SEX, AGE, INTRASPECIFIC DOMINANCE STATUS, AND THE USE OF FOOD BY BIRDS WINTERING IN TEMPERATE-DECIDUOUS AND COLD-CONIFEROUS WOODLANDS: A REVIEW

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Abstract. Most reports addressing the importance of food resources for the biology of wintering forest birds do not distinguish among sex, age, and intraspecific social dominance categories of the individuals studied, even though these can have widespread effects on the relationships between birds and their food. Here we review a selection of recent findings, emphasizing birds wintering in bark-foraging guilds in temperate-deciduous and cold-coniferous forests. We first examine how birds of different sex, age, and dominance differ in where, when, and how they look for food, and in the kinds of food they eat. We include varying tendencies to forage socially and to locate food by copying the behavior of others. We then consider how birds of different sex, age, or dominance status may store energy acquired during feeding, either externally (e.g., caching) or internally (storage of subcutaneous fat). The third section examines how stored energy is consumed by birds differing in dominance status and considers diurnal existence metabolism, nocturnal hypothermia, and roosting. This is followed by an overview of sex, age, and social dominance status and food use.

Key Words: Age; cold-coniferous forest; dominance; food acquisition; food consumption; food storage; forest birds; sex; temperate-deciduous forest.

Woodland birds have been prime material for population and community ecologists. Since the pioneering work of Hartley (1953), Gibb (1954, 1960), Betts (1955), and MacArthur (1958), dozens of reports have focused on the dimensions of species-specific niches and how such niches might overlap enough to control population sizes. Largely, it seems, because of the theoretical framework constructed by Hutchinson (1957), research on foraging niches and food has concentrated at the level of the population. Although the situation has changed enough recently to provide sufficient material for this review, the bulk of work on the foraging, feeding and physiology of terrestrial birds still lumps results for all birds of a species, regardless of sex, age or intraspecific social dominance status. Such a procedure rests on the often unappreciated assumption that niche differences among birds of different sex, age and dominance status are so minor that any population of a given species may be characterized by one realized niche. The major aim of our review will be to demonstrate that this assumption is incorrect.

We emphasize studies on bark-foraging birds wintering in temperate-deciduous and cold-coniferous forests. In practice, most of the available literature on members of this guild concerns either woodpeckers (Family Picidae) or true tits, titmice and chickadees (Family Paridae). Lesser amounts of material exist for nuthatches (Family Sittidae), creepers (Family Certhiidae), Bushtit and Long-tailed Tit (*Psaltriparus minimus* and *Aegithalos caudatus* respectively, Family Aegithalidae) and for the Goldcrest (*Regulus regulus*), Firecrest (*R. ignicapillus*) and the kinglets (Subfamily Sylviinae, Family Muscicapidae).

We begin with examples of how sex, age, and dominance status are correlated with where, when, and how such birds look for food and what they eat. We include differing tendencies to forage in the company of conspecifics and heterospecifics and to copy the food-finding activities of other foragers. In this section we first encounter a difficulty that recurs throughout the review; sex, age, or dominance status are usually autocorrelated. This makes it difficult to assign differences among birds in their relations to the food supply to any one of these variables. For example, among the parids, most of which winter in social groups larger than two, social dominance rank is highest in adult males, all males (both adult and juvenile) usually dominate all females (both adult and juvenile), and juvenile females have the lowest dominance rank (e.g., Smith 1967; Saitou 1979; Ekman 1987; Hogstad 1987a; Grubb and Waite, unpubl.). Nevertheless, we will often treat the relationships between sex, age, or dominance status and foraging separately, partly because many authors have studied only one or two of these factors.

From food acquisition, we examine how bark foragers of differing status may store energy for future use. We consider both the external storage involved with caching or hoarding food items within the home range and the internal storage of energy in the form of subcutaneous fat, as well as variations in existence metabolism during daytime, nocturnal hypothermia, and roosting.

TABLE 1. SEX-SPECIFICITY OF FORAGING BY WOODPECKERS ALONG TWO NICHE AXES

Species	Location	Tree type[a]	Sex higher in tree	Sex on smaller diameter substrate	Reference
Ladder-backed Woodpecker (*Picoides scalaris*)	Arizona	EB	F	F	Austin (1976)
Nuttall's Woodpecker (*Picoides nuttalli*)	California	DB EB	F	F	Jenkins (1979)
White-headed Woodpecker (*Picoides albolarvatus*)	California	C	M	M	Koch et al. (1970)
	California	C	M	M	Morrison and With (1987)
Downy Woodpecker (*Picoides pubescens*)	New Hampshire	DB	M	M	Kilham (1970)
	Kansas	DB	F[b]	M	Jackson (1970)
	New Jersey	DB	M	M	Grubb (1975)
	Illinois	DB	F	M	Willson (1970)
	Ohio	DB	M	M	Peters and Grubb (1983)
	Ohio (in lab)	DB		Neither	Pierce and Grubb (1981)
	Virginia	DB	M	M	Conner (1977)
Hairy Woodpecker (*Picoides villosus*)	Virginia	DB	F	F	Conner (1977)
	California	C	M	M	Morrison and With (1987)
Three-toed Woodpecker (*Picoides tridactylus*)	Norway	C	F	F	Hogstad (1976)

[a] EB = Evergreen broadleaf; DB = deciduous broadleaf; C = conifer.
[b] On live trees.

FOOD ACQUISITION: FORAGING AND FOOD

SEX

Because of noticeable differences in bill or body size between the sexes (e.g., Selander 1966) and because free-ranging birds can usually be sexed by plumage differences, sex-specific foraging in woodpeckers has been well documented. A sample of sex differences in five species of similar size, taken from studies since Selander's (1966) review (Table 1), reveals some cases in which the male forages higher in trees on thinner diameter substrates and other cases in which the opposite result holds. So far as we know, males are socially dominant to females in all the species.

Two experimental studies suggest that males may choose the more productive portion of the forest and exclude females from such sites. Pierce and Grubb (1981) showed that when isolated Downy Woodpeckers were given a choice of branch sizes under controlled laboratory conditions, both males and females foraged on 5-cm-diameter substrates most often, 2.5-, 10.0-, and 20.0-cm-diameter branches about equally, and ignored 0.5- and 1.0-cm-diameter twigs. This was approximately the range of substrates selected by free-ranging male Downy Woodpeckers in the studies cited in Table 1. Furthermore, in one study in which males were removed experimentally, females became male-like in their foraging-substrate selection, but males did not change their substrate selection after females were removed from another site (Peters and Grubb 1983). Ob-

servations by O. Hogstad (pers. comm.) suggest that sex-specific foraging is also a function of male dominance in Three-toed Woodpeckers. In a subalpine, mixed-deciduous, broadleaf, and coniferous forest in central Norway, he found that males and females often maintained separate winter territories. When in separate territories, the two sexes foraged mostly low (<5 m) on dead birch trunks with diameters >15 cm. However, when the sexes were together in a territory, females foraged mainly higher and on thinner trunks.

During the winter, those woodpeckers that are primarily insectivorous subsist chiefly on beetles and ants and, overall, the sexes do not differ markedly in their diets in any consistent fashion (Table 2). One interesting exception has been noted in Downy Woodpeckers. The old-field plant, Canadian goldenrod (*Solidago canadensis*), is host to several gall-inducing insects. Where old fields abut woodland habitat, wintering Downy Woodpeckers excavate galls and extract the larval insects (Confer and Paicos 1985, Confer et al. 1986), but the birds involved seem always to be males (J. L. Confer, pers. comm.; TCG, pers. obs.). Whether this difference occurs elsewhere and what might be the mechanism for segregation is unknown.

The reliance of certain melanerpine woodpeckers on stored mast crops during the winter will be dealt with in the section concerning food storing. It is worth noting here, though, the striking lack of sex-specific plumage in those solitary species that store food in defended "larder

TABLE 2. Sex-specificity of Diets in Wintering Woodpeckers

Species	Location	Principal foods	Differences between sexes	References
Grey-headed Green Woodpecker (*Picus canus*)	Japan	Ants, berries	Little	Matsuoka and Kojima (1985)
Black Woodpecker (*Dryocopus martius*)	Japan	Ants	Little	Kojima and Matsuoka (1985)
White-headed Woodpecker (*Picoides albolarvatus*)	California	Coleoptera, Homoptera, Hymenoptera, pine seeds	Males eat more pine seeds, fewer homopterans	Koch et al. (1970) Otvos and Stark (1985)
Hairy Woodpecker (*Picoides villosus*)	California	Coleoptera, Hymenoptera	Males eat more beetles	Otvos and Stark (1985)
Downy Woodpecker (*Picoides pubescens*)	California Illinois	Coleoptera, Hymenoptera Coleoptera, Hymenoptera	Little Males eat more ants, berries and seeds, fewer homopterans and spiders	Otvos and Stark (1985) Williams and Batzli (1979)
Three-toed Woodpecker (*Picoides tridactylus*)	Norway	Coleoptera	Little	Hogstad (1970)

hoards" rather than spreading it out through the home range in nondefended "scatter hoards," perhaps because females must defend their larder hoards against intruding males (Kilham 1978).

Much less is known about sex-specific foraging and food supplies in other types of bark-foraging birds, partially because sexual status may be difficult to ascertain. In one study of Great Tits (*Parus major*) in southern England, fewer males than females were actively looking for food at the time they were sighted (Grubb 1987). Also, males tended to forage more while solitary and less in mixed-species' flocks than did females. These differences are consistent with the idea that males monopolized the supply of hazel nuts (*Corylus avellana*) by supplanting any feeding females. Accordingly, the females turned to foraging in flocks of heterospecifics, where they presumably could reduce the proportion of time committed to vigilance for predators (Pulliam 1973).

Grubb and Waite (unpubl.) have recently examined the extent to which birds in mixed-species flocks imitate the food-finding behavior of other flock members. They made a cryptic source of mealworms available to free-ranging birds wintering in Ohio and observed how the information circulated among the members of a resident mixed-species flock. In comparing the use of this resource by males and females of four species using the same feeding site, regardless of the dominance status of birds within each sex (Fig. 1), they found that male Carolina Chickadees (*Parus carolinensis*) copied by local enhancement (*sensu* Thorpe 1963) significantly sooner than did females; such comparisons were non-significant for Tufted Titmice (*P. bicolor*), White-breasted Nuthatches (*Sitta carolinensis*) and Downy Woodpeckers. Also, the average female titmouse and woodpecker took significantly more food items than did their male counterparts; the sexes of chickadee and nuthatch did not differ. After the food source had been artificially "depleted," males and females of all four species inspected the location where the food had been about two or three times each before leaving the vicinity; none of the within-species male-female differences was significant.

Among White-breasted Nuthatches, differences in male and female foraging behavior have been observed in Colorado and Ohio. In a Colorado pine forest, McEllin (1979) found that females foraged significantly higher and on significantly smaller branches. In the deciduous forests of central Ohio in winter, males and females were statistically indistinguishable (Grubb 1982a); furthermore, no differences were detected when Ohio nuthatches were brought into the laboratory and tested in isolation (Pierce and Grubb

1981). Whether the degree of sex specificity of foraging in White-breasted Nuthatches is a response to food distribution, prevailing climate, or the interspecific social environment remains to be determined.

AGE

Age and dominance status are so tightly correlated in bark-foragers that we deferred most evidence concerning age effects to the category of dominance status. However, one finding that warrants attention here concerns differences in the abilities of adult and juvenile tits to imitate food-finding activities (Sasvari 1985). In a laboratory study, adult Great Tits copied the food-locating behavior of a "teacher" slightly sooner than did juveniles regardless of whether the teacher was a conspecific or heterospecific. Conversely, juvenile Blue Tits (*Parus caeruleus*) responded faster than did adults. Unfortunately, the results of this study are difficult to interpret because appropriate control groups were lacking. Also, every experimental group was arranged so that the "teacher" was socially subordinate to the "learner." Commonly, a potential learner stole the food item retrieved by the teacher, so that the apparent copying of food finding could have been confounded by the effects of kleptoparasitism, rather than being an unambiguous example of local enhancement.

Many woodpeckers defend territories and exist more or less independently of conspecifics during the winter. Relationships between age and foraging behavior may be more clearly disentangled from dominance status in this group, but we have not found attempts to do so.

DOMINANCE

Social dominance is a mechanism of interference competition in which one animal uses its dominant status to secure priority of use of some resource. In practice, dominance ranking among members of a social group is determined using several techniques (Dixon 1965, Smith 1976, Baker et al. 1981, Brawn and Samson 1983, DeLaet 1984, Schneider 1984). Among the woodpeckers that subsist largely on (uncached) invertebrates, males dominate females socially and apparently use their dominant status to reserve certain portions of the habitat for their own food searching. In those melanerpine woodpeckers that store mast in larder hoards, both adults and juveniles may defend small territories containing their caches. Although differences in this behavior have apparently not been examined systematically, it appears that in Ohio, beech-mast storing adult Red-headed Woodpeckers (*Melanerpes erythrocephalus*) may defend larger,
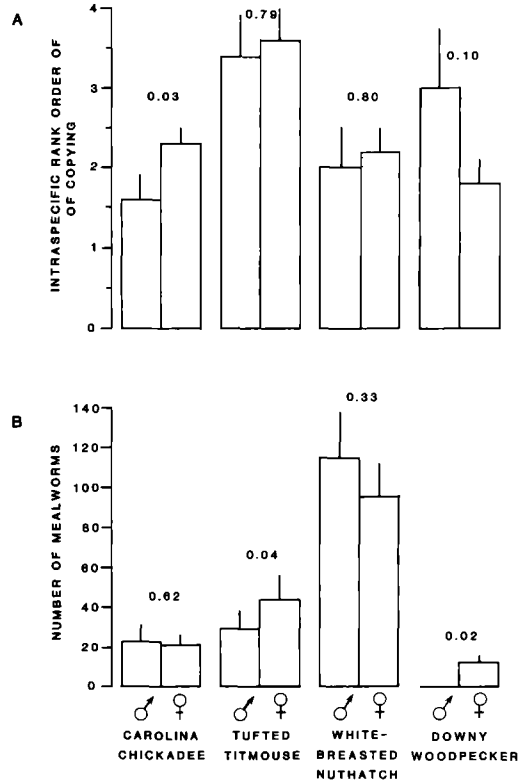

FIGURE 1.   Relationships between two measures of copying by local enhancement and sex in four species of a deciduous-forest bark-foraging guild. A. Mean rank order of copying by males and females of each species. B. Mean number of mealworms taken from the hidden supply over the course of 9 hours by males and females of each species. The vertical bars represent standard errors of the mean. All sample sizes are five, the number of different flocks studied. Numbers associated with each pair of bars are probabilities of significance derived from paired *t*-tests on the means of the sexes (from Grubb and Waite, unpubl.).

better-quality territories than juveniles (TCG, unpubl. data).

Among bark-foraging guilds, the relationships between social dominance status, food-related activity and their consequences for survival have been best studied in the Family Paridae. In virtually all species studied, birds overwinter in small parties consisting of the adult male and female that bred in the area and two or more juveniles (birds of the year). Usually juveniles disperse from their natal sites in late summer and early fall (Greenwood and Harvey 1982), so that the members in any one group are seldom parents and offspring. The number of males and females is usually the same within any given flock, and even during the early winter flock members appear to
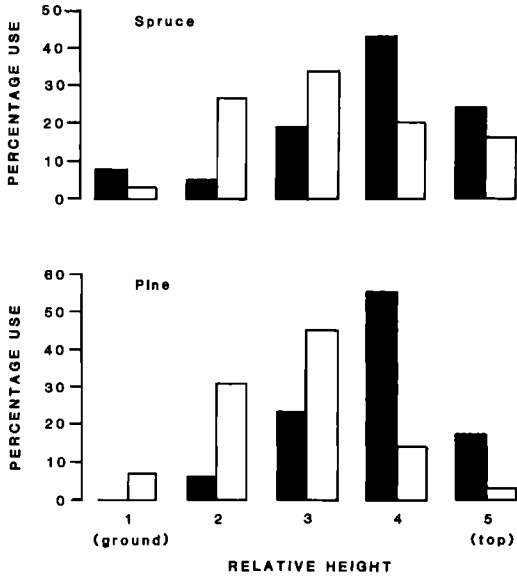
FIGURE 2.   Relative heights at which dominant (solid bars) and subordinate (open bars) Willow Tits foraged in spruce and pine trees in Sweden during December (after Ekman 1987).

be organized into male-female pairs. By midwinter, the strongest attachments are between males and females that will form breeding pairs the following spring (Ficken et al. 1981). Thus, although all males in a flock dominate all females in "one-on-one" encounters, females mated to high-ranking males attain some additional social status, which, for instance, may confer more ready access to a food supply (Dixon 1963, 1965; Ritchison 1979; Hogstad 1987a; also see below). In addition to birds integrated into sedentary nonbreeding flocks, some individuals remain as "floaters." Most are apparently juveniles of very low rank (Ekman 1979); some incorporate themselves into flocks over the course of the winter, as group members die (Ekman et al. 1981).

Ekman and his colleagues have performed an impressive investigation of the relationship between social dominance status and foraging activity in Willow Tits (Parus montanus) wintering in southwest Sweden; and Hogstad (1987c) has conducted similar work in central Norway. In both locations, the birds live in flocks that defend group territories against conspecifics throughout the winter. In Sweden, a flock usually begins in the fall with two dominant adults and two subordinate juveniles, while in Norway the two dominant adults are joined by four juveniles.

The members of the flock gain in feeding efficiency by pooling their vigilance time. However, the gain is not symmetrical, because in Swe-

den the dominant birds force subordinates to forage lower in the more open parts of conifers (Ekman 1987; Fig. 2), where they are more susceptible to predation (Ekman 1987, Ekman et al. 1981). The subordinates compensate by raising their level of vigilance beyond that of the more protected adults, but not to the level shown by birds foraging only in pairs. Thus, among juveniles, foraging with dominant conspecifics is favored over leaving their company to forage as a pair.

Hogstad (1987c) performed a removal experiment with Willow Tits that supported the hypothesis that social dominance was responsible for age-specific foraging niches. When adults were removed from flocks, the juveniles moved significantly higher in pine trees to forage in adult-like locations. In a similar experiment in Norway, Hogstad (1988) positioned feeders in a treeless bog 1, 3, 5, 10, and 20 m from the edge of a forest. Dominant tits tended to visit only those close to the woodland, forcing subordinates to feeders out in the bog. When the feeders 10 m and 20 m from cover were the only ones baited, only juveniles visited them. In general, the level of vigilance increased as Willow Tits used feeders farther from the forest, a finding consistent with the notion that predation risk increased with distance to cover. In juvenile females, however, the most subordinate category of bird, birds spent more time scanning the environment from a feeder 1 m from the woodland than from feeders 3 m and 5 m out, perhaps because they were trying to avoid supplanting attacks by dominants that preferred the feeder closest to the forest.

Waite (1987a, b) proposed that some of the vigilance time of subordinate birds is used to keep track of dominant flock mates. In laboratory experiments involving both Tufted Titmice and White-breasted Nuthatches, the dominant member of a pair scanned its surroundings more when kept in isolation than when housed with the subordinate member. However, the subordinate bird of a pair was more vigilant in the company of the dominant conspecific than when alone.

The study on imitative foraging in mixed-species flocks (Grubb and Waite, unpubl.) that we cited above provided insight into how intrasexual dominance status can affect food finding. In five different flocks tested in five different woodlots in central Ohio, a strong tendency existed for the dominant male or dominant female Carolina Chickadee, Tufted Titmouse, or White-breasted Nuthatch to take the first food item from a cryptic source. In Carolina Chickadees the dominant male or female took a food item after seeing the fewest similar items taken by other birds. In male titmice and female nuthatches, the

dominant individual took significantly more food items over the course of the experiment than did individuals of lower social rank. The same trend occurred for male and female chickadees, female titmice and male nuthatches, but was not significant.

Earlier we mentioned that the pair bond maintained in winter flocks appears to be stronger in the dominant than in more subordinate birds. This may influence the way birds find food (Fig. 3). In both Carolina Chickadees and Tufted Titmice, the two birds of the alpha pair first used the hidden food supply more quickly than did the male and female of subordinate pairs.

EXTERNAL FOOD STORAGE

Caching or hoarding behavior has been shown in 12 of 170 bird families (D. F. Sherry 1985). Two major patterns have been distinguished. Larder-hoarding, the storage of food items in large central caches in an animal's home-range, is best demonstrated by the Acorn Woodpecker (*Melanerpes formicivorous*; MacRoberts and MacRoberts 1976). Among scatter-hoarders, those animals that store food items at dispersed sites, the most studied in North America is the Clark's Nutcracker (*Nucifraga columbiana*; Tomback 1982). Several studies of scatter-hoarders have found nonoverlapping distributions of caches for individual birds but have not associated caching behavior with age, sex and/or dominance status (Cowie et al. 1981, Sherry et al. 1982, Clarkson et al. 1986).

SEX AND DOMINANCE

Because nuthatches (Family Sittidae) are typically sexually dimorphic in plumage, this group lends itself to the study of sex-specific caching behavior. Because sex, age and dominance are autocorrelated, we have combined consideration of sex and dominance. In the European Nuthatch (*Sitta europaea*), males dominate females, and adults dominate juveniles of the same sex (B. Enoksson, unpubl.). Within mated pairs of White-breasted Nuthatches in North America, males are dominant over females (Grubb 1982a).

Moreno et al. (1981) studied the hoarding behavior of one pair of European Nuthatches during autumn and winter in central Sweden. They found that the male stored food items at the periphery of the pair's communally held territory significantly more frequently than did the female, and that the female placed significantly more of her caches under lichen than did the male. The female was more generalized in all niche dimensions of hoarding, perhaps indicating the female's subordinate status, causing her to broaden the use of storage sites due to interference competition from her mate. On five occasions, they
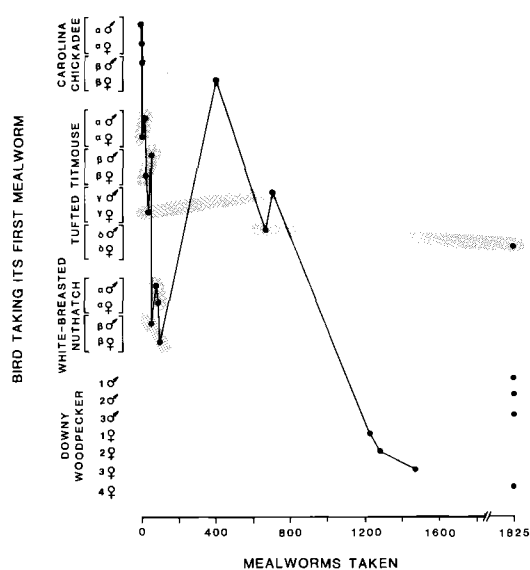

FIGURE 3. Copying by local enhancement in 23 deciduous-forest, bark-foraging birds recorded as having been in attendance during an experimental trial at one woodland site. The independent variable was the number of mealworms that other birds had removed from a cryptic supply before each bird took its first mealworm from the same place. Birds connected by stippling were mated pairs. The gamma female Tufted Titmouse and the four Downy Woodpeckers denoted by the closed circles at the far right of the figure never copied (from Grubb and Waite, unpubl.).

observed the male apparently watching the female store a food item. Each time, the male removed it and then cached it at a different site. Together, the observation of cache covering by the female and the instances of stolen caches suggest that the members of the pair did not share their caches.

Sexual differences in caching behavior of European Nuthatches have also been found by B. Enoksson (unpubl.) who found that males made longer visits to a feeder and also took more seeds per visit. This pattern was not influenced by age.

In a study of diurnal caching rhythms in free-ranging White-breasted Nuthatches, Woodrey and Waite (unpubl. ms) found that caching intensity for both the dominant male and female nuthatches at a feeder was negatively correlated with time of day. Within each alpha pair, the female cached a higher proportion of kcal than did the male (Fig. 4). In another context, Hogstad (1987c) observed five instances of adult male Willow Tits kleptoparasitizing seeds newly cached by juvenile conspecifics. Four of the seeds were eaten immediately, while the fifth was removed and cached elsewhere.
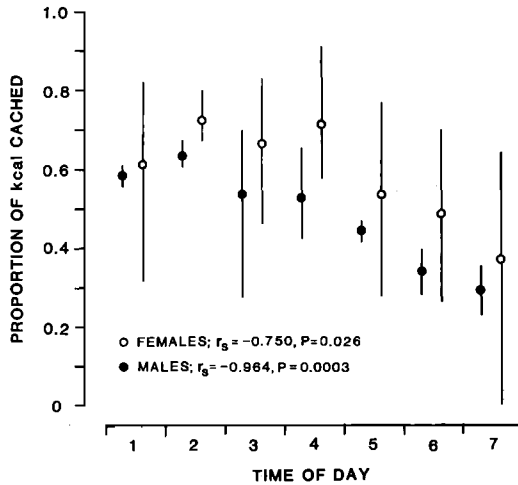
FIGURE 4. The relationship between time of day and the proportion of kcal cached by dominant male and female White-breasted Nuthatches. The circles represent means for a given septile and the vertical bars represent ranges. The P-values are for one-tailed Spearman's rank correlation tests (after Woodrey and Waite, unpubl.).

AGE

Few studies have addressed age-related differences in caching behavior. Enoksson (unpubl.) found that adult European Nuthatches collected more seeds per visit to a feeder than did juveniles during summer. Between summer and autumn, however, the juveniles increased both the number of seeds collected per unit time and the total number taken per visit. Changes in dominance status did not fully explain the observed changes because not all juveniles were subordinate to all adults. Enoksson concluded that juveniles became more proficient foragers later in the year, due both to increasing experience and to enhanced ability to handle seeds, the latter possibly associated with growth of young birds' bills.

Haftorn (1956) documented the development of scatter-hoarding in young tits. In July, juvenile Willow Tits (*Parus montanus*) and Crested Tits (*P. cristatus*) were not yet proficient in caching. Of 15 attempts by birds of both species combined, 47% were unsuccessful, largely because the young birds tended to remove a newly cached item immediately and transplant it to another site. By August, however, only 14% of attempts were unsuccessful and only 24% of newly cached seeds were transplanted.

INTERNAL FOOD STORAGE

Winter fattening is a common phenomenon in small birds in the temperate zone (King 1972; Blem 1976; Lehikoinen 1986, 1987). Although the literature is extensive (e.g., Blem 1976), few studies have distinguished among sex, age or dominance categories.

SEX

From studies of passerines in Finland, Lehikoinen (1986, 1987) proposed that the increase in minimum morning weights, a measure of the degree of winter fattening, was determined by seasonally variable risk of starvation, and that temperature and photoperiod were proximate factors that mainly regulated the daily weight amplitude. The least winter fattening was found in the Certhiidae, Sittidae and Passeridae, and in those parids with predictable food availability as a result of their hoarding behavior. Although age and sex were unrelated to fat levels in most species, Lehikoinen did find sexual differences in the Greenfinch and the Blue Tit (Table 3). In both species males showed a significantly greater increase in winter weight than did females.

AGE

Crested and Willow tits wintering in Finland showed age related differences in fat loading (Table 3). In both species, juveniles gained significantly more weight than adults. Because adults are dominant (Ekman and Askenmo 1984), the age differences in winter fattening cannot be explained by social constraints (Lehikoinen 1986), but may be connected with their habit of caching food (Haftorn 1956). Caches are presumably a predictable food resource for adults and decrease the benefit of fat deposition.

Lima (1986) modelled the body mass of small wintering birds as a trade-off between the risks of predation and starvation. Because of age differences in dominance, juveniles could be forced into areas of increased predation risk (e.g., Ekman and Askenmo 1984, Hogstad 1987c), and attain lower fat levels than adults. Lehikoinen's (1986) finding of heavier weights in juveniles seems to be inconsistent with this prediction.

FOOD CONSUMPTION: BIOENERGETICS AND ROOSTING

Food stored externally in caches or internally as subcutaneous fat is consumed by birds during the diurnal and roosting phases of their diel cycles. In light of the differences in food acquisition and storage among sexes, ages and dominance categories described above, comparison of intraspecific categories at the physiological level could prove worthwhile. Unfortunately, such comparisons have not been made, so we combine discussion of the three category types.

DIURNAL METABOLISM

Roskaft et al. (1986) studied the daytime metabolic rates of Great Tits captured in winter near Trondheim, Norway, and kept for one week in

TABLE 3. INCREASE IN THE WINTER WEIGHT AND THE SEASONAL MINIMUM MORNING WEIGHT IN PASSERINE SPECIES RETRAPPED IN SOUTHWEST FINLAND. WEIGHT IS DEFINED AS THE MEAN OF THE LOWEST INDIVIDUAL MORNING WEIGHTS IN MARCH THROUGH APRIL (AFTER LEHIKOINEN 1986)

Species	Group	Weight (g)	Increase of winter weight			Increase (%)	P[a]
			X̄	SE	N		
Great Tit (*Parus major*)	Male	18.4	0.88	0.073	125	4.8	***
	Female	17.3	0.86	0.114	85	5.0	***
Blue Tit (*P. caeruleus*)	Male	11.0	0.98	0.089	46	8.9	***
	Female	10.5	0.48	0.154	14	4.6	**
Coal Tit (*P. ater*)	All	8.9	0.70	0.210	3	7.8	0
Crested Tit (*P. cristatus*)	Adult	11.3	0.08	0.147	8	0.7	ns
	Juv.	10.9	0.54	0.014	8	5.0	**
Willow Tit (*P. montanus*)	Adult	11.1	0.45	0.136	11	4.0	**
	Juv.	10.8	0.72	0.093	32	6.7	***
Greenfinch (*Carduelis chloris*)	Male	26.5	3.33	0.472	21	12.6	***
	Female	28.3	3.09	0.798	10	10.9	**
Bullfinch (*Pyrrhula pyrrhula*)	Male	32.3	4.45	1.242	9	13.8	**
	Female	28.5	6.92	1.331	5	24.3	**
Yellowhammer (*Emberiza citrinella*)	Male	28.9	1.50	0.216	29	5.2	***
	Female	28.7	1.47	0.276	22	5.1	***

[a] P values taken from paired *t*-tests are denoted as ns if not significant, 0 if <0.1, ** if <0.01, and *** if <0.001.

an indoor aviary prior to testing. They found a positive correlation between metabolic rate and the width of a tit's breast-stripe. After noting that social dominance is correlated with and, indeed, may be indicated to other birds by the width of a Great Tit's breast-stripe, Roskaft et al. concluded that dominant birds in nature appear to have a higher energy requirement than subordinate birds. However, because the breast stripe is wider in males than in females and wider in adult males than in juvenile males (A. G. Gosler, pers. comm.; TCG, pers. obs.), Roskaft and his colleagues may have actually demonstrated a sex-related rather than dominance-related effect.

Similar results from a study of Willow Tits in central Norway (Hogstad 1987b) are more convincing, because the compositions of test flocks were natural and because the design included an experimental manipulation of dominance status. Metabolic rates were determined for Willow Tits newly captured from six different flocks. Each flock consisted of six birds in the usual arrangement for parids, with the numbers of males and females being equal, in this instance divided into one adult pair and two juvenile pairs. All males dominated all females and within a sex the adults dominated the juveniles. This order of dominance was almost perfectly correlated with the order of metabolic rates, which were highest in the most dominant male and lowest in the most subordinate female. Interestingly, when the dominant male was removed from a flock, the formerly beta male assumed the dominant position and his metabolic rate increased to that of the previous dominant. No other bird in the hierarchy changed its metabolic rate. Furthermore,

when a female was removed, no other bird, female or male, changed its metabolic rate (Fig. 5). Within a flock of wintering Willow Tits (and, apparently, in most other parids as well; e.g., Dixon 1963) the dominant adult male is most involved with defending the group's territorial boundaries and in most cases he will breed in the area in which his flock overwintered. Hogstad interprets his results as suggesting that the alpha bird of a flock requires a high metabolic rate to support the level of aggressive behavior required in boundary defense.

Related to physiological differences among sex, age, and dominance categories is the study of Silverin et al. (1984) on the hormonal levels of Willow Tits wintering in Ekman's study area east of Gothenburg. Within each flock of four birds (adult male and female and juvenile male and female), juvenile females were found to have higher levels of testosterone and corticosterone than adult birds and a higher level of dihydrotestosterone than juvenile males and adult birds, perhaps indicating that juvenile females—the most subordinate of the four age-sex categories—were the most stressed (O. Hogstad, pers. comm.).

NOCTURNAL METABOLISM AND HYPOTHERMIA

Much is known about nocturnal hypothermia in bark-foraging birds, but little of this information bears on differences among sex, age and dominance classes. We draw the following major conclusions from Reinertsen's (1983) review. (1) Nocturnal hypothermia involves the controlled reduction in nighttime body temperatures to values <10°C below body temperature during the day. (2) Such a reduction results in a 10% re-
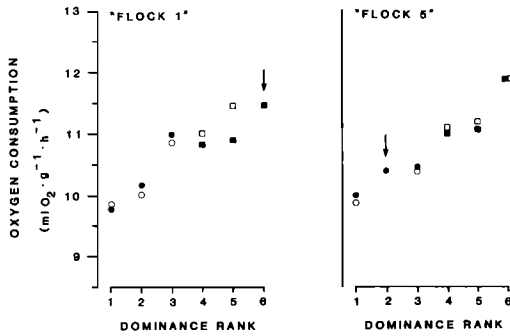
FIGURE 5. Oxygen-consumption rates of males (squares) and females (circles) in two Willow Tit flocks in Norway. Solid and open symbols, respectively, denote oxygen consumption rates before and after the bird designated by the arrow was removed from each flock (redrawn from Hogstad 1987b).

duction in consumption of stored energy. (3) Among members of the bark-foraging guild, nocturnal hypothermia is well-known among parids, having been documented in the Black-capped Chickadee and in Siberian Tits (*Parus cinctus*), Great Tits, and Willow Tits, as well as the Carolina Chickadee (Munzinger 1974). (4) No other taxa of the bark-foraging guild of temperate-deciduous and cold-coniferous woodlands appear to have been tested for nocturnal hypothermia; a search among the Picidae, Sittidae, Sylviinae and Certhidae could be successful. During midwinter, one of us (TCG) has encountered roosting Downy Woodpeckers that appeared to be in a torpid state. (5) Among the parids in which hypothermia has been shown, no published information exists for sex, age and dominance classes about either the tendency to enter hypothermia or the degree to which the body temperature is allowed to drop. However, Hogstad reports (pers. comm.) that although dominant male Willow Tits had the highest metabolic rate during the day, the metabolic rates of dominant males and subordinate females were the same while they roosted at night.

Certain results with Willow Tits suggest that the extent of nocturnal hypothermia may vary with sex, age or dominance status. The body temperature of a roosting bird is the result of an interaction among the ambient temperature, the bird's insulative properties, and its metabolic rate. In Willow Tits implanted with temperature-reading radio transmitters, it was found that the reduced resting metabolic rate and, therefore, the extent of steady-state hypothermia were apparently maintained at constant values from shortly after roosting time until arousal the following morning. Furthermore, the extent of reduction

in metabolic rate was related to a bird's fat store at roosting time. The leaner the bird, the lower the resting metabolic rate and the more profound the hypothermia (Reinertsen and Haftorn 1983). Thus, if birds of different sex, age or dominance rank go to roost with characteristically different energy reserves, as outlined above, the extent of hypothermia could vary according to their status.

ROOSTING

Wintering bark-foraging birds usually roost under some sort of protective cover. Birds wintering in northern forests generally roost in tree cavities (Kendeigh 1961) and some may burrow through snow cover to roost in underground rodent burrows (e.g., Willow Tit; Zonov 1967). Cavity roosting confers a considerable savings in metabolic expenditure because of the reduction in radiative and convective heat loss (e.g., Askins 1981). Where nighttime temperatures are warmer, birds of "cavity roosting species" and other members of the bark-foraging guild may sometimes roost outside of cavities (Red-bellied Woodpecker [*Melanerpes carolinus*], Saul and Wassmer [1983]; Red-cockaded Woodpecker [*Picoides borealis*], Hooper and Lennartz [1983]). Downy Woodpeckers wintering in Ohio dug cavities in artificial snags made of polystyrene, a highly insulative material, and roosted there throughout the winter (Grubb 1982b, Peterson and Grubb 1983), whereas only one bird of the same species wintering in the considerably milder conditions of east Texas did so (R. N. Conner, pers. comm.).

Whether in cavities or in the cover of heavy foliage or snow, most bark foragers roost in isolation, but huddling in clumps is not unknown, particularly among birds of small body size in which surface-to-volume ratios, and consequently metabolic costs, are high (e.g., Long-tailed Tit [*Aegithalos caudatus*], Lack and Lack [1958]; Bushtit [*Psaltriparus minimus*], Smith [1972]). A flock of 29 Bushtits wintering on the University of Washington campus normally maintained an individual distance of about 5 cm while roosting. However, in a 2-week period one January, during which nighttime temperature fell below freezing—an unusual occurrence in Seattle—virtually all of the birds packed tightly against one another along a perch (Smith 1972).

Little evidence points directly to differences among sex, age and dominance classes with respect to roosting. An exception is an analysis of nestbox use by Great Tits in the Netherlands. During the time of leaf-fall in late October and early November Kluyver (1957) found that Great Tits stopped roosting in the crowns of trees and began to compete for nest boxes. Sixty-nine per-

cent of adult males, 63% of adult females, 54% of juvenile males, but only 31% of juvenile females were found roosting there, a ranking that parallels dominance status. Winkel and Winkel (1980) reported similar asymmetries among Great Tits roosting in nest boxes in Germany. Kluyver (1957) concluded that competing to roost in nest boxes was adaptive because, although the overall overwinter survivorship of males (50.0%) was significantly greater than that for females (45.5%), enhanced survivorship for both sexes (67%) occurred in males and females that roosted there.

In both of these studies Great Tits were constrained to accept or reject a roost site positioned by the experimenter. It could be instructive to compare sites chosen by sex, age and dominance classes when a variety of potential sites is available. For example, Downy Woodpeckers in central Ohio were provided with trios of artificial trees or snags made from polystyrene cylinders (Grubb 1982b). Each trio was comprised of cylinders 1.21, 2.42, and 3.63 m in length, positioned vertically in a woodlot and arranged in an equilateral triangle 3 m on a side. Cylinders were checked at daily intervals until it was determined that a complete cavity had been excavated in one of each trio. While in 10 of 16 cases birds dug cavities in the snag of intermediate (2.42 m) height, there was some indication that the sexes differed in their snag preferences, with males tending to roost higher. Although the significance of the differences in cavity-site choice between the sexes of this woodpecker remains obscure, the results of this one controlled test suggest that the sexes may segregate along a niche dimension for cavity height.

CONCLUSIONS

Population and community ecologists are interested in determining why only a certain number of species or individuals occur in any given area. As the abundance and distribution of animals are at least partially the consequences of the animals' behavior, the behavioral ecologist must seek the behavioral mechanisms underlying ecological patterns, recognizing that these are affected by sex, age and social dominance. The meager literature supporting our survey prompts the conclusion that analysis has only begun.

The substantial return to be gained by studying the food-related behavior of sex, age and dominance categories is demonstrated by the pioneering studies of Ekman and his colleagues on Willow Tits and the subsequent manipulative experiments of Hogstad on the same species. It seems that population size in wintering Willow Tits, before it is pruned by predation, is set by some sort of cost-benefit analysis performed by juveniles on whether to remain in the company of a dominant pair. At least some of the factors in the "analysis" done by these young birds appear to be the harshness of the climate, presence of heterospecifics, and density of the food supply. In no other taxon or geographical locale does such a depth of analysis exist; the prospects for comparative research seem bright.