w/ bark intact, extensive decay.	Within pine growth of small ravine.
B9				Living pine w/ broken top, local decay where nest located.	Single tree in forest opening (road and parking lot).
B11	14	6.2	5.5	Mostly dead snag, some branches, bark intact.	In aspen thicket adjacent to growth of pines.
B12	59	25	1.1	Living pine with area of decay at nest.	Open grassland, other scattered pines nearby.
B13	63	20	0.9	Living pine with area of decay at nest.	Open grassland, other scattered pines nearby.

Figure 3: Blue Mountain study area and active nest sites.

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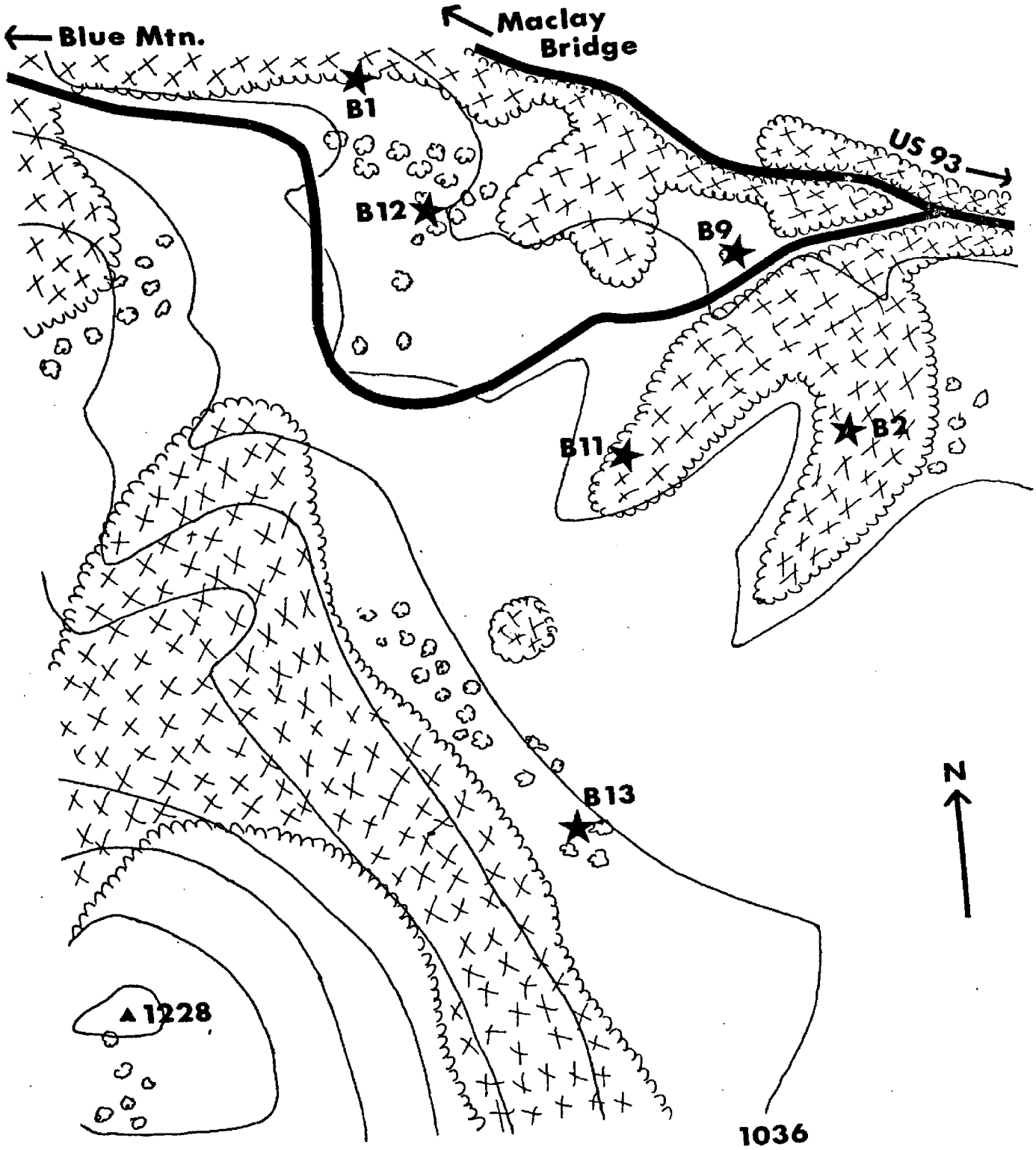

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Figure 4: Anderson study area and active nest sites.

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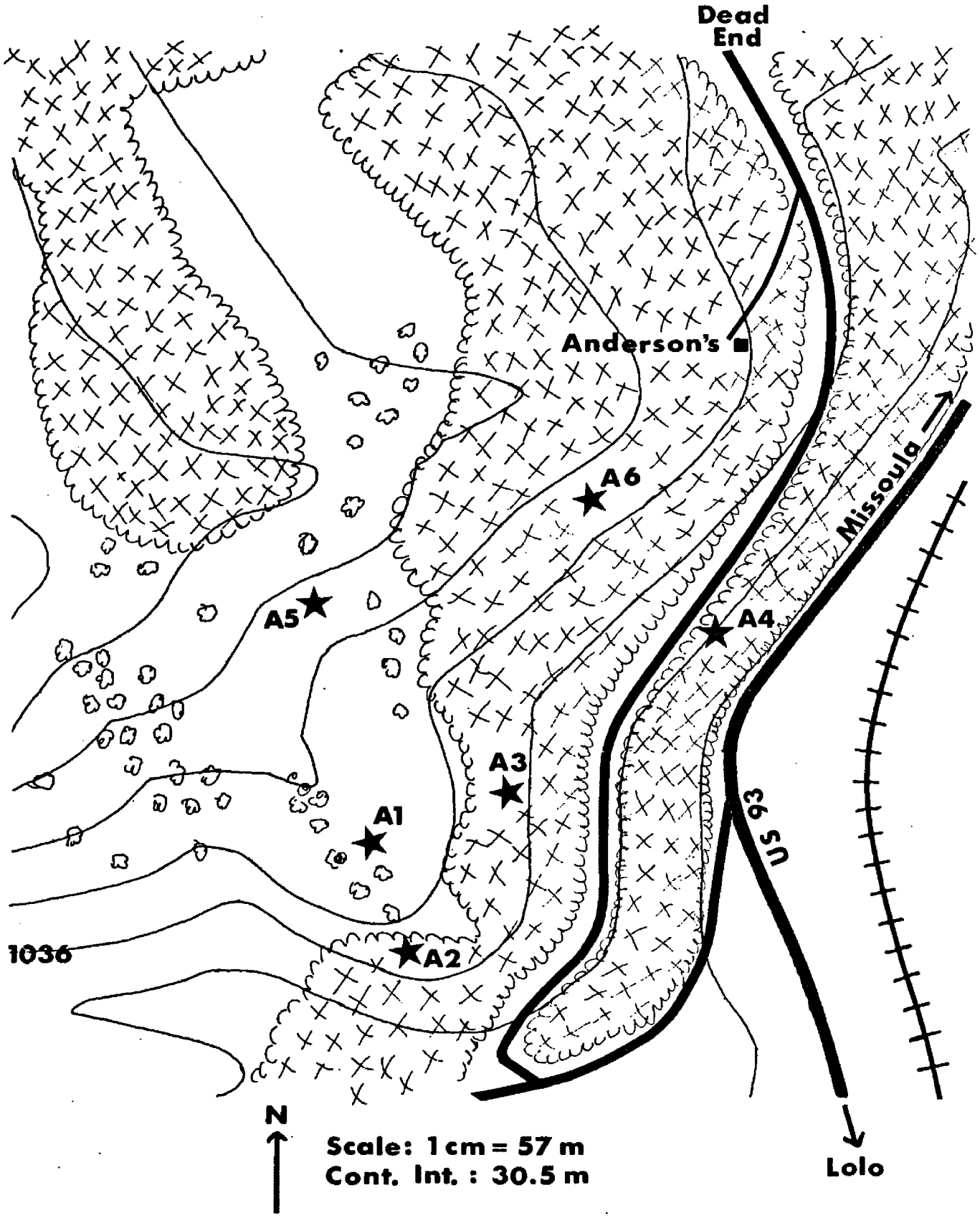

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The remaining sites, B11, B12, and B13, were not discovered until excavation activity at other sites had largely ceased, and no significant activity was observed there, although the pair at B12 did excavate at other locations.

Examination of completed nest cavities whose histories were unknown usually yielded an ambiguous indication as to whether they had been previously excavated by nuthatches or resulted from natural decay of the stub or snag.

The cavities at B12 and B13, both located at low elevation in a living pine, appeared naturally formed. Their peculiar location apparently can result from the tree being superficially damaged at an earlier time, the bark and outer cambium growing up around the wound, leaving a slit-like depression within which decay of the damaged area can occur.

The cavity at B11, cut open later in the year, appeared to have been almost entirely excavated. The sides of the cavity showed the same texture as other cavities known to have been excavated. All the other cavities of unknown origin appeared modifications to a greater or lesser extent of cavities caused by natural decay. Indeed, this is probably true of nearly all Pygmy Nuthatch cavities, as these birds are surely not capable of brute-force excavation of anything but reasonably well-decayed material. In particular, A3 showed irregularity where a branch passed outward through the cavity space. The birds had been unable to remove the heartwood of the branch, leaving it suspended in mid-air along one side of the cavity.

It appears that the Pygmy Nuthatch should thus be characterized as a primary nester (excavates its own cavity), though an opportunistic one.

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It gave no indication of being a secondary nester in the sense of using cavities excavated by other species; one reason undoubtedly being that the only primary nester that excavated on the study areas, the Common Flicker (Colaptes auratus), left cavities clearly too large to be suitable for a Pygmy Nuthatch.

Table 3 summarizes the total excavation activity at active nest sites observed during the period 8 April to 15 May. Except for B12, the birds which spent the most time excavating were those at B1 and B2, which excavated complete cavities. Data for B12 refer to excavation by the birds that nested at B12, not the site itself. This pair was encountered on three separate occasions excavating several hundred meters from B12, at sites B5 and B6. Thus the data should not be compared to that from other sites, and the percentage of time in excavation is very high because observation periods were conducted only when, by chance, the birds were encountered engaged in this unusual activity.

Activity by each sex in pairs is summarized in Table 4. The mean length of excavation bouts by males ($\bar{x}$ = 9.2 min.) is very close to that by females ($\bar{x}$ = 9.9 min.). The overall ratio of excavation bouts by males and females does not significantly differ from 1:1 (X^2 = .62, .99>p>.75).

Activity by the threesome at A6 is summarized in Table 5. It should be noted that these birds were subject to continual harassment by other species: first by a pair of Mountain Bluebirds (Sialia currucoides) that was nesting only 0.5 m. away in the same dead tree, and later by Lewis' Woodpeckers (Melanerpes lewis) that were nesting in an adjacent dead tree 25 m. away. This harassment may well account for the fact that the

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Table 3: Total excavation activity at active nest sites.

Nest site	Total observation time (min.)	Excavation activity bouts	Excavation activity minutes	Per cent time in excavation
A1	240	1	0.5	0.2
A2	100	4	32.0	32.0
A3	155	7	33.0	21.3
A5	490	23	183.0	37.4
A6	265	0	0.0	0.0
B1	350	14	183.0	52.3
B2	400	22	240.0	60.0
B9	40	1	10.0	25.0
B12**	65	10	58.0	89.3
	2105	82	739.5	35.1

Average bout length: 9.0 minutes

** see text

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Table 4: Excavation by males and females in pairs.

Nest site	Excavation by males			Excavation by females		
	bouts	minutes	per cent	bouts	minutes	per cent
A2	2	17.0	53.2	2	15.0	46.8
A3	3	13.0	39.4	4	20.0	60.6
B1	8	88.5	48.4	6	94.5	51.6
B2	8	97.5	40.6	14	142.5	59.4
B9	0	0.0	0.0	1	10.0	100.0
B12**	5	24.0	41.4	5	34.0	58.6
	26	240.0	43.2	32	316.0	56.8

** see text

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Table 5: Excavation by the birds at A5.

Birds present	Excavation by male			Excavation by female			Excavation by helper		
	bouts	minutes	per cent	bouts	minutes	per cent	bouts	minutes	per cent
3 (RO,KW,BY)	3	28.5	27.1	4	13.5	12.9	3	63.0	60.0
2 (RO,KW)	9	52.5	67.3	4	25.5	32.7			
	12	81.0		8	39.0		3	63.0	

percentage of time during which one of the threesome was excavating was lower than that for the pairs at B1 and B2, even though all were excavating complete cavities.

The sexes of the birds at A5 can be known fairly certainly even though they were not successful in breeding. On one occasion, RO was observed to feed KW, indicating that RO was a male and KW a female (see section under incubation). The third bird, BY, actually was associated with the site only a short length of time. He was first seen on 11 April, excavated on three separate occasions (though once on the wrong hole!), and was not seen after 23 April.

With three birds present it appears that the helper may have been doing the lion's share of the work, however his total includes on extraordinarily long bout of 42.5 minutes. In fact, there is no statistically significant difference in the bout lengths ($F = 2.48$, $p>.05$) or in the number of bouts by each bird ($X^2 = .20$, $.95>p>.75$). With only two birds excavating the differences are again not significant (number of bouts, $X^2 = 1.92$, $.25>p>.10$; bout length, $t = 2.14$, $.10>p>.05$).

Cavity dimensions. Several nests were opened at the end of the breeding season and measurements taken. Generally they were gourd-shaped, though with a great deal of irregularity. Figure 5 sketches the prototypical Pygmy Nuthatch cavity which might result from birds excavating in a perfectly homogeneous and workable medium.

Nest material. During the last few days of excavation, birds began to bring occasional bits of nest material into the nest cavities, at times while their mates were actively excavating. This activity was observed irregularly over the next few weeks, into the time when incubation

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Figure 5: "Composite" Pygmy Nuthatch nest cavity which might result if birds excavated in a perfectly homogeneous and workable medium.

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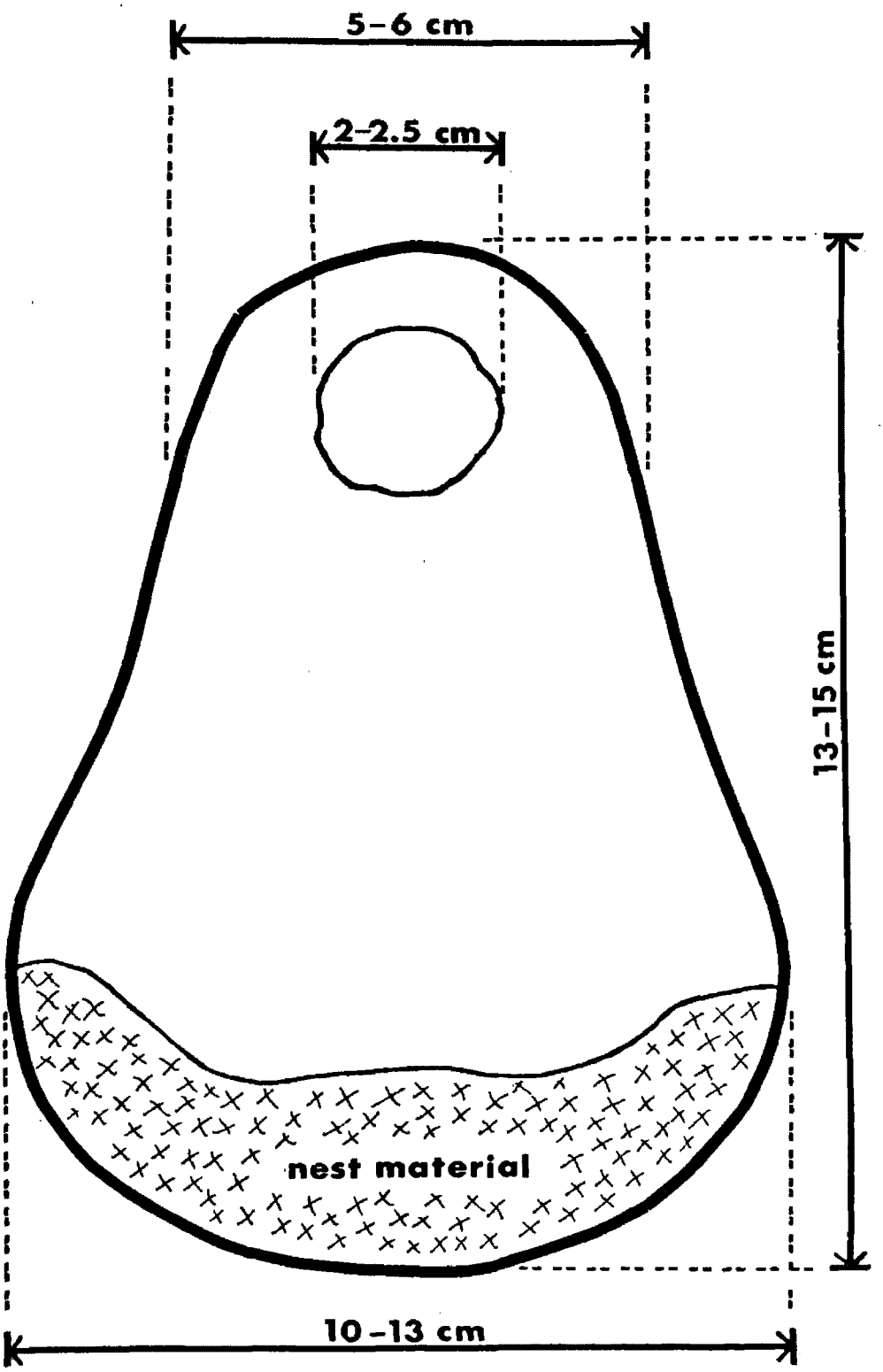

PROTOTYPICAL NEST CAVITY

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was underway. Deliveries of nest material were usually made at a rather low rate, only 2 or 3 bits per hour, although at B2 and especially A6, deliveries were sometimes made at a rate of 10 or 12 per hour.

Table 6 summarizes the bits of nest material brought at sites where this was observed. In pairs, there was no significant difference in the total number of deliveries made by males and females, either before the start of incubation (X^2 = .11, .75>p>.50), or once incubation was underway (X^2 = .62, .50>p>.25). For the threesome at A6, there was a significant difference in the deliveries made by each bird before incubation (X^2 = .6.2, .05>p>.025), with the helper delivering the least. After the start of incubation, the difference was also significant (X^2 = 15.67, .001>p), this time the female delivering the least.

No attempt was made to quantify the amount and type of nest material in the cavities, but it consisted mostly of feathers, pieces of moss, and other bits of vegetation, covering the bottom of the nest cavity to a depth of from 2 to 4 cm. Bits of similar material were stuffed into crevices in other parts of the cavity, and occasionally outside the cavity.

Incubation

Laying of eggs. Eggs were not observed in any nest until complete clutches had been laid, due to the fact that the eggs were kept covered with nest material until incubation began. Norris notes this phenomenon, but I was unaware of it at the time. The size of the nest entrance and the depth of the cavity make it difficult to view the contents, and manipulation of nest material and/or eggs would have been nearly impossible in any event. Although at two nests an additional egg was counted on the

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Table 6: Bits of nest material delivered by males, females, and helper.

Nest site	Before incubation			During incubation		
	males	females	helper	males	females	helper
B1	0	1		1	0	
B2	9	6		14	8	
B9	0	1		0	1	
B12	10	9		0	1	
A3	0	0		0	1	
	19	17		15	11	
A6	18	16	6	24	3	16

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day after the day on which eggs were first discovered, it is entirely possible that this was a result of miscounting, and not an indication that the eggs had been uncovered and incubation begun before the clutch was complete. At all other nests the number of eggs counted did not change.

During the time when eggs had been laid but were still covered, birds were generally not seen about the nest site. Frequently, however, the female was discovered on the nest early in the morning, presumably not long after that day's egg had been laid. At B12, YWR would persist on the nest even with the dental mirror stuck into the nest entrance. Re-examination of the nest later in the day with the female gone, however, would reveal no sign of eggs.

Dates of laying and clutch sized are listed in Table 7. For A3 the dates are inferred on the basis of the behavior of the birds about the nest, since the nest was inaccessible. B11 was not examined during this period.

Length of incubation period. Despite uncertainty at some nests as to the first day on which the eggs were uncovered, the length of the incubation period can be fairly well established as somewhat more than 14 days. This assumes that eggs were laid during the early morning hours and that the incubation period is considered as extending from the time at which the last egg of a clutch is laid until the time at which the last egg hatches.

On the late afternoon or early evening of day 15 of incubation, clutches at B1, B12, and A2 had nearly completed hatching, with perhaps two or three eggs unhatched. Again, the precise contents of the nests

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Table 7: Dates of egg laying and incubation; clutch sizes.

Nest site	Start of incubation	Clutch size	Probable date of first egg
A2	18 May	7	12 May
A3	16 May	?	?
A6	23 May	6	18 May
B1	21 May	8	14 May
B2	17 May	7	11 May
B9	16 May	9	8 May
B12	30 May	7	24 May
B13	20 May	7	14 May
	median: 19 May	mean: 7.3	median: 14 May

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were difficult to ascertain. An incubation period of between 14.5 and 15 days appears reasonable for those nests. At B13, five of seven eggs had hatched by the evening of day 16. At B2, only one egg remained unhatched at 1100 hours on what was either day 15 or day 16. At B9 and A6, hatchlings were discovered during what was probably day 15, but could possibly have been only day 14.

All possible lengths of incubation periods, therefore, could be included in a range from 13.5 to 16 days, with the most typical length very probably lying between 14.5 and 15 days.

Attentive periods and time on the nest. Only one bird of a pair or threesome was observed to incubate, and on the basis of Norris' collected birds and the few instances of copulation which I observed, there can be no reasonable doubt that this bird was and is always a female.

Attentive and inattentive periods for each nest are summarized in Table 8. Only complete periods are included in these data, for which both the entrance of the female at the start of the period and her exit at the end of the period were observed. Occasionally entrances or exits were missed, thus a summation of lengths of attentive and inattentive periods would be less than total minutes of observation. The per cent time on the nest includes all complete attentive periods, as well as other times during which the presence or absence of the female was known.

Lengths of attentive periods covered a very wide range. Average lengths of attentive periods also varied considerably from nest to nest, but the overall time on the nest showed much less variation.

Figure 6 plots the mean length of attentive periods for all nests combined versus the day of incubation, with no apparent trend. A plot

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Table 8: Attentive and inattentive periods of females during incubation.

Nest site	Total minutes of observation	Attentive periods			Inattentive periods			Per cent time on nest
		No.	Length (minutes) Range	Length (minutes) Mean	No.	Length (minutes) Range	Length (minutes) Mean	
B1	476	7	13-59	38.6	8	3-44	10.3	79.2
B2	1290	22	13-70	31.7	23	2-37	10.7	72.8
B9	379	7	6-33	18.6	7	2-8	4.7	89.7
B12	505	4	18-73	39.0	6	5-10	6.8	88.6
A3	505	11	14-42	24.6	10	3-15	8.3	81.8
A6	879	16	6-54	31.1	17	2-11	6.8	84.6
	4034	67	6-73	30.2	71	2-44	8.5	80.7

Figure 6: Mean length of female attentive periods vs. day of incubation. Data for all nests are combined (A3, A6, B1, B2, B9, B12).

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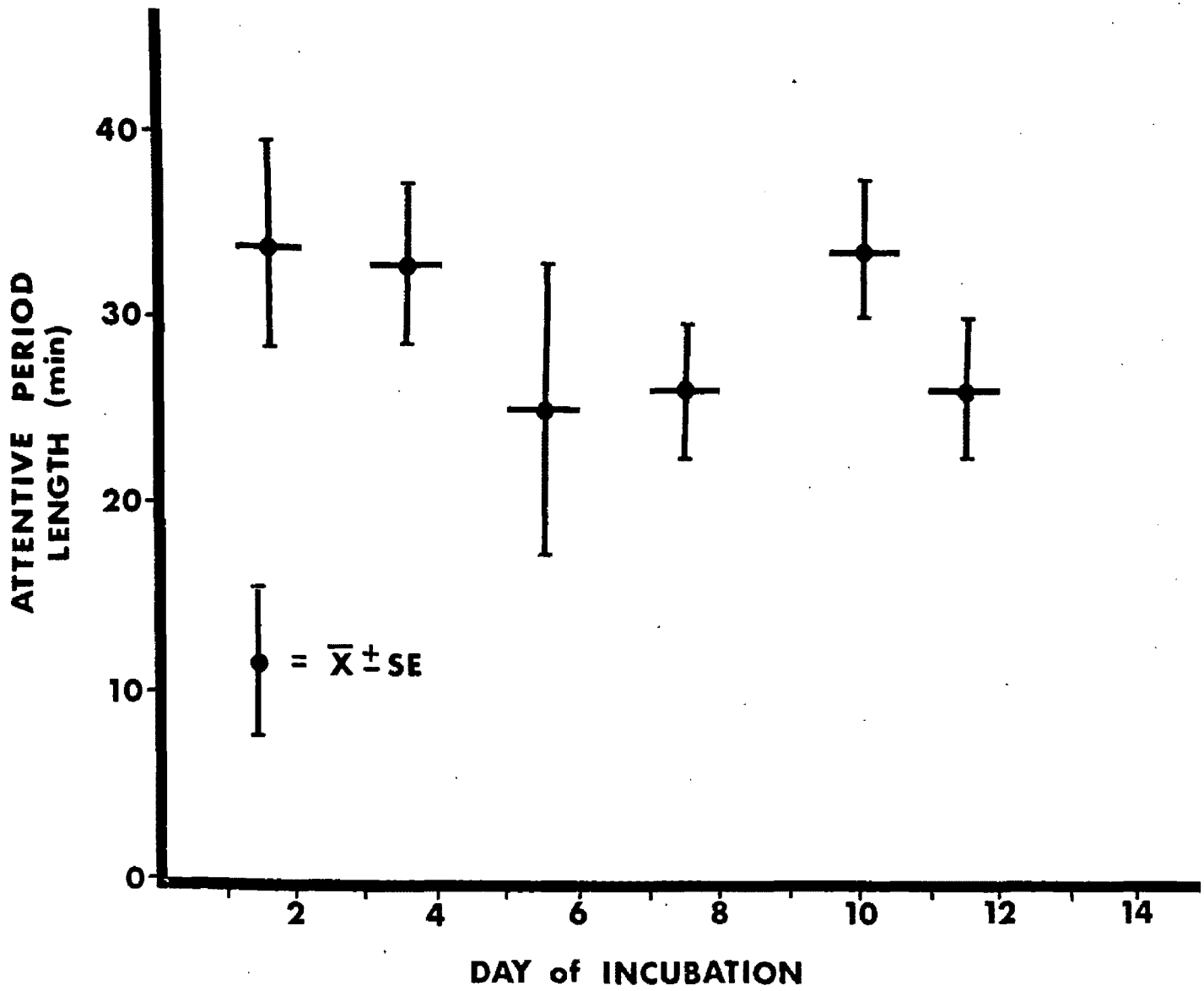

of per cent time on the nest versus day of incubation (Fig. 7), however, reveals a significant tendency for birds to spend a greater amount of time on the nest as the incubation period progresses ($t = 3.57$, $.005>p$), although only a moderate amount of the variability among all observation periods can be explained on this basis ($r^2 = .41$).

Feeding of the female. Feeding of the female by the male or helper occurred during all stages of incubation and was accompanied by a stereotyped display and vocalization by the female. Although usually the female was fed from the nest entrance, and only her head was visible, she was occasionally fed while perched on a branch just outside the nest entrance, at which time the entire display could be observed.

As the male approached the female, she faced him with bill open and uttered a drawn-out, high-pitched call. At the same time the wings were held slightly away from the side of the body and shaken. The display would be interrupted by the process of receiving and swallowing the food item, usually resuming for a short time afterwards, after which the female would enter the nest or fly off with the male. The male also occasionally gave the wing-shake display before and/or after feeding the female.

This display involved with feeding was very similar to that given by both birds before the two observed instances of copulation; the latter in general being more exaggerated, the wings held further from the side, more stiffly, and the shaking more vigorous. During the copulation display the tail was also held stiffly erect.

At A6, the female responded with vocalization and display when being fed by both BW and WG. Both of these birds also displayed at times

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Figure 7: Female per cent time on the nest vs. day of incubation. Each point represents one observation period at one nest (A3, A6, B1, B2, B9, B12).

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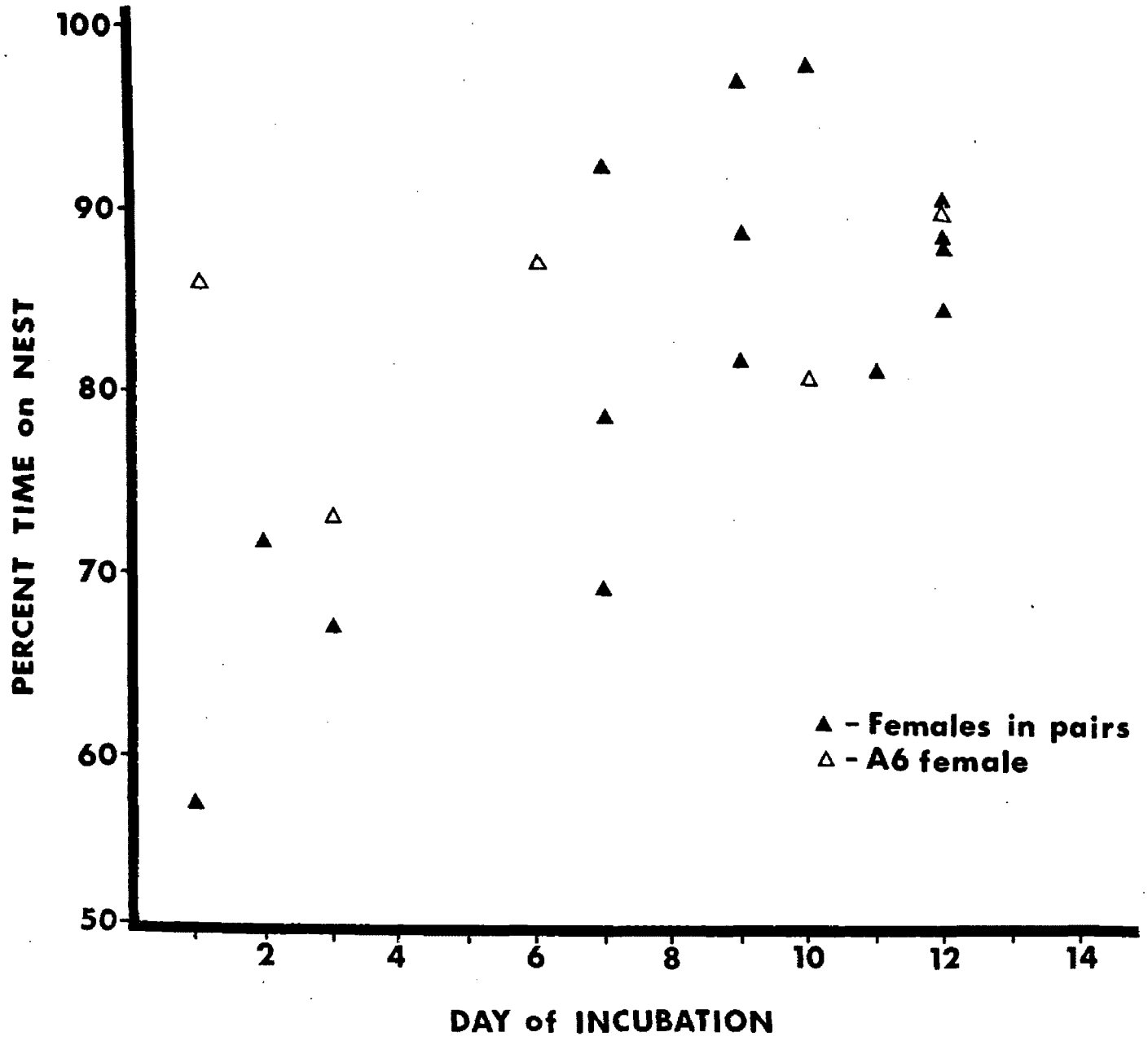

during the feeding process, and on a few occasions, all three birds were present outside the nest entrance and simultaneously engaged in the wing-shake.

At all nests there was considerable variation in the intensity of the feeding display, as characterized by the loudness and length of vocalizations and the duration of the wing-shaking. The vocalization was also heard at times when the birds were away from the nest, although the feeding which was presumably occurring then was never seen. During the early stages of incubation, when the male was still bringing bits of nest material, the female frequently responded to these visits with vocalizations and display, and even grabbed bits of nest material from the male and attempted to eat them.

Figure 8 plots the feeding rate at each observation period as it varied over the course of the incubation period. Both males in pairs and the male at A6 show a significant and similar increase in feeding rate with time (pairs, $t = 3.5$, $.005>p$; A6, $t = 4.92$, $.01>p>.005$). In contrast, the helper at A6 shows no increase in feeding rate with time ($t = .076$, $p>.40$), in addition to feeding at a much lower rate than other males.

Nestling Stages

Brooding. During the first few days after hatching, females remained on the nest nearly as much as during the last days of incubation (Fig. 9). Time on the nest rapidly declined, however, and after day 12 females no longer spent any time on the nest during the day. Per cent time on the nest for the female at A6 falls within the range for females in pairs, except for day 6, when it was higher.

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Figure 8: Feeding rates for males feeding females during incubation. Each point represents one observation period at one nest (A3, A6, B1, B2, B9, B12).

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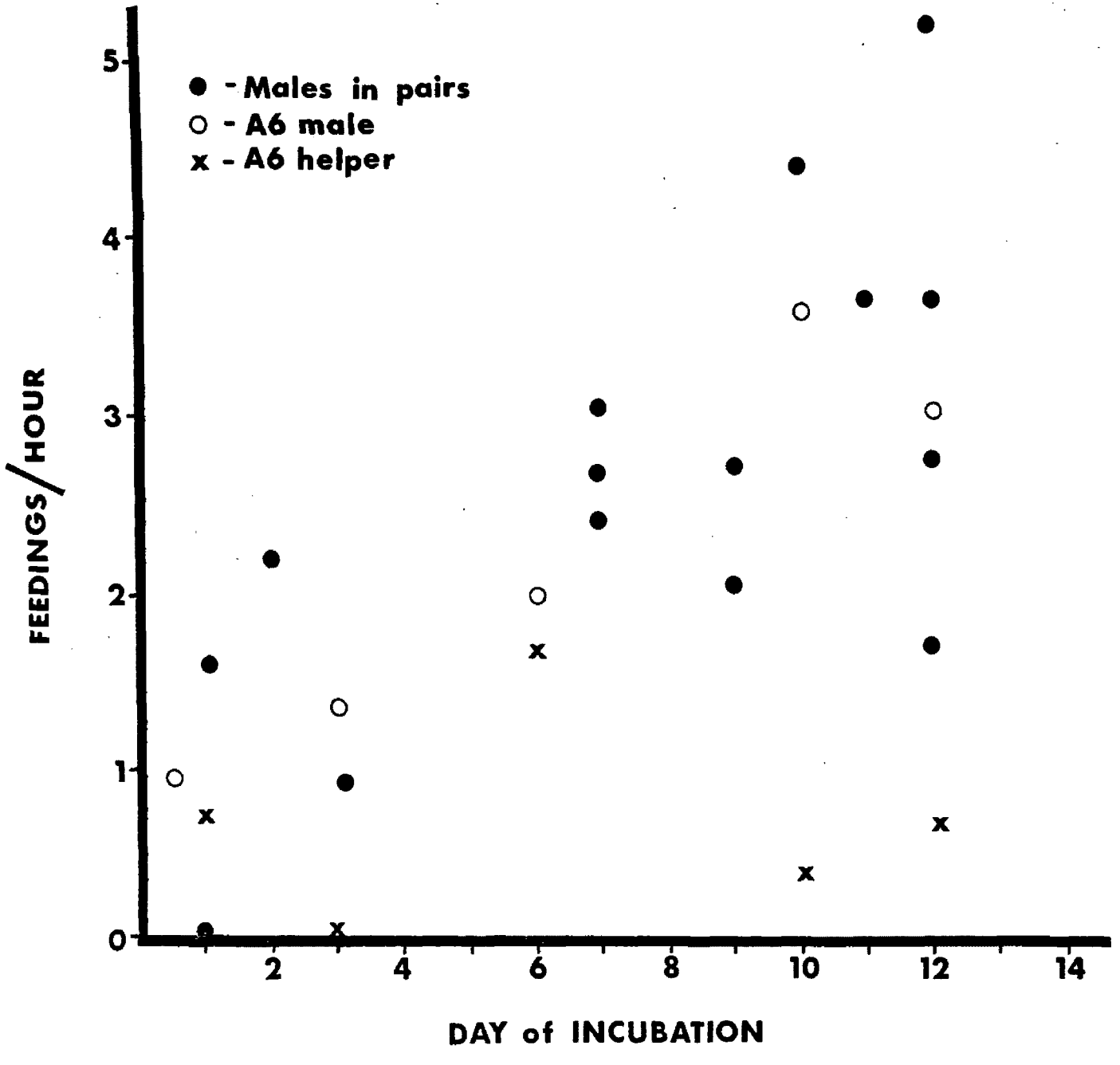

Figure 9: Female per cent time on the nest vs. day from hatching. Each point represents one observation period at one nest (A3, A6, B1, B2, B9, B12).

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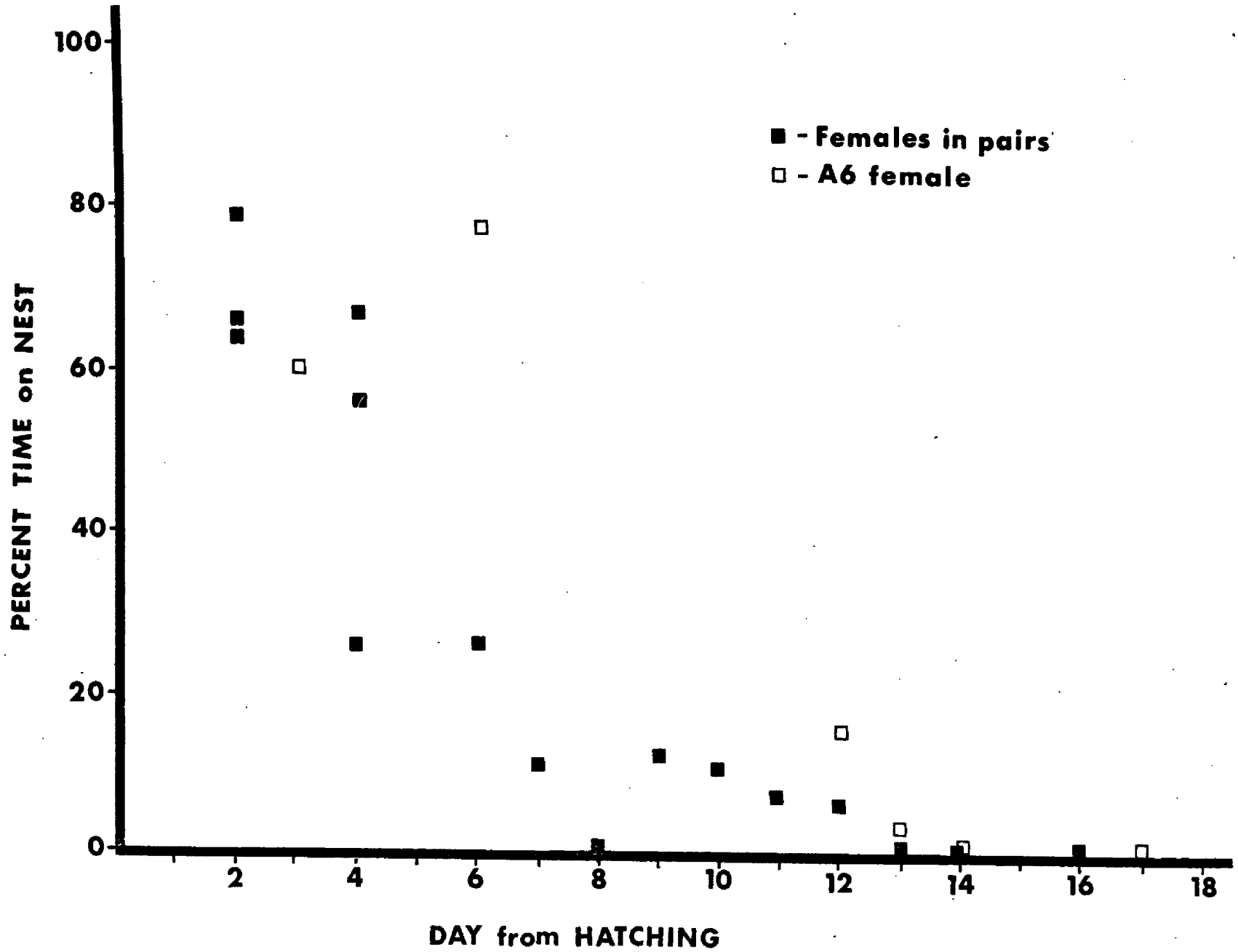

With one exception, none of the males nor the helper at A6 spent any time on the nest during the day. The one exception occurred during a late evening observation period at B9, when RY was on the nest for three separate periods totaling only 5 minutes. Shortly after the last of these, at 2100 hours, he entered the nest and presumably remained there with the female during the night. Observations during the evening hours at other nests would undoubtedly have revealed similar patterns.

The decrease in total time on the nest reflected a similar decrease in the length of brood periods, plotted in Figure 10. Average length of brood periods immediately after hatching was only half of that typical during incubation, declining rapidly to a point where periods on the nest usually did not exceed 5 minutes.

Feeding of nestlings. Males and females and the helper at A6 participated actively in the feeding of nestlings.

During that time when they were brooding, females invariably brought a food item with them when returning to the nest. Also during this period it was common for males to deliver food items to the female when she was on the nest. Very rarely the female appeared to eat these items herself; usually, though, she disappeared with them into the nest, presumably to deliver them to the nestlings. Food calls were occasionally given by the female when accepting deliveries from the male, though these calls were weaker than those given when being fed during incubation. Birds which met while approaching or leaving the nest frequently gave the wing-shake display, including the helper at A6.

No attempt was made to identify the food items being delivered, other than to note that they consisted mostly of small insects, spiders,

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Figure 10: Mean length of female brood periods vs. day from hatching. Data for all nests are combined (A3, A6, B1, B2, B9).

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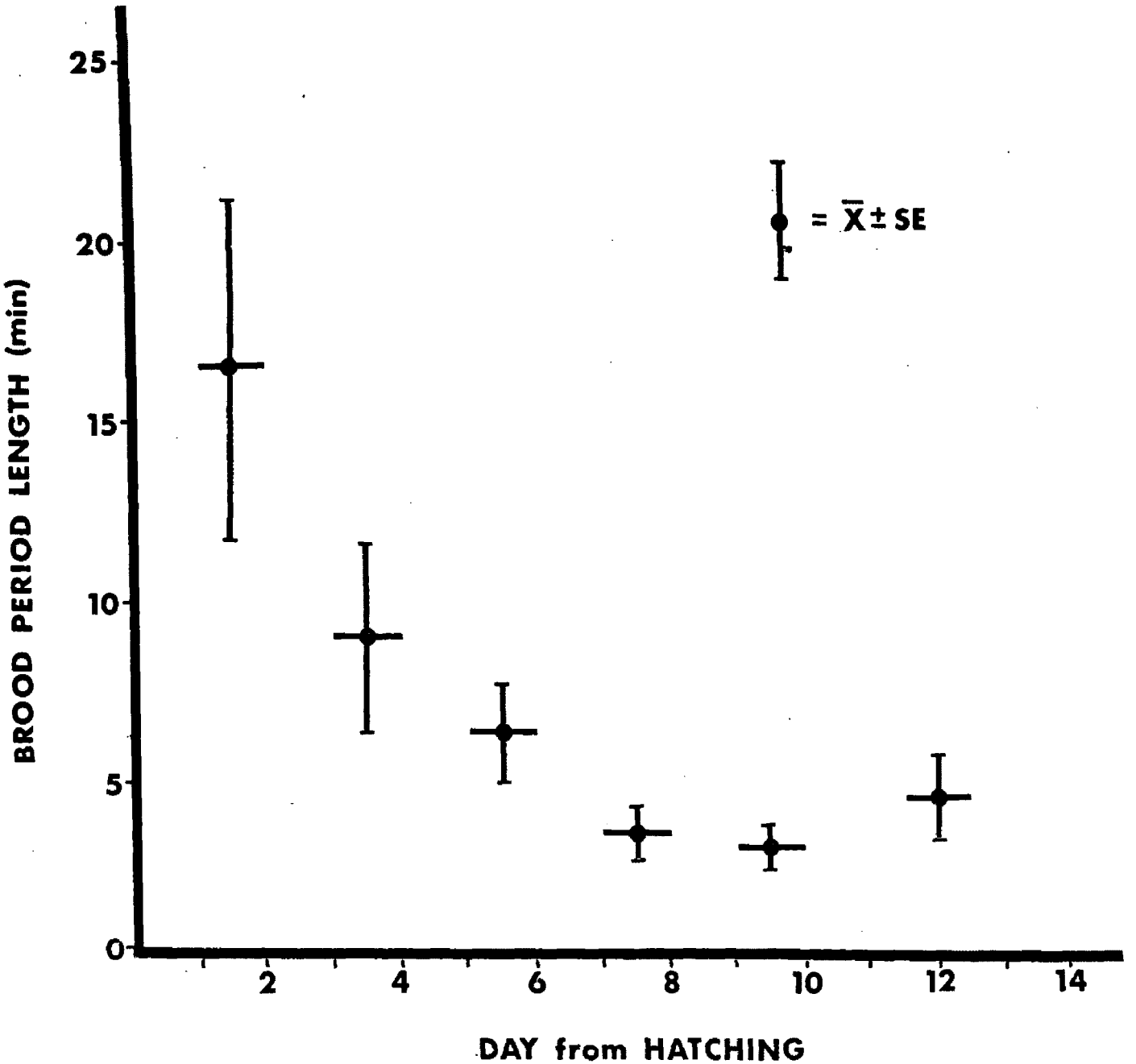

larvae, pupae, and the like. These was an obvious increase in the size of food items as the nestling period progresses. Occasionally during earlier stages of feeding a bird entered the nest with an item, only to fly out shortly to a nearby branch, hammer at the item, and then return to the nest with the results. At later stages of feeding birds no longer entered the nest to feed, but instead perched at the nest entrance. At about this same time calls of the nestlings could be heard when an adult bird appeared at the nest entrance. These calls were similar in quality, though weaker, than food calls given by the female.

Figures 11 and 12 plot feeding rates for males at nests B2, B9, B1, and A6. Data for A3 are not included since the number of nestlings was unknown at this nest. Data for B1 are only included for that period of time when both parents were feeding. The male at B1, Y, disappeared between day 10 and day 13.

When plotted as simple feeding rate (Fig. 11) great variation is apparent, both from male to male and from day to day. The male in the threesome at A6, however, appears to feed at a distinctly lower rate than males in pairs. Feeding rates for the helper at A6 fall more within the range for other males, though tend towards the low side.

Figure 12 plots the same data with simple feeding rates converted to feeding rates per nestling. Variation in feeding rates among males in pairs is reduced and the rates show a clear increase with time from hatching. This trend is matched fairly well by a linear regression (r^2 = .64), with a slope significantly different from zero ($t = 3.99$, $.005>p$). Points for the individual birds at A6 do not change position in relation to each other, of course, because the number of nestlings is the same.

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Figure 11: Simple feeding rate vs. day from hatching - all males. Each point represents one observation period at one nest (A6, B1, B2, B9).

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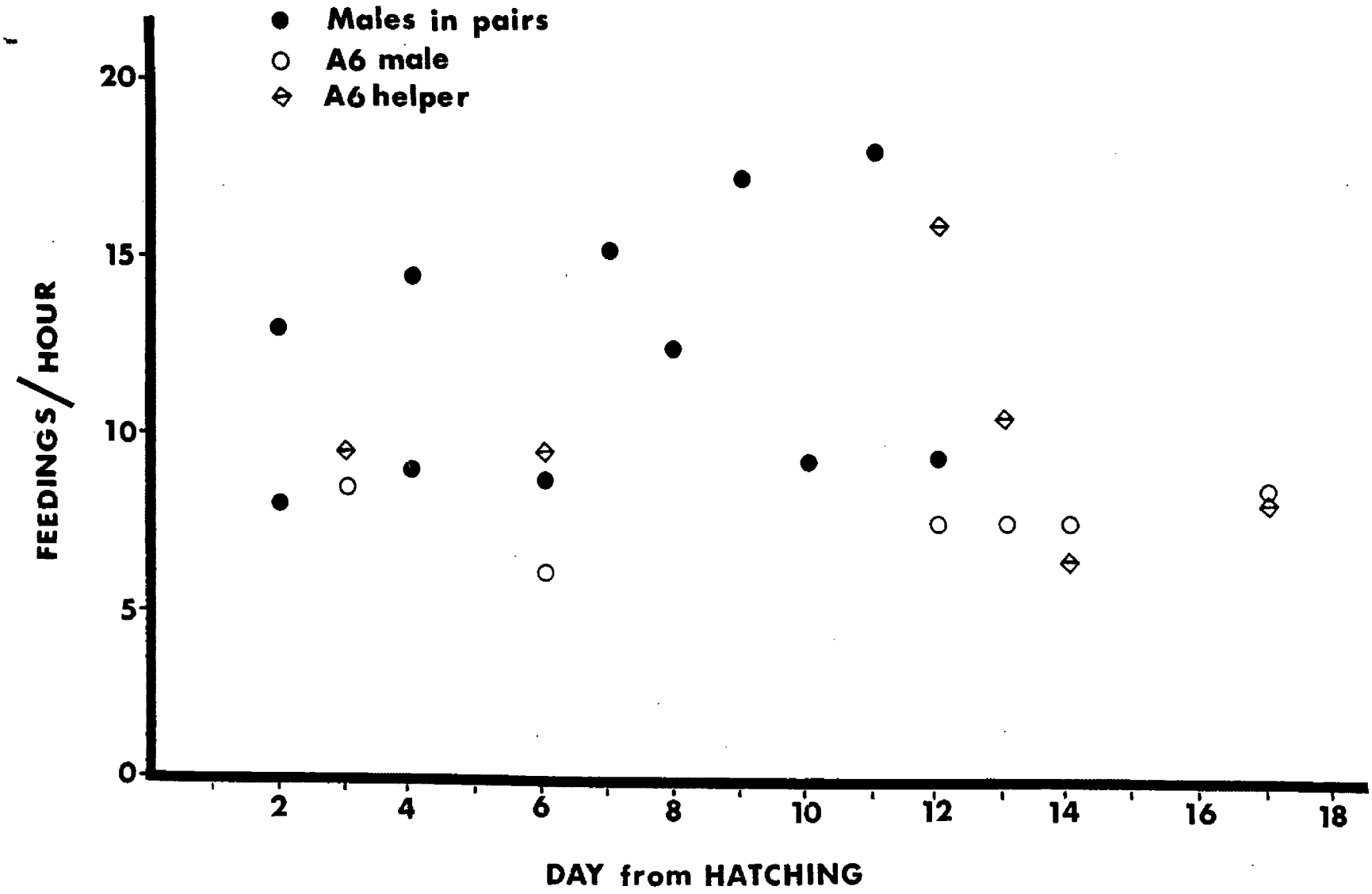

Figure 12: Feeding rate per nestling vs. day from hatching - all males. Each point represents one observation period at one nest (A6, B1, B2, B9).

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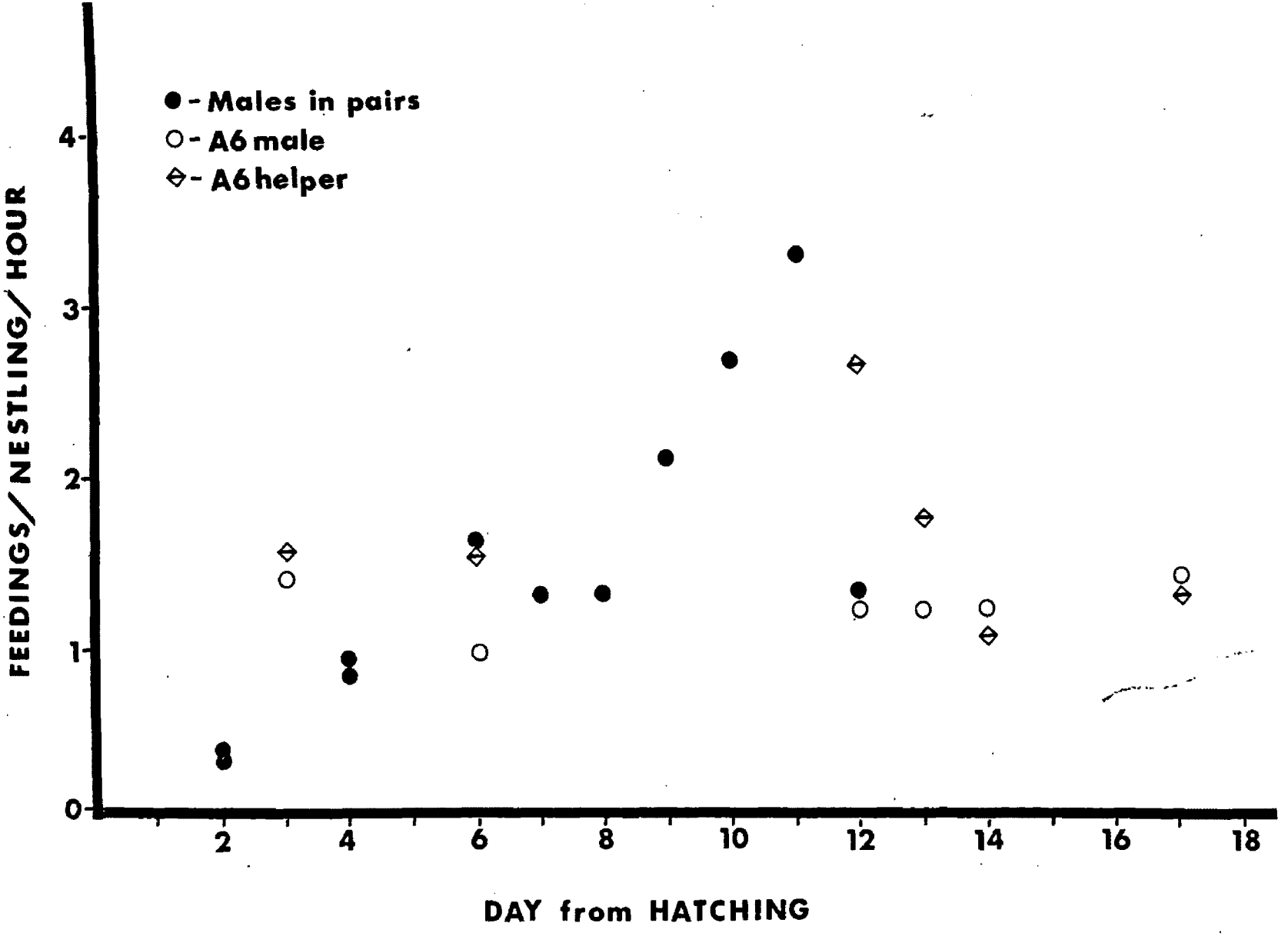

There is even more of a suggestion, though, that the male at A6 was feeding at a lower rate than males in pairs. Unfortunately, data for males in pairs were not obtained beyond day 12, due to my absence from Missoula and/or the destruction of the nests.

Similar data for females are plotted in Figures 13 and 14. Since during the first few days of feeding females spent time on the nest and were thus unable to feed during a portion of the observation period, the feeding rates have been computed only on the basis of that time when females were not on the nest.

Females in pairs show a significant increase in simple feeding rate with day from hatching ($t = 2.51$, $.025>p>.01$), though accompanied by considerable variation ($r^2 = .41$)(Fig. 13). When rates are expressed as rates per nestling (Fig. 14), the variation remains ($r^2 = .43$) as does the significance of the increase ($t = 2.26$, $.025>p>.01$). This suggests that females may not be responding to the number of nestlings, as males seem to do. During the later stages of feeding the female at A6, like her mate, shows both simple and per nestling feeding rates lower than those which would be expected for pairs based on an extrapolation of the trend from days 1 to 12.

Figures 15 and 16 plot the total (male, female, and helper combined) simple feeding rate and total feeding rate per nestling, respectively, at all nests. Variation remains high, particularly during the later stages. This may be due to the greater range of food item sizes which the nestlings can accept during this period. Rates for A6 fall within within the range for pairs.

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Figure 13: Simple feeding rate vs. day from hatching - all females. Data are time-adjusted (see text). Each point represents one observation period at one nest (A6, B1, B2, B9).

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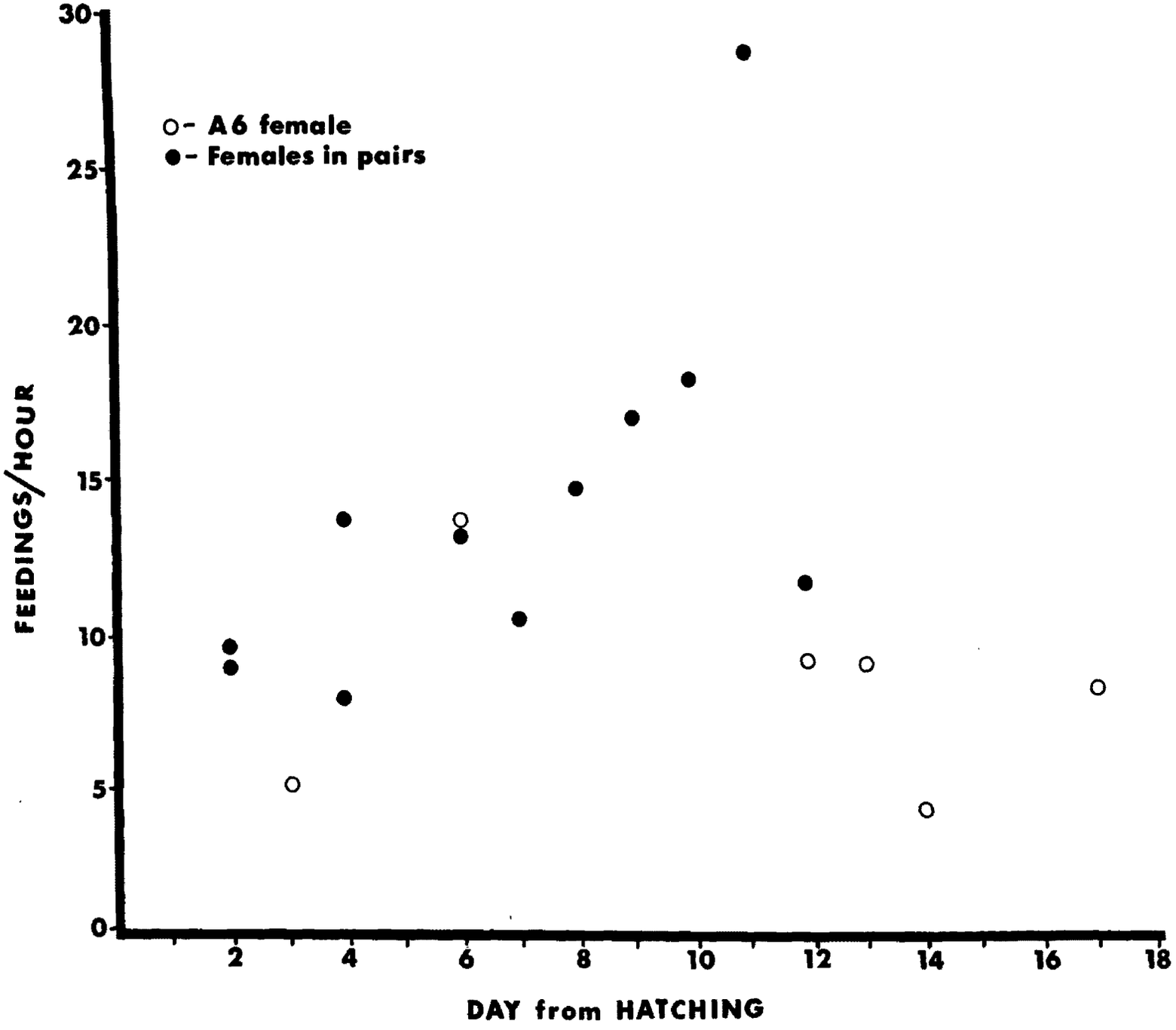

Figure 14: Feeding rate per nestling vs. day from hatching - all females. Data are time-adjusted (see text). Each point represents one observation period at one nest (A6, B1, B2, B9).

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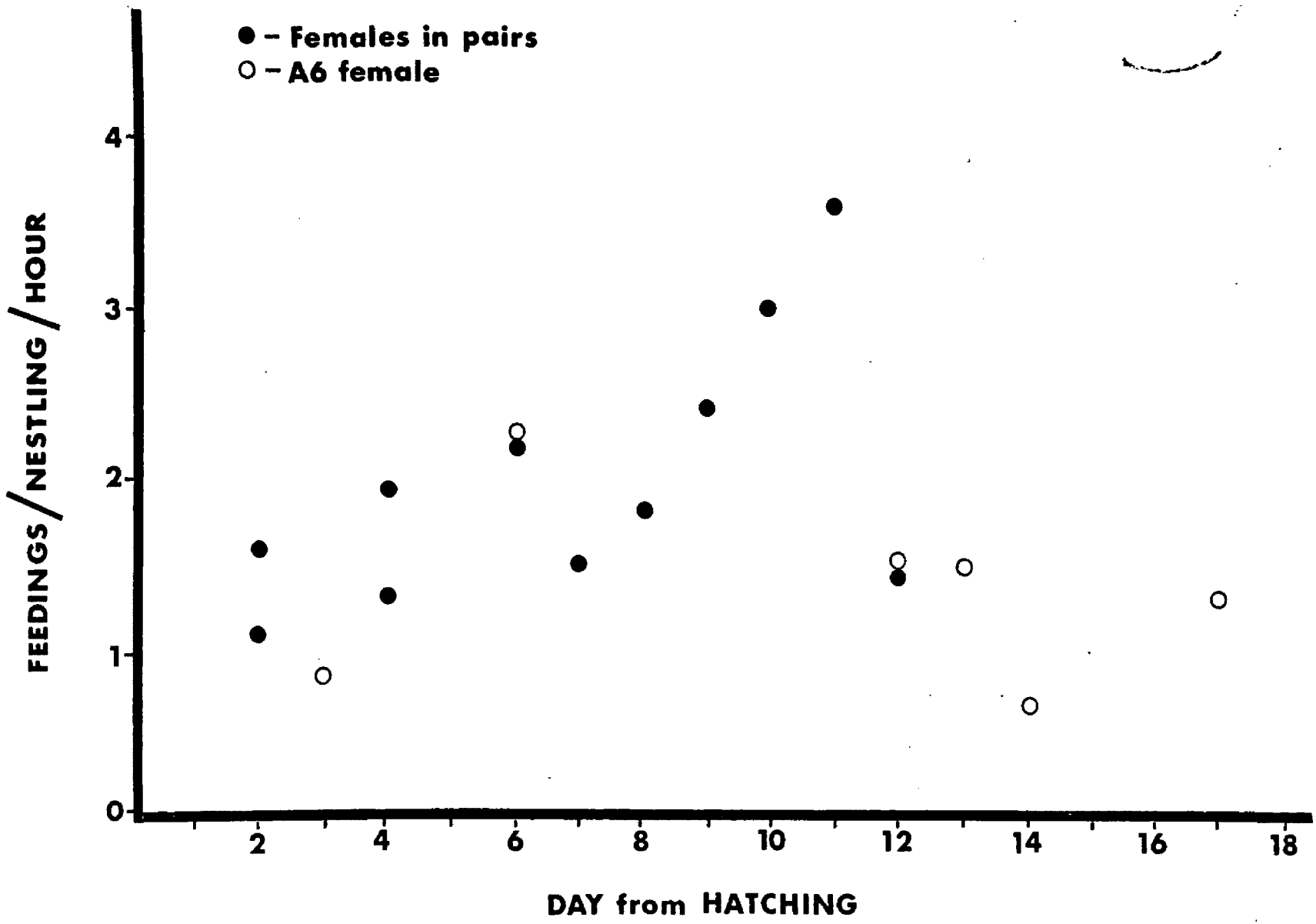

Figure 15: Total simple feeding rate vs. day from hatching. Each point represents one observation period at one nest (A6, B1, B2, B9).

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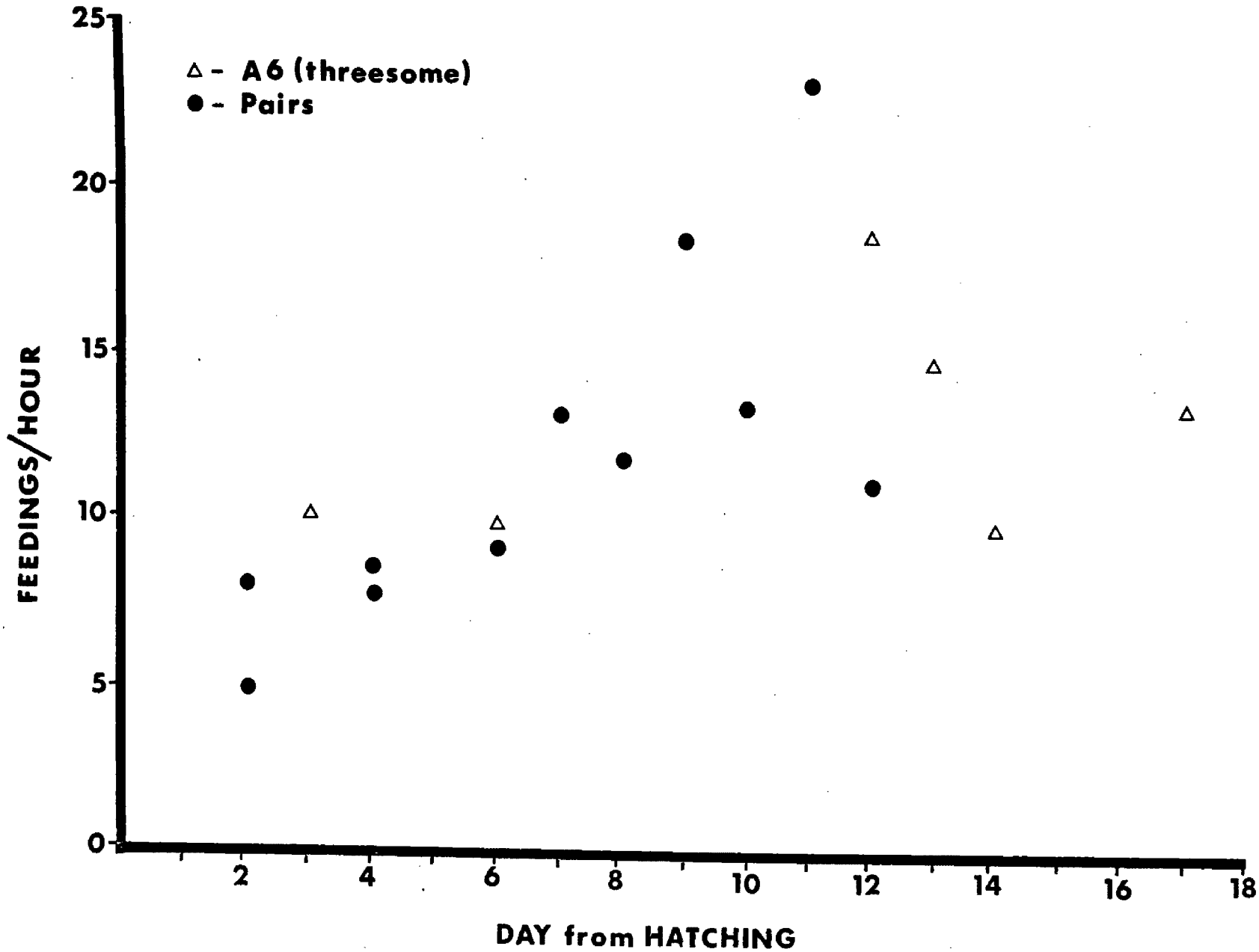

Figure 16: Total feeding rate per nestling vs. day from hatching. Each point represents one observation period at one nest (A6, B1, B2, B9).

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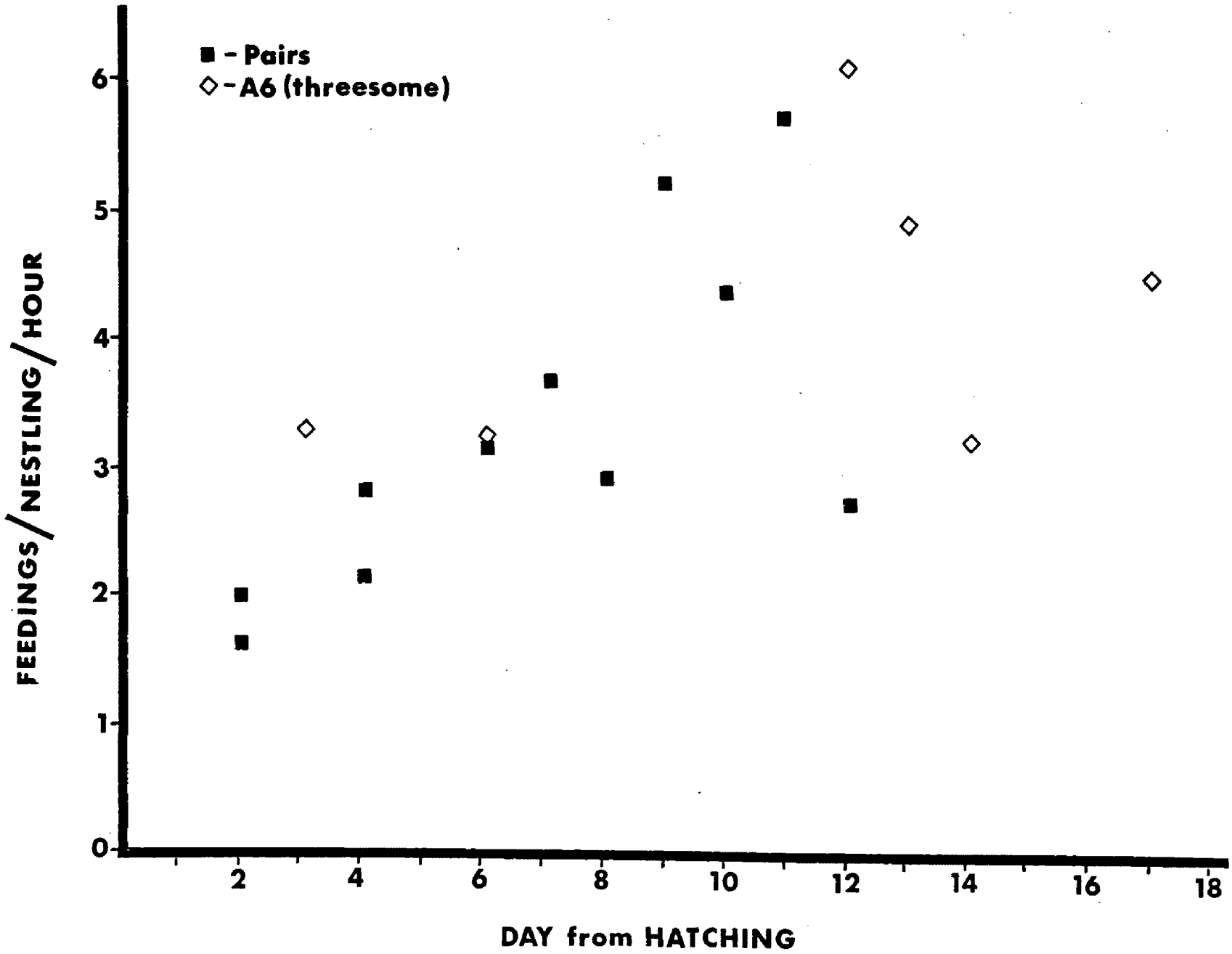

In order to facilitate comparison between feeding rates for males and females in pairs, simple feeding rates for both males and females in pairs are plotted in Figure 17. The rates for the females are again adjusted for the time they were actually available to feed. Data for A3 are also included. Variability is high, but there are no apparent differences between males and females. Rates for males and females were compared using the Wilcoxon test for paired data, with no significant differences resulting ($T(+) = 66$, $p \approx .76$).

Figure 18 plots the same type of direct comparison for the three birds at A6, the female rates still adjusted for time. Friedman's two-way analysis of variance shows no significant difference among the rates for male, female, and helper ($S = 1.6$, $.57>p>.43$).

Fecal sac removal. Fecal sacs were regularly carried from the nest by males, females, and the helper at a rate which increased fairly linearly with time (Fig. 19). Table 9 lists total fecal sacs removed by each sex and the helper during the course of the nestling period. No differences were found between males and females in pairs ($X^2 = 1.64$, $.25>p>.10$), or between the three birds at A6 ($X^2 = .15$, $.75>p>.50$).

Territory

The boundaries of three territories were determined during the nestling period as described under methods, with results as follows:

B2 (pair) - 3.9 hect.
A6 (threesome) - 2.9 hect.
A3 (pair) - 1.8 hect.

Territorial encounters were very rarely observed, but corresponded nicely with boundaries established on the basis of foraging flights. It was not possible to determine the identity of the individuals involved in

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Figure 17: Simple feeding rate vs. day from hatching - males and females in pairs. Data for females are time-adjusted (see text). Each point based on one observation period at one nest (A3, A6, B1, B2, B9).

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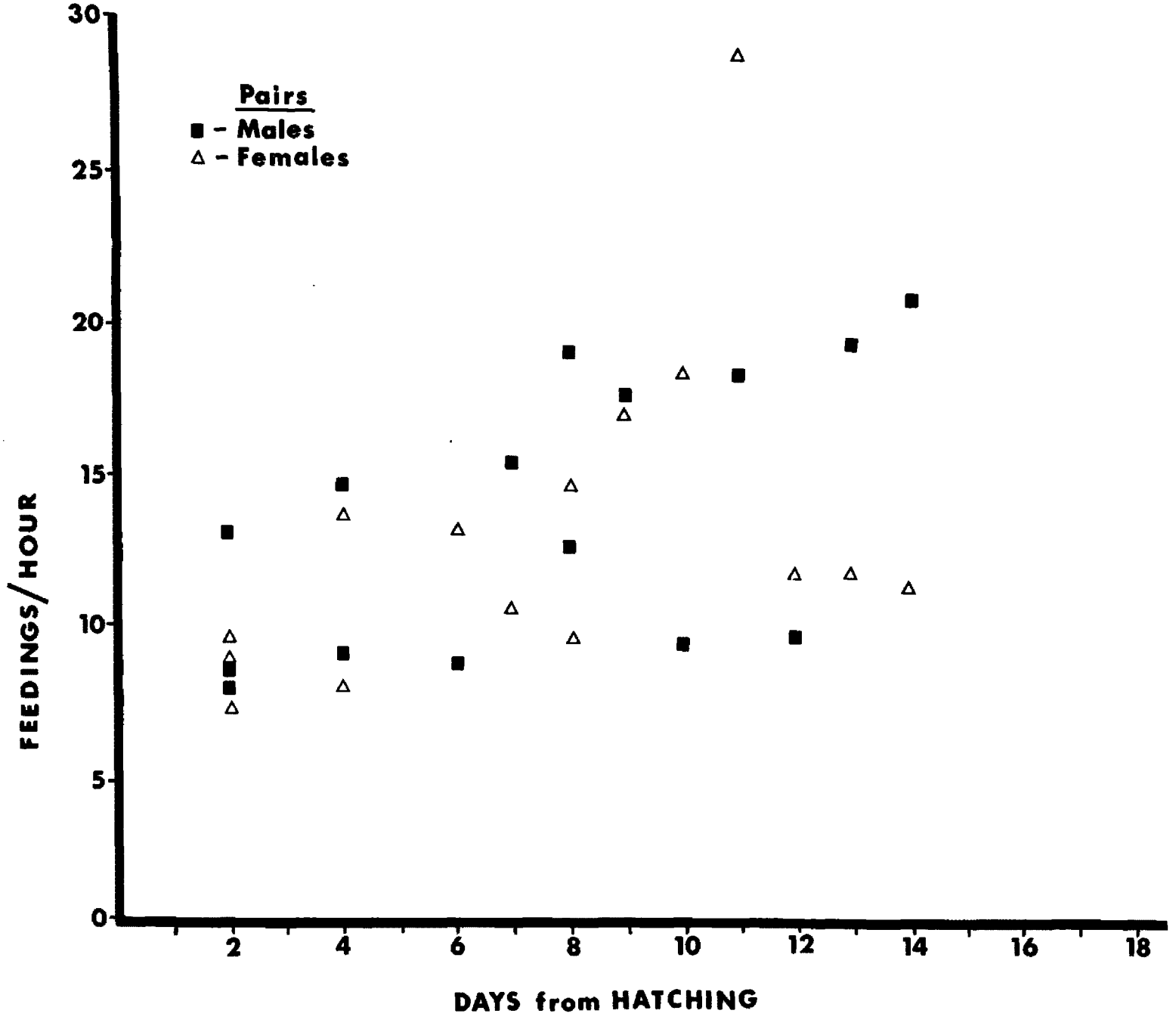

Figure 18: Simple feeding rate vs. day from hatching - male, female, and helper at A6. Data for female are time-adjusted (see text). Each point based on one observation period.

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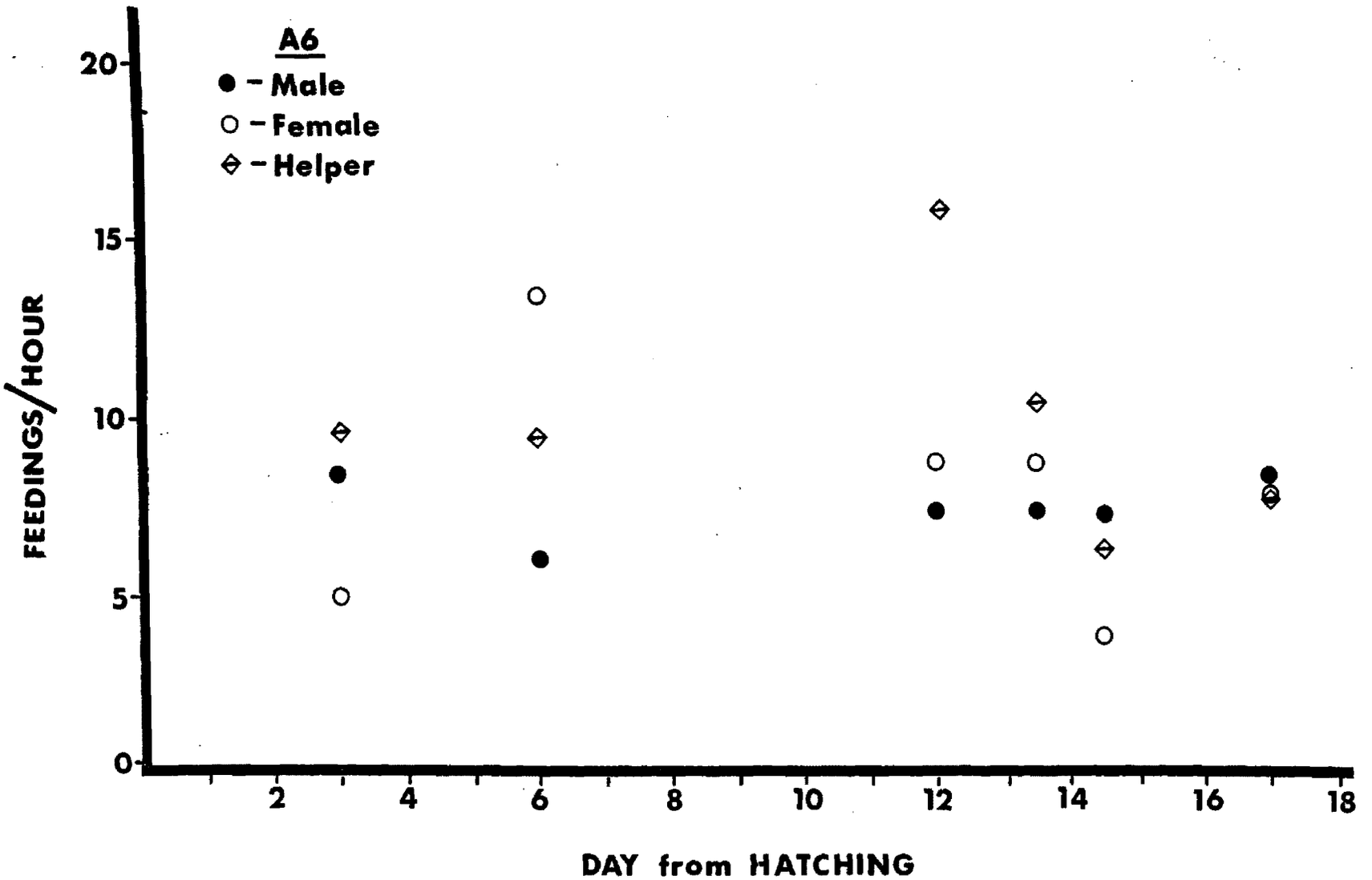

Figure 19: Total fecal sac removal vs. day from hatching. Data for all nests are combined (A3, A6, B1, B2, B9).

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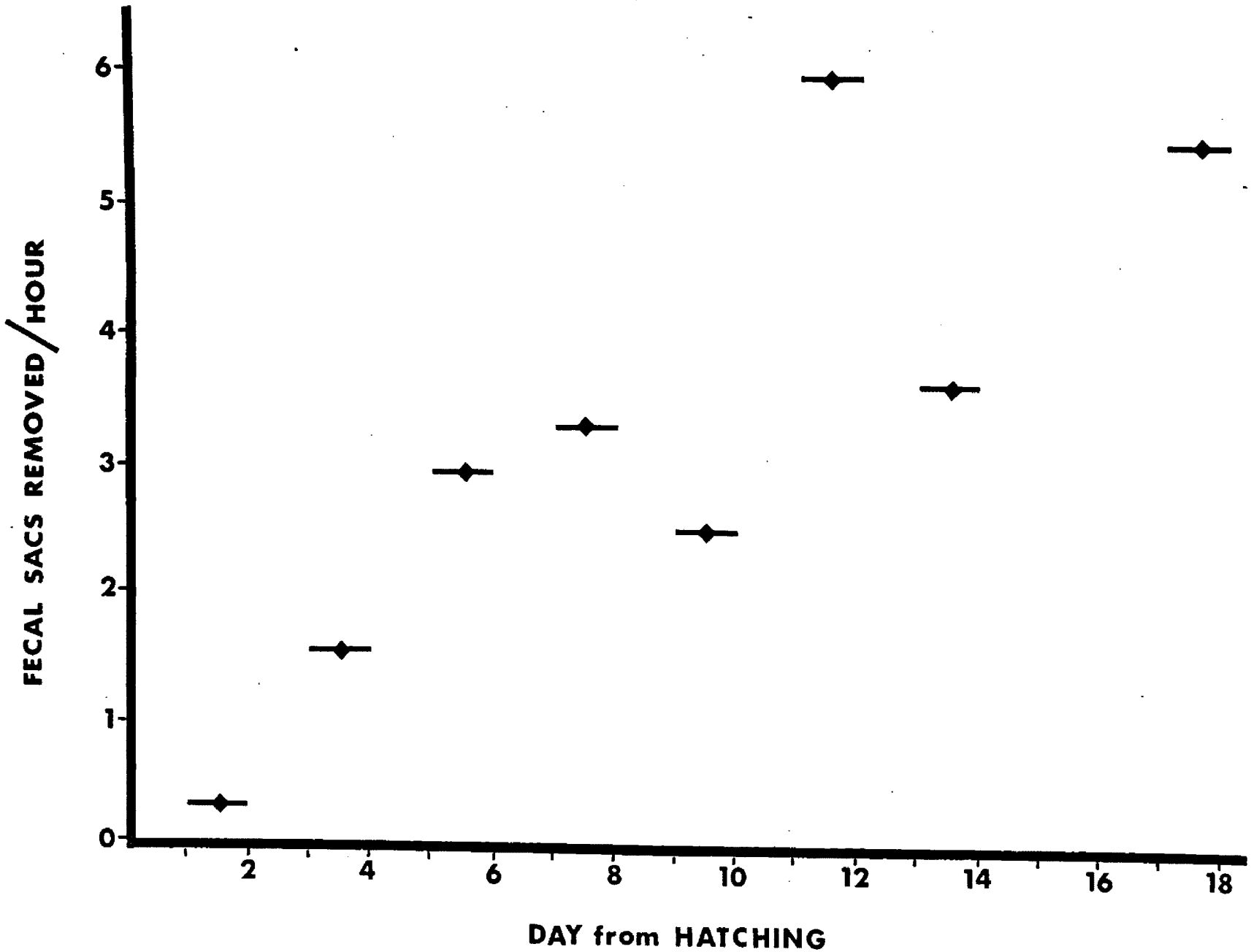

Table 9: Fecal sac removal by males, females, and helper.

Nest site	Fecal sacs removed		
	males	females	helper
B1	5	14	
B2	2	10	
B9	16	18	
A3	15	8	
	38	50	
A6	14	13	12

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encounters. No birds were ever identified on the study areas (while breeding was in progress) which were not associated either with the territory they were on or with an adjacent territory.

No attempt was made to measure the habitat structure of territories. However, I feel confident in stating that the density of ponderosa pine cover was not equal on all territories; that it was definitely greatest for B2, which had the largest territory; and that it was probably least for A3, which had the smallest. A large area of relatively homogeneous and preferably contiguous breeding habitat would be necessary to assess the possible significance of an additional bird in acquiring larger and/or more desirable territories.

Fledging Success

In 1976 there was a very high rate of nest failure prior to fledging, although at most nests failure did not occur until nestlings were at least several days old. My absence from the study areas for three or four days at a time precluded knowledge of many events which may have been associated with nest failure. The known events involved with the success or failure of the various nest sites are summarized below.

A1: Birds persisted in the vicinity of this nest site throughout the breeding period, but no eggs were ever laid, at least in the nest. A single egg was found at the base of the nest stub on 1 June. The shell was very thin, and the egg broke immediately when I tried to pick it up. There seems no way that this egg could have been laid inside the nest and transported to the ground outside without being broken, indicating that it had been laid on the ground where found, and that the female involved was reproductively incompetent. The third bird which had been associated

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with the other two was never observed again after the initial sighting on 7 April.

A2: This nest was not closely followed after the presence of nestlings had been ascertained. When opened on day 18, four dead nestlings were found inside. Their primaries were still sheathed, indicating that they had died several days previously. There was no evidence that the nestlings had been killed by a predator, nor were the parents about the nest.

A3: This nest was opened on day 23. Although the nest entrance had been enlarged, there was no evidence as to whether this had occurred before or after fledging. The female, YG, and another bird YB, had been seen on the nest snag the previous day. Since YB was not her mate, it seems possible that this nest was destroyed by predators, with YG the only survivor.

A4: No information on the progress or success of this site.

A5: The harassment of this nest site by other species has been noted earlier. Since the nest was inaccessible, it is not known whether RO and KW actually completed excavation or laid eggs. Behavior associated with incubation was never observed, although the instance of RO feeding KW is evidence that eggs could have been present, as this behavior was not observed at other nests until eggs were present or incubation had begun. On 2 June the nest was discovered to have been broken into by some unknown agent, probably the Lewis' Woodpeckers. On 6 June both birds were observed excavating a new cavity adjacent to the first, but this activity was not seen again, the site apparently having been abandoned.

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A6: On day 25 a small flock of immature birds was seen near the nest site. Although banded birds could not be identified among them, the presence of the immatures would seem to be strong circumstantial evidence that fledging was successful. Examination of the nest cavity revealed nothing unusual.

B1: The male at this nest disappeared between day 10 and day 13. The female continued to feed the nestlings alone and was observed in this activity on day 16. On day 18 the nest was opened and seven dead nestlings discovered inside. All seemed to have been about the same age at death, based on the stage of development of primaries, with no evidence of predation. The female was still bringing food items to the nest at this time, apparently eating them herself when unable to feed them to nestlings. The surviving male from adjacent B12, YW, was around the nest site on day 18 and excavated briefly on the nest stub. YW had also been around the nest site on day 16, as had WRW, a bird not known to have been breeding on the study area. Although both of these birds appeared interested in the activity of the female, calling and peering into the nest, neither was observed to feed the nestlings.

B2: Six nestlings and the male, RV, were discovered dead in the nest cavity on day 17. Three of the nestlings and RV had had the fleshy parts completely eaten, while the other three nestlings were partially eaten. The nest entrance was enlarged and showed evidence of gnawing around the edges. An unbanded bird was in the vicinity, presumably the unbanded female.

B9: On day 20, eight nestlings flew from the nest as I was attempting to open it to band the nestlings. The parents had been feeding the

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nestlings just prior to this, and the nestlings flew and perched rather unsteadily, indicating that this may have been a premature first flight. A flock of young birds was in the vicinity on day 31.

B11: This nest was opened at a time unknown in relation to hatching. Two nestlings were barely alive inside, with five others dead underneath in a wet, stinking mass of nest material. The entrance to this nest was angled in such a way that rain, which had been heavy during the previous few days, would have been able to enter.

B12: On day 7 the female, YWR, was found partially eaten at the base of the nest tree. Only two dead nestlings could be recovered from the inaccessible interior of the nest cavity, although at least five were known to have hatched.

B13: Nestlings were not present in the nest on day 17, a time when fledging would not have been expected to have already occurred. The cavity was partially opened and nest material had been dragged out, an indication that this nest had also been a victim of predation.

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CHAPTER IIIB

RESULTS: WINTER FLOCKING

A total of 20 flocks were encountered during the period 7 January to 9 February, 1977. From 18 of those flocks 219 discrete observations of foraging birds were obtained.

Flock Composition

The estimated composition of flocks by species is listed in Table 10. Due to the rapid movement of birds within the flocks and the ease with which birds were obscured by foliage, precise or absolute counts were impossible. The numbers presented therefore represent a best guess based on the number of birds actually visible and vocalizations heard. They are very probably biased towards underestimating the true number of individuals present, but should be fairly consistently biased.

Four species (Pygmy Nuthatch, Mountain Chickadee, Black-capped Chickadee, and Red-breasted Nuthatch) accounted for about 85 per cent of all birds seen. An additional five species (White-breasted Nuthatch, Downy Woodpecker, Hairy Woodpecker, Brown Creeper, and Golden-crowned Kinglet) accounted for the remaining 15 per cent.

Based on casual observations during the winter of 1976, it was expected that a fair percentage of flocks encountered would be single-species flocks of Pygmy Nuthatches, single-species meaning no chickadees present but perhaps a few of the less frequent auxilliary species present.

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Table 10: Composition of 20 flocks by species.

Species	Number of flocks in which present	Mean number of individuals when present (± S.E.)	Per cent of flock when present
Pygmy Nuthatch	14	8.4 ± 1.0	45.0
Mountain Chickadee	14	5.0 ± 0.4	27.7
Black-capped Chickadee	11	4.5 ± 0.6	25.3
Chickadee sp.	17	7.0 ± 0.5	52.8
Red-breasted Nuthatch	15	2.9 ± 0.3	15.2
White-breasted Nuthatch	9	1.7 ± 0.2	8.5
Downy Woodpecker	8	1.0 ± 0.0	4.8
Hairy Woodpecker	3	1.3 ± 0.3	5.7
Brown Creeper	7	1.6 ± 0.2	7.5
Golden-crowned Kinglet	4	2.5 ± 0.6	10.5
	Mean flock size:	14.6 ± 1.6	

This was not the case during the winter of 1977, at least not during that month when I was in the field. Only three Pygmy Nuthatch flocks were encountered; eleven flocks contained both Pygmy Nuthatches and chickadees, and six contained only chickadees.

In general, variations in flock size were not accompanied by a proportionate increase or decrease in the number of individuals of each species, rather by the presence or absence of species; ie., large flocks were large because they had more species (particularly chickadees and Pygmy Nuthatches), not more of each species.

Temperature had no effect whatever on flock size, as shown in Figures 20 and 21. Total flock size, number of Pygmy Nuthatches, number of chickadees, and number of species all varied completely independently of temperature.

Use of Foraging Zones

Frequency distributions of the proportion of observations in each of the six foraging zones within ponderosa pines are shown in Figure 22. A few observations which did not occur in one of the six zones are not included, for instance birds feeding on the ground or in adjacent bushes. The few instances in which Pygmy Nuthatches foraged on the trunks of pines are also not included, since this zone is essentially unavailable to chickadees for morphological reasons and represents isolation on a different level.

Clear differences exist in the way the three species use the six foraging zones, particularly with respect to height of the zones. Whereas Pygmy Nuthatches used the upper zones a highly significant proportion of the time (X^2 = 42.6, .001>p), Black-capped Chickadees preferred zones in

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Figure 20: Number of total individuals, number of Pygmy Nuthatches, and number of chickadees present in flocks vs. temperature. Each point based on one flock.

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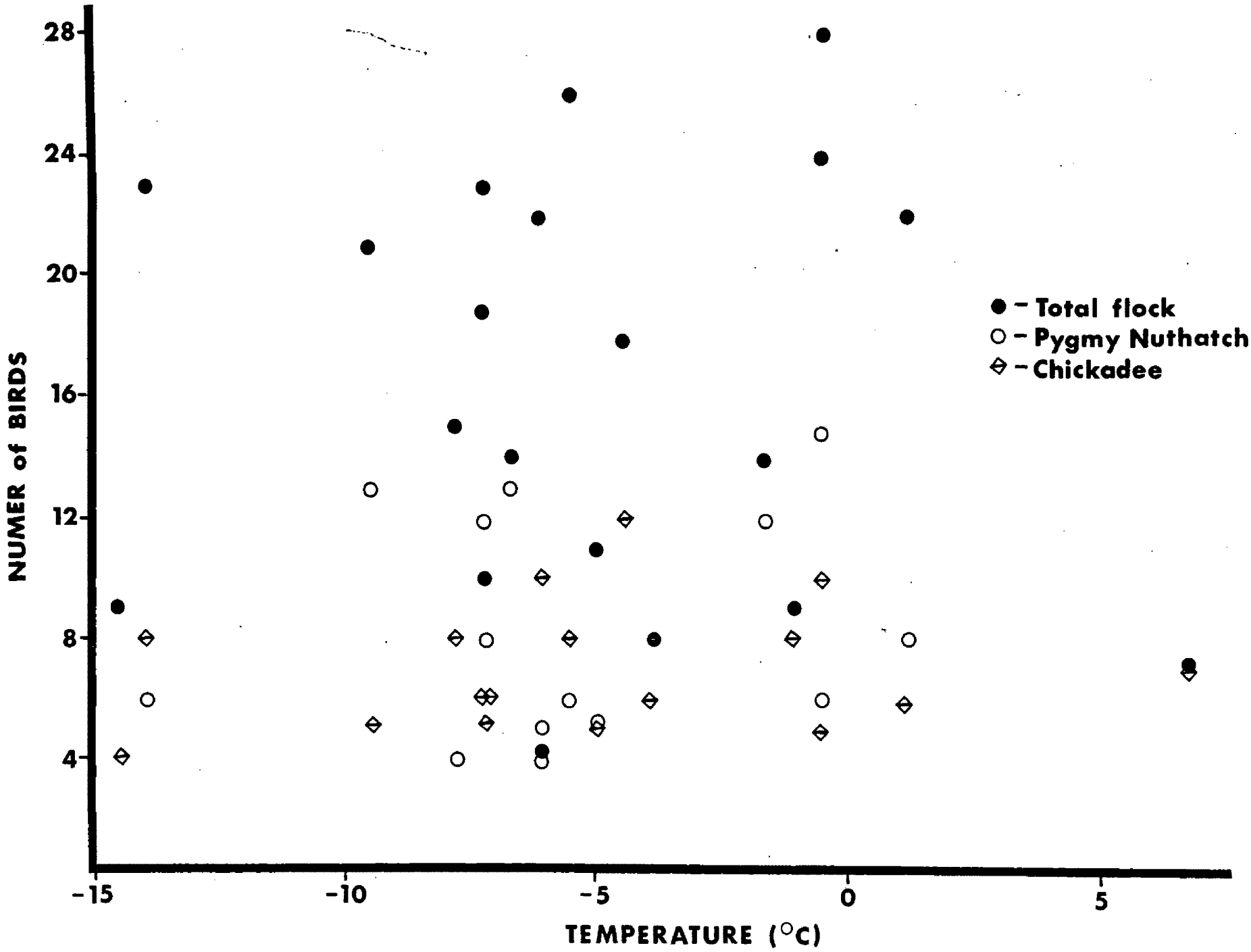

Figure 21: Number of species present in flocks vs. temperature. Each point represents one flock.

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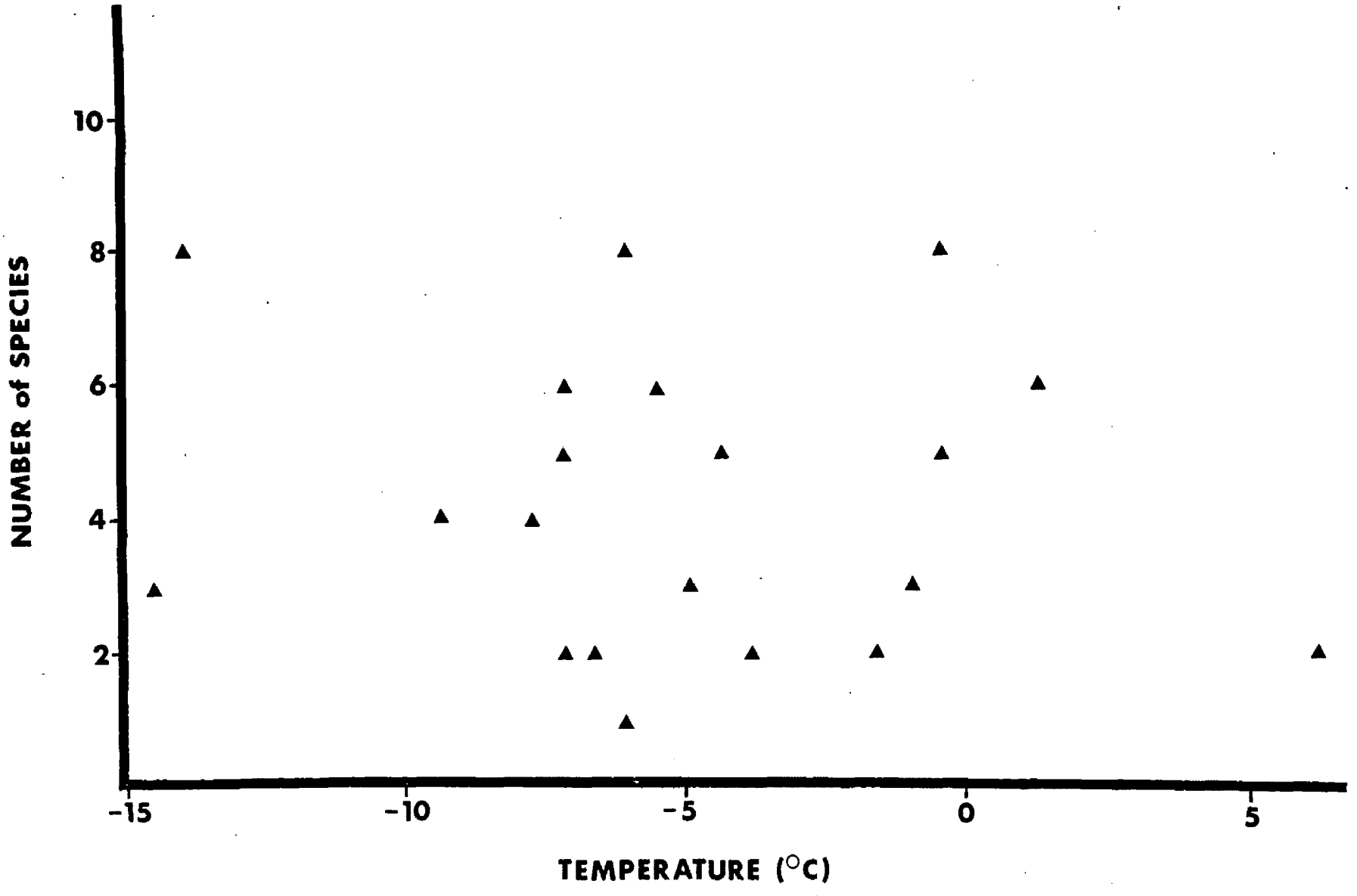

Figure 22: Proportion of observations in each foraging zone - Pygmy Nuthatch, Black-capped Chickadee, and Mountain Chickadee. (BC = Black-capped Chickadee, MC = Mountain Chickadee, PN = Pygmy Nuthatch)

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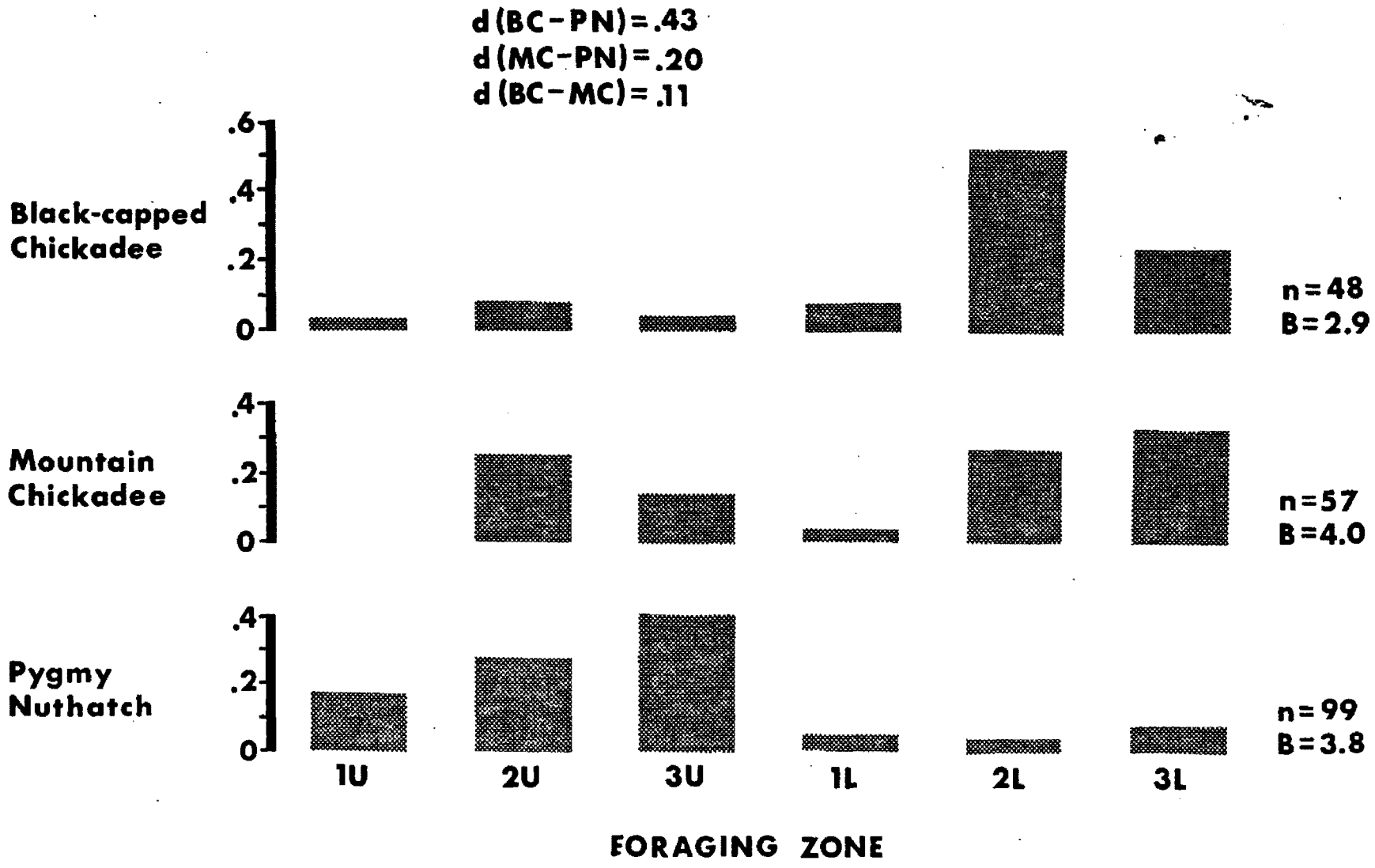

the lower half (X^2 = 21.3, .001>p). Mountain Chickadees show no preference for upper or lower zones (X^2 = 2.96, .10>p>.05), but in this respect are significantly different from both Pygmy Nuthatches (X^2 = 27.7, .001>p) and Black-capped Chickadees (X^2 = 6.11, .025>p>.01).

Significant differences also exist in the way the species used the zones when the zones are classified as to nature of foraging substrate (type 1 - primary branches, type 2 - secondary branches, type 3 - foliage, cones, and smallest branches; see Fig. 2). Pygmy Nuthatches had the greatest equitability among zones, but showed a preference for type 3 and a lack of preference for type 1 (X^2 = 9.88, .005>p>.001). Black-capped and Mountain Chickadees were not significantly different from each other in the way they used foraging-substrate types (X^2 = 3.78, .10>p>.05). Both had a significant lack of preference for type 1 (Bl.-cap., X^2 = 17.4, .001>p; Mtn., X^2 = 23.1, .001>p), but Mountain Chickadees used types 2 and 3 about equally, whereas Black-capped Chickadees had a preference for type 2.

Niche width, calculated as $B = \sum_i \frac{1}{p_i^2}$ (Levins, 1968), is lowest for Black-capped Chickadees and about equal for Mountain Chickadees and Pygmy Nuthatches. Niche differences, calculated as $d = \Sigma\ (p_{iA} - p_{iB})^2$ (Levins, 1968), are greatest between Pygmy Nuthatches and Black-capped Chickadees, as would be expected from looking at the proportionate frequency distributions (Fig. 22). By this measure Mountain Chickadees are more similar to Black-capped Chickadees than to Pygmy Nuthatches.

Differences Between Single- and Mixed-species Flocks

I had hoped that the foraging niches of Black-capped and Mountain Chickadees would be similar enough that observations could be combined

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for comparisons between niches in single-species and mixed-species flocks. Unfortuneately this was not the case, and the relatively small sample sizes obtained for single-species flocks must be made even smaller by considering Black-capped and Mountain Chicadees separately. Also because of the small sample sizes, it is necessary to group the observations either into upper and lower zones or into zones of the same foraging-substrate type when making comparisons with Chi-square.

Figure 23 shows the proportion of observations in each foraging zone for each species of chickadee, both with Pygmy Nuthatches present in the same flock and absent from the flock.

Mountain Chickadees show no differences in use of either upper and lower zones (X^2 .42, .75>p>.50), or foraging-substrate type (X^2 = .01, .95>p>.90, types 1 and 2 combined). Both niche width and difference between the Mountain Chickadee niche and the overall Pygmy Nuthatch niche (ie., as in Fig. 22) are virtually unchanged.

Black-capped Chickadees show no difference in the use of foraging-substrate types (X^2 = 1.08, .50>p>.25, types 1 and 2 combined); but do show a significant difference (p = .021) in the use of upper and lower zones, occurring in the upper zones when Pygmy Nuthatches are present. Fisher's exact probability test was used for this comparison, since Chi-square gave ambiguous results depending on the use of Yate's continuity correction. Niche width broadened considerably in the presence of Pygmy Nuthatches, and the difference between the Black-capped Chickadee niche and the Pygmy Nuthatch niche decreased. The small sample size involved, however, undoubtedly overemphasizes the significance of these changes.

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Figure 23: Proportion of observations in each foraging zone - species pairs compared on the basis of whether or not they were observed together in flocks. (BC = Black-capped Chickadee, MC = Mountain Chickadee, PN = Pygmy Nuthatch, CH = either or both species of chickadee)

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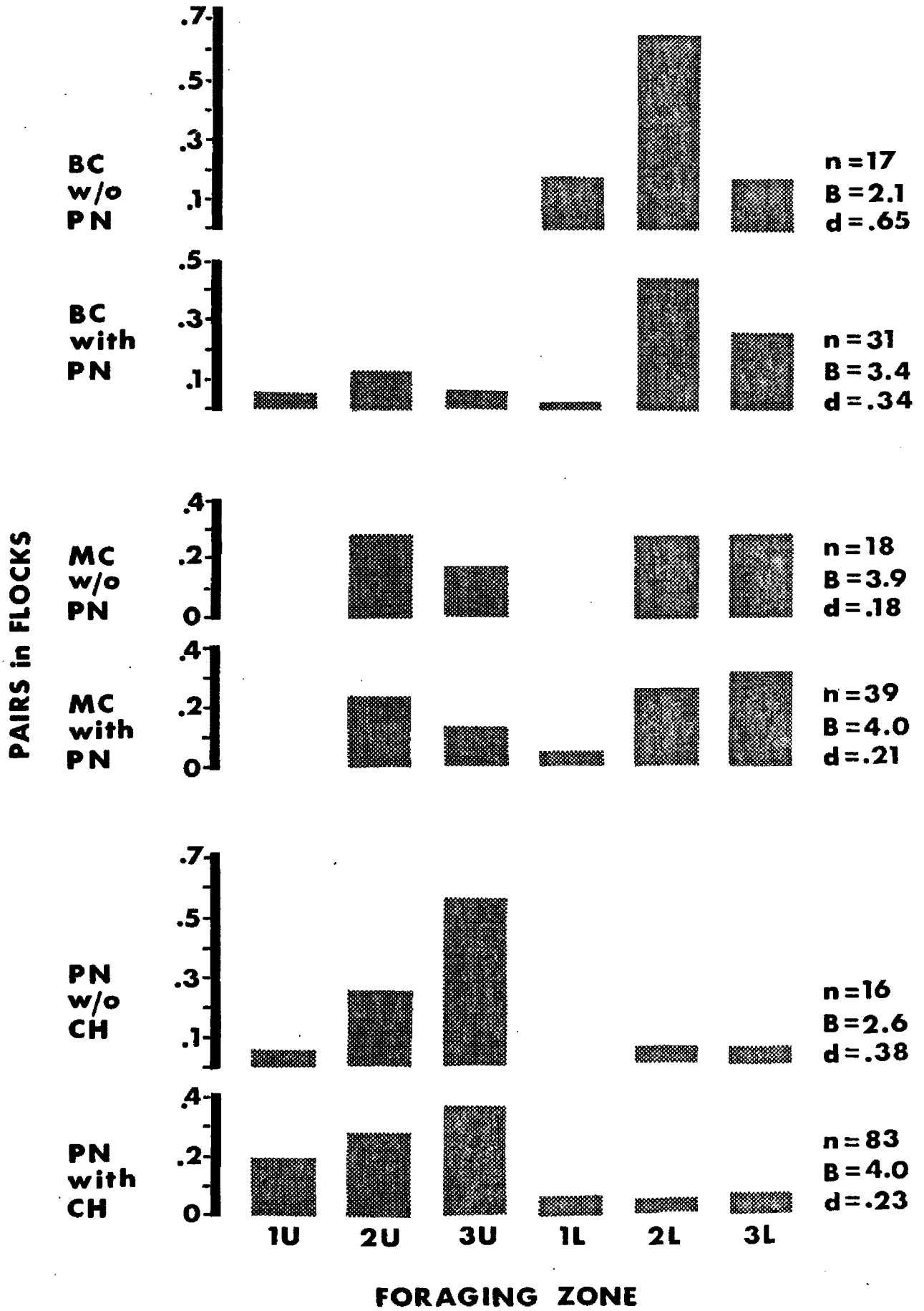

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Observations of Pygmy Nuthatches were segregated on the basis of the presence or absence of either or both species of chickadee in the same flock (Fig. 23). Although the distributions appear quite different, there are no statistically significant differences in the way Pygmy Nuthatchesused upper and lower zones (X^2 = .34, .75>p>.50) or foraging-substrate types (X^2 = 3.17, .25>p>.10). Again, though, the trend is for the Pygmy Nuthatch niche to broaden in the presence of chickadees and to become more like that of chickadees. Chickadee species were combined for this comparison.

The above comparisons were then repeated with observations segregated on the basis of whether or not pairs of species were recorded together on individual scans of ponderosa pines. This was thought to better represent the actual proximity of species, since two species could occur together in the same flock yet remain some distance apart. The absence of a species in a scan is not an absolute indication that it was not present in the tree being scanned, but it should at least indicate that it was not conspicuously present.

When considered on the basis of scans, the relative numbers of "with" and "without" observations are oppostie from those considered on the basis of flocks, ie., in most scans the other species was not present. Comparisons of the frequencv distributions again show no significant differences (.05<p in all cases), except, again, for Black-capped Chickadees occurring significantly more in the upper zones when Pygmy Nuthatches are present (p = .026, Fisher's exact). The proportionate frequency distributions are shown in Figure 24.

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Figure 24: Proportion of observations in each foraging zone - species pairs compared on the basis of whether or not they were observed together in scans of individual pines. (BC = Black-capped Chickadee, MC = Mountain Chickadee, PN = Pygmy Nuthatch, CH = either or both species of chickadee)

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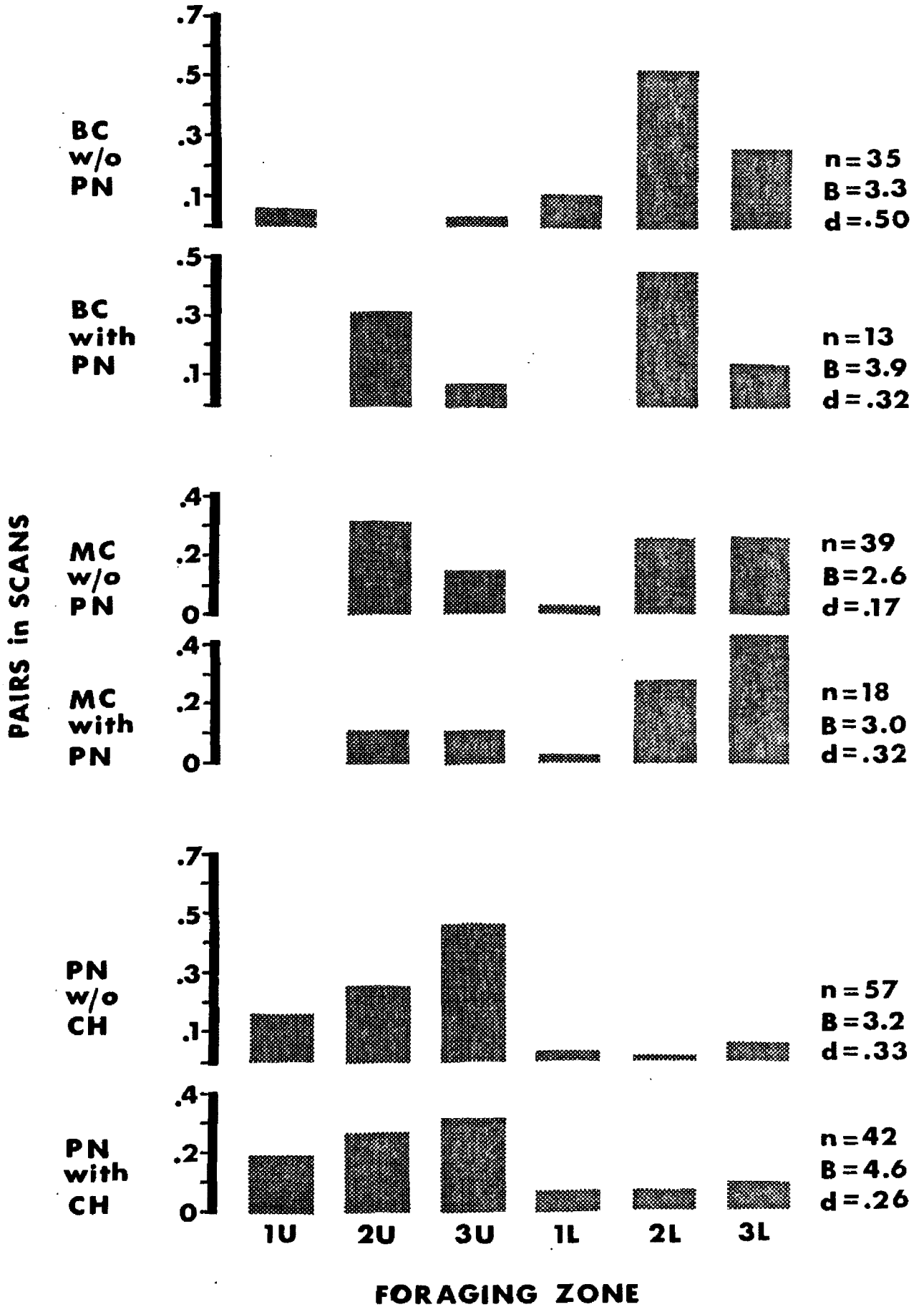

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The trend in most cases is for niches to broaden and for differences between species to decrease, when those species occur together. Again, however, it must be emphasized that no great significance can be placed on this point, due to the small sample size on which at least one of the underlying frequency distributions is based and the lack of statistically significant differences between those distributions.

Finally, observations were segregated on the basis of temperature, one group being those that occurred below the mediam temperature of -6°C. and the other group being those that occurred above it. No significant differences were found for any species ($.05<p$ in all cases).

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CHAPTER IV

DISCUSSION

The discussion of the breeding study will have three parts: (1) a brief comparison of the general biology of the Pygmy Nuthatch in Montana with that in California; (2) a consideration of the question of how the helper helps, and whom, both generally and in the Pygmy Nuthatch; and (3) a consideration of helpers in the Pygmy Nuthatch in terms of ideas which have been advanced concerning the evolution of helpers.

General Biology

Nearly all aspects of Pygmy Nuthatch breeding biology which I examined in western Montana are very similar to those reported for California birds (Norris, 1958). Most specific quantitative measurements, such as length of attentive periods, feeding rates, etc., are within 10 to 20 per cent of each other. In any event, statistical comparisons are impossible because of the lack of raw data or the small sample sizes involved. For instance, Norris reported the length of the incubation period to be 15.5 to 16 days, one day longer than the 14.5 to 15 days which I found typical, but this information was based on only one nest. The only point for which clear differences exist is in the size of the territories. For six territories that Norris measured, average area was 1.1 hectares, compared to 2.9 hectares for the three that I measured. This difference could be due to differences in habitat density, nest site

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availability, or even habitat productivity, but no good data are available for comparison. Norris did estimate, apparently without measuring, that canopy coverage on his study area was about 60 per cent; I would estimate, again without measuring, that canopy coverage on my study areas was less than 60 per cent for the smaller territories, but more than 60 per cent for the largest, an inconsistent trend.

With particular regard to the occurrence of threesomes, Norris reported that 8 of 36 nest sites had helpers (22%), and implied that birds were successful in completing cavities and laying eggs at all of those 36 sites. By the same criterion of successfully laid clutches, 1 of 7 nests which I studied had helpers (14%), a ratio completely consistent with that for California. Associations of three birds at A1 and A5 were short-lived, and in any event breeding was not successful at either site. The other three active nest sites were not studied in sufficient detail to permit absolute knowledge of the number of birds involved.

Do Helpers Help, and Whom?

Before considering the specific ways in which the Pygmy Nuthatch helper may actually have helped, a general orientation is in order as to the ways in which helpers might help, and the relative selective advantages of helping to the helper and the helpee. All of these will be strongly influenced by the sex of the helper, its reproductive condition, and its genetic relationship to the helper.

Consider first the advantages and disadvantages to a nesting pair of permitting a helper to help; these may be different for each sex. Both sexes would be disadvantaged, of course, if the helper actually decreased their reproductive success by breaking eggs, mishandling nestlings, or

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attracting predators to the nest sites, and there is some evidence that "helpers" can exhibit such incompetence (Zahavi, 1974; but see Brown, 1975). A helper should help both sexes if its activities increased their reproductive success, either by increasing the number of offspring raised in the year in which it helps, or by increasing the ability of the parents to raise more offspring in the future (most likely by increasing the chances that they would survive to do so). The latter point is very difficult to assess, but there is some evidence for the former (Ligon, 1970; Fry, 1972; Smith and Ridpath, 1972; Woolfenden, 1975). Only in one case though, has the number of offspring raised by pairs with helpers been higher in a statistically significant way than the number raised by pairs without helpers (Woolfenden, 1975). It should also be noted that the question of the number of offspring raised involves more than the number of young fledged, but must also take into account their ability to survive to reproductive age.

If the helpers are reproductively immature, as in the Mexican Jay (Brown, 1972) and frequently in the Florida Scrub Jay (Woolfenden, 1975), then from the parents' point of view there should be little else to consider besides the relative ability of a helper to help or hinder. The relationship of the helper should be relatively unimportant, although if helpers increase their <u>own</u> reproductive success in later years it would be an additional advantage to permit this benefit to accrue to one genetically related. Of course, as Brown (1975) has pointed out, in the extreme conservative view the <u>only</u> benefit to the parents may be in the enhanced reproductive experience and maturity of the helper in subsequent breedings of its own.

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If the helpers are potentially reproductive, however, then additional disadvantages could be involved for the parent the same sex as the helper. For the male this disadvantage would have to consider the probability that the helper could be the father of the offspring, weighed against the probable degree of genetic relatedness of the helper, and the degree to which the helper actually increases the males reproductive success. Smith and Ridpath (1972) have calculated the outcome for some of the possible conditions, and concluded that if the helper helps, and is of known close genetic relationship (offspring or sibling), then there will be a net advantage to the male to permit the helper to help even if there is some probability that it, and not the male, will be the father of the collectively raised offspring.

For the female, her relationship to her offspring is never in question, but the presence of another female could possibly result in her being deserted by the male, and would be a clear disadvantage. The point is moot, however, since there do not appear to be any cases of reproductivitely active female helpers.

The helper may be advantaged in helping for two reasons. One is through kin selection, if the help is directed toward close relatives. (At this point it should be made clear that advantages and disadvantages do not really refer to individuals, but to genotypes. There would not, of course, be any advantage to a helper as an individual in terms of its own offspring; but there is an advantage for its genotype, dependent on the degree to which the genotypes which receive help are similar to its own). Since the helper, to the degree to which it makes an investment in raising young, suffers the same diminution of future reproductive

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potential as does a parent; then, if there is no other advantage in helping, it is clear that helpers should evolve to help only those very closely related to themselves.

It is also possible, though, that non-breeders which participate in raising young may increase their reproductive potential in subsequent years over non-breeders which do not help. This might occur either if they are more likely to acquire a mate, or, once mated, more capable of raising a brood. There is no evidence to support or refute this idea, however. It is also true that this particular advantage does not necessarily involve helping relatives, although the additional advantage in so doing would always be high.

It should also be noted that an additional advantage for the helper will exist in the possibility, particularly for males, that it could actually fertilize the female. Arrayed against this is the possibility, and the consequences, of being caught, and the co-evolving ability of the male to reject helpers with the inclination to try.

The question of who benefits the most from helping, parents or helper, relates to the suggestion of Alexander (1974) that helpers are a result of manipulation by the parents. If all the benefits accrue to the parents, and none to the helper, than parents should evolve the ability to "cultivate" some of their offspring to act as future helpers to themselves or other offspring. Conversely, if all the benefit accrues to the helper, then presumably birds should evolve strategems which would cause parents to tolerate them in such a capacity. More likely it would seem that the benefits are not dichotomously divided, with the net benefit going to either parents or helper depending on the ecological and behavioral conditions peculiar to each species.

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Information on the Pygmy Nuthatch relative to the above questions of sex, reproductive ability, and genetic relationship of the helper is inconclusive.

All of the unspecified number of helpers that Norris collected were males; the others were described as males on the basis of "protracted study." I would concur that WG behaved like a male (eg. he fed the female); however, this bird was not collected, in deference to the wishes of the property owner. The best reason for believing that all helpers are males lies in the sex ratio, which appears strongly skewed in favor of males (Norris, 1958). Tabulation of over 900 museum specimens resulted in a male:female ratio of 1.52:1 for juvenal birds and 1.75:1 for adults. Assuming that first year birds are reproductively mature, and Norris mentions several instances of first year birds successfully breeding, then with a sex ratio so skewed in favor of males it is hard to see how any females could remain unmated and be available to act as helpers.

Norris also believed that most helpers were first year birds, though some were older. Part of this belief was based on knowledge of birds banded as nestlings or fledglings, and thus of unquestionable age. In other cases, first year birds were identified on the basis of unspecified plumage characters. Information available in Ridgway (1904) and Bent (1948), however, indicates that the first basic plumage is essentially definitive. Hence, I have some reservations about the accuracy of identifications made in this manner.

If, for whatever reason, threesomes are more successful than pairs, and the sex ratio reported by Norris reflects the actual situation in the population, then the question arises as to why helpers do not occur with

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greater frequency. Theoretically (and perhaps quite unrealistically, depending on the normal kin relationships of the helper and the number of pairs successfully raising broods the previous year), helpers could be available for up to 70 per cent of nesting pairs, instead of the 15 to 20 per cent actually observed. Perhaps some first year birds are not reproductively mature, and are more likely to be inclined or to be allowed to serve as helpers. On the other hand it seems doubtful that second year or older helpers, which do occur, would be incapable of breeding if they could acquire a mate. It would be interesting to know the relative reproductive condition of first year breeders, first year helpers, and first year non-breeding non-helpers, as well as of any older helpers.

It is also possible, of course, that the measured male:female ratio is too high, because of some bias for male birds to be collected more easily or identified more easily. The sex ratio at fledging would also be a valuable piece of information.

No information is available on the genetic relationship of Pygmy Nuthatch helpers, though one would be surprised if they were anything but offspring from a previous year or siblings. Fledged young remain with the parents in family groups throughout the winter, and it seems reasonable to believe that helpers would be young which were retained from this group, the other young dispersing on their own or being driven off.

Finally, as to the question of how, or whether, the helper actually helps in the Pygmy Nuthatch, the major points are summarized and discussed below. It should be borne in mind that although the activity of the helper apparently does result in some reduction in investment by the

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parents, at least in terms of energy expenditure, it is not clear that this necessarily has any significant effect in terms of increased reproductive potential in later years. Rather, more important investments may be those which involve a high risk of mortality, such as defending the nest against a predator, but little actual energy expenditure as compared to activities such as excavation or feeding (Trivers, 1972).

Excavation. For the brief time during which a helper was present at A5, it excavated more than the male and female combined, although this could easily be an artefact of the small amount of excavation observed. Norris gives no quantitative data on this point, other than to state that helpers were observed excavating. The data are inadequate to indicate whether time spent in excavation by a helper reduces the contribution of the male, the female, or both. The highly variable amount of excavation from site to site and the variability of the proportion done by each sex in a pair suggest that the reduction in effort by the male and/or female would also be variable, and in any event of limited significance in terms of overall reproductive effort. With the exception of some bank-dwelling species of bee-eater (Fry, 1972), helpers described in other species do not participate in excavation or nest building.

Provision of nest material. Before the start of incubation the helper brought less material than either the male or the female, who brought about the same amount. Norris described the same situation. After the start of incubation, however, the female's role was reduced compared to that for females in pairs. Conceivably a female in a threesome might thus gain the advantage of being able to spend more time foraging while off the nest. The nest materials used, though, are not so

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exotic that one would expect that an appreciable amount of time would be required for their acquisition.

Incubation. Overall time on the nest and lengths of attentive periods for the female in the threesome were well within the range for females in pairs. This should be expected if helpers are males, and there is every indication that they are.

Feeding of female. Contribution by a helper could be of substantial importance to a bird which spends up to 90 per cent of the day on the nest; however, the helper at A6 fed little compared to the male, yielding a total feeding rate for the two combined only somewhat higher than achieved by males in pairs feeding alone. This pattern is similar to that reported for the Florida Scrub Jay (Woolfenden, 1975) and may be an indication that the bond between female and helper is not as great as that between female and male. Norris also reported that helpers, unlike males, did not participate in "courtship feeding" of the female away from the nest.

Feeding of nestlings. The threesome at A6 did not feed nestlings at a higher overall rate than did pairs. Norris does not make a specific quantitative comparison between feeding rates for pairs and threesomes.

Since each bird in a threesome feeds at roughly the same rate (though females deliver fewer items when spending time on the nest brooding), then on the average a bird in a threesome needs to gather 1/3 fewer food items than a bird in a pair. This could result either in additional time spent searching for each item (hence a larger or qualitatively better item?), or additional time available for the bird's own foraging. There is some evidence that time spent in acquiring a food item may be of considerable

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importance in determining the quality of that item. This is the case of the female at B1 feeding nestlings after her mate had disappeared. Although she fed at the highest rate observed for any bird during the study, equaling that for birds in a pair combined, the size of the food items being delivered was obviously smaller than that of food items being delivered by other birds to nestlings of the same age; and the nestlings subsequently died. Of course, the smaller food items could have resulted from abnormal foraging behavior under stressful conditions rather than from a lack of time.

At times I also observed birds in both pairs and threesomes foraging with a food item held in the bill. Possibly these birds can collect and carry more than one food item at a time, but it is also possible that when another food item was encountered, one would be eaten and the other retained for delivery to the nestlings. If the latter pattern were common, then additional time between delivery of food items should enable a parent bird to acquire more food for itself and still deliver optimal items to nestlings.

Although feeding of nestlings is the most common activity in which helpers participate, few studies have made quantitative comparisons of feeding rates at nests with and without helpers. In one which did (Gaston, 1973), feeding rates were the same at nests of the Long-tailed Tit. Equally useful, if not more so, would be comparisons of growth curves for nestlings. The only available data on this point is for the Red-cockaded Woodpecker (Ligon, 1970), in which nestlings fed by three helpers (1 case) weighed more at fledging than nestlings fed by one helper (1 case) or by the parents alone (3 cases). However, weight at

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fledging may not necessarily be relevant to subsequent survival (Woolfenden, pers. comm. in Wilson, 1975).

Territory. Norris reported that of six territories which he measured, the two largest belonged to two threesomes. Of three which I measured, the one belonging to a threesome was intermediate in size. My own impression is that in many locations the local distribution of habitat and availability of nest sites will be more important in determining territory size than the unproven ability of threesomes to defend a larger area.

As mentioned previously, the above points do indicate some reduction in the energy expenditure of parents assisted by a helper, but there is no way to assess the significance of this in terms of their long-term reproductive success.

Because of the high rate of nest failure, and the fact that all nests failed completely, there is no evidence concerning the ability of helpers to increase the number of young fledged. If the pattern of all-or-nothing fledging success is the typical one, then I would not expect that the average number of young fledged from a successful nest would be higher for threesomes than for pairs (which says nothing about the more important number which survive to breed). I do suspect, however, that threesomes will fail less often than pairs, because of the hypothetical ability of a helper to assume the role of a deceased parent and the proven inability (at least in one case, the female at B1) of a single parent to raise a brood.

Evolution of Helpers

Finally, I wish to consider rather briefly the phenomenon of helpers

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at the nest in the Pygmy Nuthatch vis-a-vis some of the broader contexts which have been proposed as conducive to the evolution of helpers. A common theme of these contexts is the existence of a reproductively inactive segment of the population, inactive either because its members are not able to find mates or because they are physiologically immature. From this population of non-breeders helpers may be drawn, subject to the selective advantages and disadvantages for the helper and helpee reviewed previously.

Brown (1974) considers that, among several possible evolutionary trends, a skewed sex ratio is one which, at least in monogamous species, results in a non-breeding population from which helpers can be drawn. The Pygmy Nuthatch clearly fits this category, as do various species of bee-eaters, which have helpers when the sex ratio is skewed (in favor of males) and do not have helpers when the sex ratio is unity (Fry, 1972). Why the sex ratio may be skewed in the first place is a question which has not been resolved, but Trivers (1972) has argued that the monogamous mating system which characterizes most species of birds will, as a direct result of the reproductive strategies involved, tend to produce a differential mortality by sex which will result in an excess of males in many species. This by no means implies that in all such species we should expect to find helpers, because the relative advantages and disadvantages will be different in each species depending on other factors. For instance, we might expect helpers to develop in a sedentary permanent resident with a social organization built around family groups (ie., Pygmy Nuthatch) in which kin are available and are known as kin; we should not expect helpers in a migratory species or any species in which mixture or

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dispersal of individuals results in a low probability that kin are available and that they are known as kin (Brown, 1974).

It has also been suggested (Fry, 1972) that a reserve of experienced individuals could be a means of finely regulating population numbers when environmental conditions are stable and recovering from crashes when conditions fluctuate widely. Apart from the dependence of the entire concept on group selection, the latter hypothesis would seem to be of limited significance if, as in the Pygmy Nuthatch, all the reserve were of one sex.

Ricklefs (1975) proposed that in species with high annual recruitment and/or low adult mortality, delayed reproduction would result from competition of young birds with experienced adults. Helpers would evolve from this non-breeding population. In the Pygmy Nuthatch it appears that mortality is high (approaching 60 per cent per year for adults, Norris, 1958), and that recruitment is low (56 per cent at time of fledging, present study). Norris does not give figures for nest mortality, although he notes that several nests were lost to predators. Also reproduction is not delayed beyond the first year, at least in some cases, and in any event it hardly seems likely that this would be an advantage in a small passerine bird whose average life span includes only two breeding seasons (Norris, 1958). This theory may be applicable, however, to the jays studied by Brown (1972) and Woolfenden (1975).

It should be apparent by now that I accept the idea that an excess of males in Pygmy Nuthatch populations, combined with a tight-knit social organization and environmental conditions which may tax the ability of pairs to raise young, are conditions which make the appearance of helpers

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somewhat inevitable. It remains to be demonstrated, however, in precisely what ways advantages accrue to parents, helpers, or both. Unfortunately this information can only be obtained by detailed study, over several years, of large numbers of birds. Although the Pygmy Nuthatch is in some ways a tractable species (common, sedentary, easily banded) it is in many ways also a very difficult species to work with (small, nests sometimes inaccessible, nests always in cavities, low proportion of pairs with helpers, high mortality). Potential future studies would have to carefully weigh the considerable effort which would be involved against the value of the information which might be obtained.

Winter Flocking

In spite of some overall trend towards niche broadening, in light of the small sample sizes obtained it seems unwarranted to infer that my data support or refute ideas that birds in mixed-species flocks gain some advantage, either through increased foraging efficiency resulting from increased niche specialization or through the opportunity to exploit new areas by copying other species. Evidence in the literature also does not give strong support to either idea.

Although "social learning" among species which flock has been demonstrated experimentally, both intraspecifically (Krebs, MacRoberts, and Cullen, 1972; Turner, 1965) and interspecifically (Krebs, 1973), it can be argued that these artificial conditions are an unrealistic reflection of normal patterns in the wild. Also, social learning would only seem possible between species which were already similar ecologically, such as Mountain and Black-capped Chickadees. It would not be expected to occur between Hairy Woodpeckers and Mountain Chickadees, or between

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White-breasted Nuthatches and Golden-crowned Kinglets; yet all these species occur together. Different species of sea birds will congregate when one finds a local concentration of food (Sealy, 1973), but this is a short-lived phenomenon which is not comparable to mixed-species flocks which habitually forage together.

Morse (1970) studied foraging patterns in mixed-species flocks of woodland birds over all sections of the country, yet actual changes in foraging pattern occurred only in a few combinations of species where one species was clearly subordinate to another, and narrowed its niche through avoidance of the dominant. Conversely, Austin and Smith (1972) found that dominant species in flocks might be increasing foraging diversity by avoiding interactions with other species and seeking new areas. However, even accepting the fact that these sorts of interactions do occur between some flock members, it is hard to see a general mechanism whereby this could lead to interspecific flock development. If a narrowed foraging niche were advantageous, then it should be advantageous with or without other species present, and should not require that a bird should join with other species, there to be forced into a narrower niche than it would otherwise occupy. In fact, interspecific encounters between flocking birds are very infrequent (Morse, 1970; Austin and Smith, 1972; Bock, 1969).

Again, making the same point as was applied to the idea of niche broadening, it seems that even if niche specialization might occur in flocks through the interaction of ecologically similar species, it would have no relevance to those which are ecologically quite dissimilar to begin with, ie., the aforementioned woodpeckers and chickadees.

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We should also remind ourselves that any idea proposing advantages to changes in foraging location, even among similar species, implicitly assumes that the species involved are generalists enough to be able to change foraging location. There can be no species-specific dependence on location-specific kinds of food items; nor can there be any species-specific restriction to specific locations because of finely tuned morphological differences. For the particular species in question these appear to be reasonable assumptions, but if they are not, then one should expect changes in foraging location to be much less likely.

The hypothesis which at this point appears most logical to me is that proposed by Moynihan (1962). If the primary advantage of flocks, whatever that is, is achieved in simple numbers of individuals, then mixed flocks of ecologically diverse species should reduce the intraspecific competition that would otherwise result. Furthermore, birds which are sedentary, permanent residents - and all of the species forming the flocks that I looked at are in this category - might also gain an additional advantage by reducing the distance they have to travel from their home territory in order to join a flock of optimal size. In this regard, I would expect that the relative numbers of individuals of each species in a flock would directly reflect the relative population density of those species.

As for the advantage of flocking itself, I will state my present inclination to accept the idea that flocking is an adaptation which permits each individual bird to invest more time in foraging or other beneficial activity, while the flock as a whole maintains the same level of alertness for predators and other hazards. In the temperate zone this

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would be of particular importance during the winter months when thermoregulatory demands on metabolism are greatest and food availability usually low. Above a certain number, however, additional birds in a flock would not significantly increase the time which each could spend foraging (Pulliam, 1973), and might increase competition to unaccaptable levels. Various studies of insectivorous bird flocks have shown an average flock size ranging from 10 to 17 (reviewed in Austin and Smith, 1972). The average from the present study falls nicely within that range.

It is also interesting to note that among the smaller birds occurring in these flocks, for whom thermoregulatory demands would be greatest, many form small, stable social units during the winter months, thus assuring the benefits of an at least minimal flock size. Family units may form the basis for these units in the Pygmy Nuthatch, though apparently not in the Black-capped Chickadee (Weise, in Ficken and Witkin, 1977; Smith, 1976) and Mountain Chickadee (Minock, 1971, 1972).

This hypothesis of increased foraging time resulting from reduced surveillance does not seem to have been explicitly tested for insectivorous woodland birds; however, in experimental groups of Starlings, birds in flocks spent less time in surveillance and detected predator models more rapidly than did solitary birds (Powell, 1974). Single Starlings in flocks of Tri-colored Blackbirds also reduced surveillance. It has also been found that individual Wood Pigeons feed at lower rates than those in flocks (Murton, 1968).

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CHAPTER V

SUMMARY

Breeding activity of the Pygmy Nuthatch was studied in an attempt to gain more information concerning the occurrence and role of helpers at the nest reported in this species (Norris, 1958).

Fifty-five birds were banded on two study areas near Missoula, Montana during February of 1976. Twelve active nest sites were subsequently located and observations continued at some of these through June, 1976. Helpers were observed at two nest sites, but at only one did it persist at the site throughout the breeding period. At the other site the helper disappeared after participating in cavity excavation over a period of two weeks.

The helper, probably a male, participated in excavation of nest cavities, delivery of nest material, feeding of the female during incubation, feeding of nestlings, and removal of fecal sacs. Participation by all three birds in a threesome was roughly equal, although the helper was less active than the male in feeding the female. The pair with helper did not feed nestlings at a higher rate than pairs without a helper. Territories were mapped for three nest sites; the area for the pair with helper was intermediate in size. Only two nest fledged successfully, one of them the one with the helper.

In sum, the data indicated that activities of the helper reduced somewhat the energy expenditure of the parents, however, the significance

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of this in terms of the future reproductive potential of the parents is unknown. It was also impossible to assess the possible benefits or risks to the helper in terms of its future reproductive potential. As for the conditions which lead to the evolution of helpers in this species, it is suggested that these include the excess of males in the population, the stable, closely knit social organization, and environmental conditions which may tax the ability of pairs to successfully raise a brood.

Additional information was collected during January of 1977 on the foraging niche of Pygmy Nuthatches, Black-capped Chickadees, and Mountain Chickadees occurring together in flocks of varying composition. This was done with the hope of being able to test alternate hypotheses that niches of ecologically similar species might narrow (Morse, 1970) or broaden (Krebs, 1973) when they forage together.

Comparisons of frequency distributions of observations of birds in six foraging zones showed no statistically significant differences when species were together or alone in the same flock, except that Black-capped Chickadees used upper zones more in the presence of Pygmy Nuthatches. The same comparisons were made when species were alone or together in the same tree, with the same result. Temperature had no effect on foraging location, or on flock size.

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LITERATURE CITED

Alexander, R. D. 1974. The evolution of social behavior, p. 325-383. In R. G. Johnston (ed.), Annual review of ecology and systematics, vol. 5. Annual Reviews, Inc., Palo Alto.

Austin, G. T., and E. L. Smith. 1972. Winter foraging ecology of mixed insectivorous bird flocks in oak woodland in southern Arizona. Condor 74: 17-24.

Balda, R. P.. and G. C. Bateman. 1971. Flocking and annual cycle of the pinyon jay, Gymnorhinus cyanocephalus. Condor 73: 287-302.

Bent, A. C. 1948. Life histories of North American nuthatches, wrens, thrashers, and their allies. U.S. Nat. Mus. Bul. 195, 435 p.

Bleitz, D. 1951. Nest of pygmy nuthatches attended by four parents. Condor 53: 150-151.

Bock, C. E. 1969. Intra- vs. interspecific aggression in pygmy nuthatch flocks. Ecology 50: 903-905.

Brackbill, H. 1971. Tufted titmouse breeding behavior. Auk 87: 522-536.

Brown, J. L. 1972. Communal feeding of nestlings in the mexican jay (Aphelocoma ultramarina): interflock comparisons. Anim. Beh. 20: 395-403.

_____. 1974. Alternate routes to sociality in jays, with a theory for the evolution of altruism and communal breeding. Am. Zool. 14: 63-80.

_____. 1975. Helpers among arabian babblers Turdoides squamiceps. Ibis 117: 243-244.

Cody, M. L. 1971. Finch flocks in the Mojave Desert. Theor. Pop. Biol. 2: 142-158.

Ficken, M. S., and S. R. Witkin. 1977. Responses of black-capped chickadees to predators. Auk 94: 156-157.

Fry, C. H. 1972. Social organization of bee-eaters and co-operative breeding in hot-climate birds. Ibis 114: 1-14.

Gaston, A. J. 1973. Ecology and behavior of the long-tailed tit. Ibis 115: 330-351.

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Gignoux, C. 1924. Nesting of pygmy nuthatches at Lake Tahoe. Condor 26: 31-32.

Knorr, O. A. 1957. Communal roosting of the pygmy nuthatch. Condor 59: 398.

Krebs, J. R. 1973. Social learning and the significance of mixed-species flocks of chickadees. Can. J. Zool. 51: 1275-1288.

Krebs, C. J., M. H. MacRoberts, and J. M. Cullen. 1972. Flocking and feeding in the great tit (Parus major). Ibis 114: 507-530.

Lazarus, J. 1972. Natural selection and the functions of flocking in birds, a reply to Murton. Ibis 114: 556-558.

Levins, R. 1968. Evolution in changing environments. Princeton Univ. Press, Princeton.

Ligon, J. D. 1970. Behavior and breeding biology of the red-cockaded woodpecker. Auk 87: 255-278.

MacArthur, R. H., and J. W. MacArthur. 1961. On bird species diversity. Ecology 42: 594-598.

Minock, M. E. 1971. Social relationships among mountain chickadees (Parus gambeli). Condor 73: 118-120.

_____. 1972. interspecific aggression between black-capped and mountain chickadees at winter feeding stations. Condor. 74: 454-461.

Morse, D. H. 1970. Ecological aspects of some mixed-species foraging flocks of birds. Ecol. Monog. 40: 119-168.

Moynihan, M. 1962. Organization and probable evolution of some mixed-species flocks of neotropical birds. Smith. Misc. Coll. 143(7): 1-40.

Murton, R. K. 1968. Some predator-prey relationships in bird damage and population control, p. 157-169. In R. K. Murton and E. N. Wright, (ed.), The problems of birds as pests. Academic Press, London.

_____. 1971. Why do some bird species feed in flocks? Ibis 113: 534-536.

Norris, R. A. 1958. Comparative biosystematics and life history of the nuthatches Sitta pygmaea and Sitta pusilla. U. of Cal. Publ. in Zool. 56: 119-300.

Powell, G. V. N. 1974. Experimental analysis of the social value of flocking by starlings (Sturnus vulgaris) in relation to predation and foraging. Anim. Beh. 22: 501-505.

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Pulliam, H. R. 1973. On the advantages of flocking. J. Theor. Biol. 38: 419-422.

Ricklefs, R. E. 1975. The evolution of co-operative breeding in birds. Ibis 117: 531-534.

Ridgway, R. The birds of North and Middle America, Part 3, U.S. Nat. Mus. Bul. 50, 801 p.

Sealy, S. G. 1973. Interspecific feeding assemblages of marine birds off British Columbia. Auk 90: 796-802.

Skutch, A. F. 1961. Helpers among birds. Condor 63: 198-226.

Smith, J. M., and M. G. Ridpath. 1972. Wife-sharing in the Tasmanian native hen Tribonyx mortierii: a case of kin-selection? Am. Nat. 106: 447-452.

Smith, S. M. 1976. Ecological aspects of dominance heirarchies in black-capped chickadees. Auk 93: 95-107.

Trivers, R. L. 1972. Parental investment and sexual selection, p. 136-179. In B. Campbell, (ed.), Sexual selection and the descent of man, Aldine Pub. Co., Chicago.

Turner, E. R. A. 1965. Social feeding in birds. Behaviour 24: 1-45.

Wilson, E. O. 1975. Sociobiology: the new synthesis. Belknap Press, Cambridge.

Woolfenden, G. E. 1975. Florida scrub jay helpers at the nest. Auk 92: 1-15.

Zahavi, A. 1974. Communal nesting by the arabian babbler. Ibis 116: 84-87.

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