ECOLOGY OF NON-BREEDING SOCIAL SYSTEMS OF *PARUS*

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ABSTRACT.—Most parids of temperate regions during the non-breeding season associate in small, generally non-kin, flocks. The typical pattern is discrete social units, often with stable composition and high coherence among the members. Exceptions are the Great Tit (*Parus major*) and the Blue Tit (*P. caeruleus*) with a more loosely organized system of "basic flocks" which may intermingle, and where space is divided into overlapping ranges rather than territories. This dichotomy in social organization may be linked to food hoarding where low tolerance toward conspecifics is associated with the value of protecting hoarded food. Discrete social units in territories are known only among hoarding species. The selective advantages for conspecific flocking are unclear. Benefits of flocking involving lower vigilance time have been verified, but predator protection can also be obtained from flocking with heterospecifics as well as conspecifics. Further, costs of being of low rank suggest that joining a flock with dominants may be a poor option for subordinates. Flocking in parids may be associated with steep gradients in quality of the habitat, causing a sharp reduction of options that are alternatives to settling as a low-ranking flock member. Habitat constraints should then be a main ecological factor affecting flocking among parids, and flock size may vary with habitat structure.

Over the years descriptions of social patterns of many different *Parus* species have accumulated. The social organization in individually marked populations has been studied for more than a dozen species. My intention is to do a synthesis of this information to identify general patterns. Parids of temperate regions may be a suitable group in which to study ecological factors relating to the evolution of sociality. Few species live in kin groups (Ekman, in press), hence the evolutionary approach will not be plagued by difficulties in separating direct from indirect fitness components operating through relatives.

Most parid studies describe general social patterns, and objectives have differed considerably as social organization is such a broad concept. Pioneering studies of social dominance outside the laboratory were done with parids (Hamerstrom 1942, Odum 1942). Recent studies have involved more systematic approaches to testing ecological theories (e.g., Saitou 1978, Drent 1983, Smith 1984, Ekman 1987, Hogstad 1988).

PATTERNS

The Dichotomy

All *Parus* species studied so far are social to a varying extent during the non-breeding season (Table 1). Among species studied, there is a strong

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TABLE 1

SIZE OF NON-BREEDING SOCIAL UNITS IN THE PARIDAE. * = DATA FROM STUDIES WITH INDIVIDUALLY COLOR-BANDED BIRDS. N = NUMBER OF UNITS STUDIED

Species		Number of members	(N)	Location	Season	Reference
Black Tit (*Parus niger*)	*	2.7–3.9	(19)	South Africa	Pre and post-breed.	Tarboton 1979, 1981
Black-capped Chickadee (*P. atricapillus*)	*	6–8	(?)	Massachusetts, USA	Winter	Wallace 1941
	*	5.0	(4)	Minnesota, USA	Jan	Hartzler 1970
	*	3.3	(42)	Michigan, USA	Feb–Mar	Robins & Raim 1970
	*	6.4	(23)	New York, USA	Autumn	Glase 1973
	*	6.6	(?)	Massachusetts, USA	Autumn	Smith 1976
	*	7.7	(3)	Pennsylvania, USA	Winter	Samson & Lewis 1979
	*	8.1	(37)	Massachusetts, USA	Winter	Smith, in press
		3.3	(16)	Illinois, USA	Winter	Brewer 1961
		4–8	(?)	Wisconsin, USA	Winter	Weise & Meyer 1979
Blue Tit (*P. caeruleus*)		2[a]	(?)	S. Sweden	Dec–Feb	Alerstam et al. 1974
		7[a]	(?)	Gotland, Sweden	Dec–Feb	Alerstam et al. 1974
		2.5	(4)	S. Sweden	Jan–Feb	Ulfstrand 1975
		6.6	(207)	Oxford, England	Winter	Morse 1978
Boreal Chickadee (*P. hudsonicus*)		6	(?)		Winter	Cade 1953
Bridled Titmouse (*P. wollweberi*)		4.1	(?)	Arizona, USA	Sep–Dec	Austin & Smith 1972
Carolina Chickadee (*P. carolinensis*)	*	4.2	(13)	Texas, USA	Winter	Dixon 1963
	*	6	(1)	Pennsylvania, USA	Sep–Mar	Smith 1972
		3.3	(21)	Illinois, USA	Winter	Brewer 1961
Coal Tit (*P. ater*)	*	3	(2)	W. Sweden	Winter	Ekman unpubl.
		2[a]	(?)	S. Sweden	Winter	Alerstam et al. 1974
		4–23[a]	(?)	Gotland, Sweden	Winter	Alerstam et al. 1974
		4.1–6.7	(?)	Japan	Winter	Nakamura 1975

TABLE 1
CONTINUED

Species		Number of members	(N)	Location	Season	Reference
Crested Tit (*P. cristatus*)		2.6	(26)	S. Sweden	Jan–Feb	Ulfstrand 1975
		3.2	(38)	Middle Norway	Jan–Mar	Hogstad 1978
		1.5	(115)	Oxford, England	Winter	Morse 1978
	*	2.9	(28)	W. Sweden	Autumn	Ekman 1979
	*	3.3	(6)	Belgium	Winter	Jans 1980
		2[a]	(?)	S. Sweden	Winter	Alerstam et al. 1974
		2.3	(32)	S. Sweden	Jan–Feb	Ulfstrand 1975
		1.5	(24)	Middle Norway	Jan–Mar	Hogstad 1978
		1.5	(4)	N. Sweden	Mar	Alatalo & Carlsson 1987
Great Tit (*P. major*)	*	3.2–8.4	(?)	Japan	Winter	Nakamura 1975
	*	4.8	(169)	Japan	Winter	Saitou 1978
		→50	(?)	England	Winter	Hinde 1952
		20[a]	(?)	S. Sweden[b]	Dec–Feb	Alerstam et al. 1974
		2[a]	(?)	S. Sweden[c]	Dec–Feb	Alerstam et al. 1974
		2.3	(15)	S. Sweden	Jan–Feb	Ulfstrand 1975
		1.8	(108)	Oxford, England	Winter	Morse 1978
		1.4–1.6	(15)	N. Sweden	Mar	Alatalo & Carlsson 1987
Marsh Tit (*P. palustris*)	*	2	(?)	Oxford, England	Winter	Southern & Morley 1950
	*	2–3	(?)	Germany	Winter	Löhrl 1950
	*	2	(?)	Germany	Winter	Ludescher 1973
	*	2–9	(?)	S. Sweden	Sep–Mar	Nilsson & Smith 1988
		2[a]	(?)	S. Sweden	Dec–Feb	Alerstam et al 1974
		1.3	(3)	S. Sweden	Jan–Dec	Ulfstrand 1975
		1.7	(130)	Oxford, England	Winter	Morse 1978

TABLE 1
CONTINUED

Species		Number of members	(N)	Location	Season	Reference
Mountain Chickadee (P. gambeli)	*	4	(3)	Utah, USA	Winter	Dixon 1965
	*	3	(4)	Utah, USA	Winter	Minock 1971
Plain Titmouse (P. inornatus)	*	2	(?)	California, USA	Winter	Dixon 1949, 1956
Siberian Tit (P. cinctus)		2.6	(48)	N. Sweden	Mar	Alatalo & Carlsson 1987
Sombre Tit (P. lugubris)		2	(2)	Yugoslavia	Autumn	Löhrl 1966
Tufted Titmouse (P. bicolor)	*	2–6	(?)	Pennsylvania, USA	Winter	Gillespie 1930
	*	8	(1)	Ohio, USA	Winter	Nice 1930
	*	3	(1)	Tennessee, USA	Winter	Laskey 1957
	*	4.8	(4)	Pennsylvania, USA	Sep–Apr	Condee 1970
	*	6.7	(3)	Pennsylvania, USA	Winter	Samson & Lewis 1979
	*	2.9	(14)	Missouri, USA	October	Brawn & Samson 1983
Varied Tit (P. varius)	*	3.0	(11)	Japan	Oct–Nov	Higuchi 1976
	*	1.9	(10)	Japan	Nov	Higuchi 1976
Willow Tit (P. montanus)	*	2	(3)	Oxford, England	Winter	Foster & Godfrey 1950
	*	2–4	(?)	Germany	Winter	Ludescher 1973
	*	4.1	(32)	W. Sweden	Dec	Ekman 1979
	*	6	(10)	Middle Norway	Winter	Hogstad 1987a
		2[a]	(?)	S. Sweden	Dec–Feb	Alerstam et al. 1984
		1.6	(17)	S. Sweden	Jan–Feb	Ulfstrand 1975
		2.3–2.4	(?)	Japan	Winter	Nakamura 1975
		3.7	(54)	Middle Norway	Jan–Mar	Hogstad 1978
		2.9	(117)	N. Sweden	Mar	Alatalo & Carlsson 1987

[a] Median values.
[b] Deciduous habitat.
[c] Coniferous habitat.

TABLE 2
CHARACTERISTICS OF WINTER SOCIAL SYSTEMS AMONG PARIDS

"Basic flock" system	Discrete flocks
Social units mingle	Non-mixing flocks
Non-exclusive ranges	Flock areas exclusive
Exchange of individuals	Stable group composition
Site-related dominance	Linear hierarchies
Small–large (→50) units	Small units (mostly <10)

bias towards the temperate zones of Europe and North America. Two main patterns emerge among these species studied in individually marked populations, where detailed information is available on associations among individuals and their use of space. One characteristic of most temperate zone parids is discrete units with high coherence among members which reside within non-overlapping territories. The other, represented by the Great Tit, and probably also the Blue Tit, has a looser organization (Saitou 1978) characterized by semi-stable flocks which often intermingle and live in overlapping home ranges (Table 2). These differences pertain to the established population cohort where individuals are resident within defined areas. Both systems have in common floaters which move between flocks.

For some species listed in Table 1, such as the Boreal Chickadee (*Parus hudsonicus*), the Bridled Titmouse (*P. wollweberi*), the Siberian Tit (*P. cinctus*), and the Sombre Tit (*P. lugubris*), the information is still too meager to allow any conclusions concerning where they fit in this system.

Discrete Units and Territories

Group cohesion and space use. — The majority of temperate zone *Parus* species live in tightly knit social units using a common exclusive area ("discrete units, territories"; Table 3). The coherence is high among permanent members of a social unit. This pattern is shown in the social organization of the Black-capped Chickadee (*P. atricapillus*), the Carolina Chickadee (*P. carolinensis*), the Coal Tit (*P. ater*), the Crested Tit (*P. cristatus*), the Marsh Tit (*P. palustris*), the Mountain Chickadee (*P. gambeli*), the Plain Titmouse (*P. inornatus*), the Varied Tit (*P. varius*), and the Willow Tit (*P. montanus*) (Table 3).

The social organization of the Tufted Titmouse (*P. bicolor*) fits the description above, but this species probably should be considered separately as there is evidence for kin associations during winter (Tarbell

TABLE 3
FEATURES OF THE NON-BREEDING SOCIAL ORGANIZATION OF PARIDS

Species	Units		Exclusive ranges (c)	Dominance structure (d)	Juvenile dispersal (e)	References—evidence for
	Discrete (a)	Stable (b)				
"Basic flock" system						
Blue Tit	no	no	no	?	yes	Colquhoun 1942—abc Goodbody 1952—e
Great Tit	no	no	no	site-dependent	yes	Brian 1949—d Goodbody 1952—e Dhondt 1978—e Saitou 1978—abc Greenwood et al. 1979—e Drent 1983—cd
Discrete flocks						
Black Tit	yes	yes	yes	?	not always	Tarboton 1979, 1981
Black-capped Chickadee	yes	yes	yes	linear	yes	Butts 1931—e Wallace 1941—abc Smith 1967—c Hartzler 1970—abc Glase 1973—abcd Holleback 1974—e Smith 1976—abd Weise & Meyer 1979—d Ficken et al. 1981—ab Smith 1984—abc
Carolina Chickadee	yes	yes	yes	linear	yes	Brewer 1961—d Dixon 1963—abcde Smith 1972—abcd

TABLE 3
CONTINUED

Species	Units Discrete (a)	Stable (b)	Exclusive ranges (c)	Dominance structure (d)	Juvenile dispersal (e)	References—evidence for
Coal Tit	yes	yes	yes	?	yes	Ekman unpubl.
Crested Tit	yes	yes	yes	?	yes	Ekman 1979
Marsh Tit	yes	yes	yes	linear	yes	Southern & Morley 1950—abc Nilsson & Smith 1985—e, 1988—abcde
Mountain Chickadee	yes	yes	yes	linear	?	Dixon 1965—abcd Minock 1971—abc
Plain Titmouse	yes	yes	yes	pair territorial	yes	Dixon 1949, 1956
Tufted Titmouse	yes	yes	yes	linear	not always	Gillespie 1930—ab Nice 1930—c van Tyne 1948—e Laskey 1957—e Condee 1970—abc Samson & Lewis 1979—abc Brawn & Samson 1983—abcd Tarbell 1983—e
Varied Tit	yes	yes	yes	?	yes sometimes late	Higuchi 1976—abc Higuchi & Momose 1981—e
Willow Tit	yes	yes	yes	linear	yes	Foster & Godfrey 1950—c Ludescher 1973—c Ekman 1979—abce Hogstad 1987a—c

1983). The Tufted Titmouse appears to differ in other respects as well. Flock territories are exclusive, but individual members seem to prefer different subareas (Samson and Lewis 1979, Brawn and Samson 1983). As a corollary, coherence within Tufted Titmouse groups appears lower (Brawn and Samson 1983) relative to other group-territorial parids.

Age and sex.—Sex ratios have generally proved to be equal in these discrete social units (Dixon 1963, Glase 1973, Ekman 1979, Brawn and Samson 1983, Smith 1984) suggesting that pairs form before winter. Winter groups are sometimes formed around the nucleus of a former breeding pair remaining in their territory (Dixon 1963, Glase 1973, Ekman 1979, Brawn and Samson 1983), but winter groups in which several adult pairs occur in the same unit have been reported (Glase 1973). Still, pure juvenile groups may also form in territories without survivors from the previous winter (e.g., Nilsson and Smith 1988).

Winter groups are dominance-structured. Several workers have reported what appears to be a general pattern where males dominate females, and within sexes adults generally dominate juveniles (Dixon 1963, 1965; Glase 1973; Brawn and Samson 1983; Hogstad 1987a), although there may be exceptions to such a clearcut dominance structure. There is at least one example where linear and stable dominance relationships did not develop in a Carolina Chickadee population (Mostrom pers. comm.).

Juvenile dispersal takes place shortly after fledging (e.g., Nilsson and Smith 1985), and most recoveries of juveniles which have become permanent winter group members are made at a distance of just a few territories from their natal territory (Weise and Meyer 1979, Ekman and Askenmo 1984, Nilsson 1988). Further, the overwhelming majority of permanent members in coherent and discrete winter groups become established within a month after independence (Weise and Meyer 1979, Ekman, in press, Nilsson and Smith 1988). Longer movements may occur, but the general rule appears to be early establishment. Early establishment as a permanent member of a winter group may have survival value as new members are recruited from the bottom of the rank order (Nilsson and Smith 1988), suggesting strong competition for positions in hierarchies. Still early establishment and prior occupancy may not always bring benefits through high rank, as there are populations of Carolina Chickadees where early settlers have no advantage (Mostrom pers. comm.).

Although a large fraction of juveniles rapidly become permanent members of a winter group some juveniles do not become permanent members of a specific group but remain "floaters" (Ekman et al. 1981, Smith 1984, Nilsson and Smith 1988). Apparently some floaters finally find a vacant position and become a permanent member of a flock (Smith 1984, Ekman,

in press, Nilsson and Smith 1988). In the Crested Tit, the Marsh Tit, and the Willow Tit, the cohort of floaters finally disappears during the autumn (Ekman et al. 1981, Nilsson and Smith 1988), while they are present throughout the winter in Black-capped Chickadees (Smith 1984).

Although patterns appear remarkably constant among species with this social organization, some studies of the Black-capped Chickadee (Brittingham pers. comm., Howitz pers. comm.) and the Carolina Chickadee (Mostrom pers. comm.) suggest substantial intraspecific plasticity. One problem in interpreting this variability is to sort out the effect of supplemental food which has been used in many North American studies. Food provisioning can profoundly affect social organization (Ekman 1987) and introduce intraspecific variability.

The Loose "Basic Flock" System

In winter the Great Tit and the Blue Tit are organized in a looser system than the majority of temperate parids. A description of the main characteristics of the social organization of the Blue Tit is provided by Colquhoun (1942) and for the Great Tit by Saitou (1978, in press) and Drent (1983). Great Tits belong to "basic flocks" (Saitou 1978) composed of either several birds or just a pair (Drent 1983). The area used by "basic flocks" appears more like a home range than an exclusive territory. "Basic flocks" readily intermingle when they meet and utilize a communal area. A similar pattern seems likely among Blue Tits as well, or quoting Colquhoun, ". . . when breeding is over flocking occurs, territories are invaded and, superficially, have ceased to exist" (1942:239). Space thus appears not to be as rigidly partitioned into exclusive areas among Great Tits and Blue Tits as in parids with discrete social units.

Great Tits do not adhere strictly to their late summer range and may abandon it for long periods in the winter (Perrins 1971, Drent 1983). In this respect, they differ from parids organized in discrete units within exclusive territories. The latter species are sedentary and stay within their winter ranges even during adverse conditions. Linked to the organization in a "basic flock" system is site-dependent social dominance (Brian 1949, de Laet 1984), so that the outcome of interactions shifts in favor of the bird on home ground. It is not clear whether Blue Tits also have this site-dependent dominance. Low-ranked individuals bred farther away from the feeders (Colquhoun 1942), but they may just as well have been subordinates that were evicted. Aggressive behavior by Great Tits and Blue Tits during the non-breeding season may serve primarily the purpose of securing priority to resources within a bird's home range rather than excluding intruders (Drent 1983). Due to lack of defense of an area, Great

Tit and Blue Tit flocks have a potential of becoming much larger than those of most parids and flocks of about 50 conspecifics (Great Tits) have been reported (Hinde 1952).

Juveniles of Great Tits or Blue Tits also disperse shortly after fledging (Goodbody 1952), but they often spend their first winter without becoming a regular member of a "basic flock" and only settle permanently their first breeding season (e.g., Dhondt and Schillemans 1983).

CAUSATION—A TENTATIVE SKETCH

The route to sociality among parids consists of several steps. I will consider the following ones: (1) whether to become sedentary, (2) to share a range with conspecifics, or (3) to be gregarious. Several questions may thus be asked in order to understand the evolution of sociality; these questions may be relevant to the diversity of social organizations on different levels. They may refer to differences between species, populations of a species or individuals within a population. The prime goal will be to identify the factor(s) generating the main dichotomy of discrete and non-discrete social units within the genus *Parus*. To understand each system further, we have to identify the options open to individuals and the factors determining their value.

Exclusive Ranges—the Impact of Hoarding

The main dichotomy between a discrete and a loose "basic flock" system among parids is a matter of exclusive ranges. Non-overlapping ranges will necessarily entail that units do not intermingle. Exclusive access to resources usually has been interpreted in terms of economic defendability (Brown 1964). In parids, there is no apparent difference in the distribution of resources for species using exclusive and those having overlapping ranges. This pattern does not suggest large differences in economic defendability. Species with territories and discrete flocks are dependent largely on sparse and widely scattered insect food (Palmgren 1932; Haftorn 1954, 1956a, b; Betts 1955; Gibb 1960; Jansson 1982). In such cases the costs of defense are low relative to the value of the resource.

Economic defendability generally is assumed to vary mainly with costs of defense (Brown 1964), but many parids improve the value of their resource by hoarding large amounts of food in summer and autumn (Butts 1931; Bent 1946; Löhrl 1950; Haftorn 1953, 1954, 1956a, b, 1974; Laskey 1957; Lawrence 1958; Löhrl 1966; Davis et al. 1973; Higuchi 1977; Alatalo and Carlsson 1987). The value of resources then largely depends on the time and energy invested in accumulating supplies. Efforts devoted to hoarding are only rewarded if the hoarder retrieves its supplies, and exclusion of potential scroungers should be strongly favored (Andersson

TABLE 4

THE LINK BETWEEN FOOD HOARDING AND NON-BREEDING SOCIAL ORGANIZATION

Social system	Species	Hoarding		Reference
		Yes	No	
"Basic flock"	Great Tit		*	Perrins 1979
system	Blue Tit		*	Perrins 1979
Discrete	Black-capped Chickadee	*		Butts 1931, Lawrence 1958
flocks	Coal Tit	*		Haftorn 1956a
	Crested Tit	*		Haftorn 1954
	Marsh Tit	*		Löhrl 1950
	Mountain Chickadee	*		Haftorn 1974
	Plain Titmouse	*		Davis et al. 1973
	Tufted Titmouse	*		Bent 1946, Laskey 1957
	Varied Tit	*		Higuchi 1977
	Willow Tit	*		Haftorn 1956b
	Σ	9	2[a]	

[a] Significant difference in social organization between hoarders and non-hoarders ($P < 0.02$, Fishers exact probability test).

and Krebs 1978). There is also a link to sociality, as parids that hoard are organized in discrete territorial units (Table 4). Territoriality could conceivably be an evolutionary response to the risk of scrounging. This inference is based on a correlation, and as such does not prove any causal relationship. Further, it is not clear whether hoarding has evolved separately for each *Parus* species or if its occurrence represents a single evolutionary event. However, territoriality in an unrelated hoarding species, such as the Eurasian Nuthatch (*Sitta europea*) (Enoksson 1988, Matthysen, in press), strongly suggests that the relationship between hoarding and sociality is a real one. The hypothesis of relationship between hoarding and a social system suggested in Table 4 needs further testing. The prediction is that the social organization of hoarding species such as the Boreal Chickadee, the Siberian Tit, and the Sombre Tit should conform to a pattern with discrete units within exclusive territories.

It should be noted that hoarding is only a behavioral response for efficient resource use, and conditions generating hoarding are the factors fundamentally driving the social system. Temporary abundance of a rich food resource can be one factor favoring hoarding (Sherry et al. 1982), but little is presently known about all factors which generate hoarding, especially the long-term hoarding reported for other parids (Haftorn 1956c).

It is important to note that hoarding can account only for exclusive ranges, but not for the formation of groups. Additional individuals will

merely increase the risk for scrounging. One of the unsolved riddles of parid biology is how hoarding can be reconciled with sociality. The memory capacity demonstrated for Marsh Tits and Black-capped Chickadees, allowing individuals to remember their own specific hoarding sites (Shettleworth 1983, Sherry 1984), is a possible mechanism making hoarding within groups possible. Individually specific foraging sites as in Black-capped Chickadees (Glase 1973) and Willow Tits (Ekman and Askenmo 1984) are another possibility, although the evolutionary consequences of such foraging have not been evaluated.

Gregariousness

All parids are social despite some differences in social organization. Formation of kin groups is confined to a few species, and sociality for most parids must therefore be associated with factors other than kin selection.

Kin groups. — Prolonged juvenile association with the parents is known only for the Black Tit (*P. niger*) (Tarboton 1981), Tufted Titmouse (van Tyne 1948, Laskey 1957, Tarbell 1983), and the Varied Tit (Higuchi and Momose 1981), and this association is only known to lead to cooperatively breeding units in the Black Tit (Tarboton 1981) and the Tufted Titmouse (Tarbell 1983). The frequency of juvenile retention and cooperative breeding in these species is not known. It might be relatively common in the Tufted Titmouse, while it seems clear that not all Black Tit groups consist of relatives.

The ecology of flocking. — Ecological benefits of gregariousness have generally been coined in terms of either improved predator protection like the "many eyes" hypothesis (Pulliam 1973) or improved efficiency at locating food such as local enhancement (Thorpe 1963). Direct measurements of the value of gregariousness in parids are still in their infancy and there are hardly any actual field data. From aviary experiments, it is known that Great Tits do find clumped food faster through the information conveyed during social foraging (Krebs et al. 1972). Further, free-ranging Willow Tits allocated less time to scanning for predators per capita the more conspecifics in the group (Ekman 1987), as is found in a number of other studies (e.g., Powell 1974, Caraco 1979).

Predator protection. — Sociality allows savings in vigilance time without suffering increments in risk of predation (Caraco 1979). Still, there must be a substantial risk of predation in the first place for increased protection to have any value. Further, the forager must be stressed for time in order to benefit from reduced vigilance time. These conditions may well both be met during the non-breeding season. The information available on predation by Sparrowhawks (*Accipiter nisus*) on Great Tits in Britain

(Perrins and Geer 1980) and by Pygmy Owls (*Glaucidium passerinum*) on Willow and Crested tits in Sweden (Ekman et al. 1981, Ekman 1986) both suggest that predation risk can be substantial. Evidence for predation on North American parids is meager (e.g., Brawn and Samson 1983), but predation risk has not been thoroughly studied. For instance the Saw-whet Owl (*Aegolius acadicus*), the Screech Owl (*Otus asio*) and the North American Pygmy-Owl (*Glaucidium gnoma*) in the West are potential winter predators on small passerines. Conceivably there is a shortage of foraging time for temperate parids in winter. Great Tits and Black-capped Chickadees start foraging earlier relative to sunrise and cease foraging later relative to sunset in winter as compared to summer (Kluijver 1950, Dunnet and Hinde 1953, Kessel 1976). Additional food also roughly doubled winter survival for Willow and Crested tits (Jansson et al. 1981) by mitigating their time stress in balancing foraging against predator vigilance (Ekman 1987). Extra food allowed Willow Tits to abandon exposed foraging sites requiring high vigilance levels, and to reallocate time from vigilance to searching (Ekman 1987), thus providing the mechanism linking starvation and predation risks, and demonstrating the value of savings in vigilance time through gregariousness. Conceivably other tit species make the same time profit, although it has not been studied in detail. It is known only that predation risk will influence access to feeders for Great and Blue tits (de Laet 1985, Hegner 1985). Predation may be more substantial among parids than recognized, and it may be an important factor shaping their social behavior.

Willow Tits save vigilance time not only from flocking with conspecifics but also by associating with other tit species, Goldcrests (*Regulus regulus*) and Treecreepers (*Certhia familiaris*). Heterospecifics in such mixed-species flocks are generally considered to substitute for conspecifics as predator protection at low competition cost. The number of coexisting *Parus* species available for predator protection could thus be one determinant of conspecific flock size. The data available to test this possibility are limited and not very conclusive. Group size increases for the Willow Tit from two in Germany and Britain, through four in Sweden to six in Norway, as the number of congeners decreases (Fig. 1). The substantial increase in Coal Tit group size from the Swedish mainland to the island of Gotland (Alerstam et al. 1974) also parallels a decline in the number of coexisting congeners from two to none.

There is a tendency for larger group size in North American parids. For instance, the number of conspecifics in a flock ranges from six to eight in the Black-capped Chickadee and the Tufted Titmouse (Fig. 2). Larger conspecific groups may be interpreted as a compensation for the fewer coexisting *Parus* species in North America (Lack 1971) to uphold the
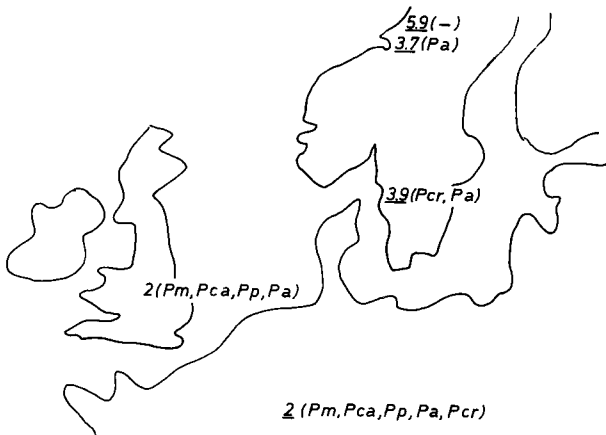
FIG. 1.   Regional trends in the group size of the Willow Tit in northern Europe in relation to the number of coexisting congeners. Pa = Coal Tit, Pca = Blue Tit, Pcr = Crested Tit, Pm = Great Tit and Pp = Marsh Tit. Data from Foster and Godfrey (1950), Ludescher (1973), Ekman (1979), Hogstad (1987c).

joint vigilance to predators. Still, other factors such as habitat complexity and predator skill should contribute to variations in group size as an anti-predator device. More data are badly needed for a more rigid test of whether the set of coexisting congeners influences sociality. The only data available actually trying to quantify the influence of conspecific and heterospecific company for the value of sociality do not show any decisive advantage of heterospecific company (Hogstad 1988), and the higher cost of conspecific company further remains to be shown.

   Social foraging. — Social foraging may reduce the risk of energetic shortfall (Caraco 1981; Pulliam and Millikan 1982; Clark and Mangel 1984, 1986; Ekman and Rosander 1987) which could be another reason for parids to be social during the non-breeding season when survival is the main fitness component. Benefits of social foraging in reducing starvation risk require clumped food distribution where foraging individuals convey information about its location (Local enhancement—Thorpe 1963). It is, however, doubtful if food of parids in general is clumped sufficiently for social searching to bring benefits. A diet which is largely insectivorous (Palmgren 1932; Haftorn 1954, 1956a, b) consists of food items which cannot be shared and which often occur sparsely and spaced out (Jansson and von Brömssen 1981). Information about the location of food should then be of little value. Response to information about the location of food has been verified in the Great Tit (Krebs et al. 1972) which is largely
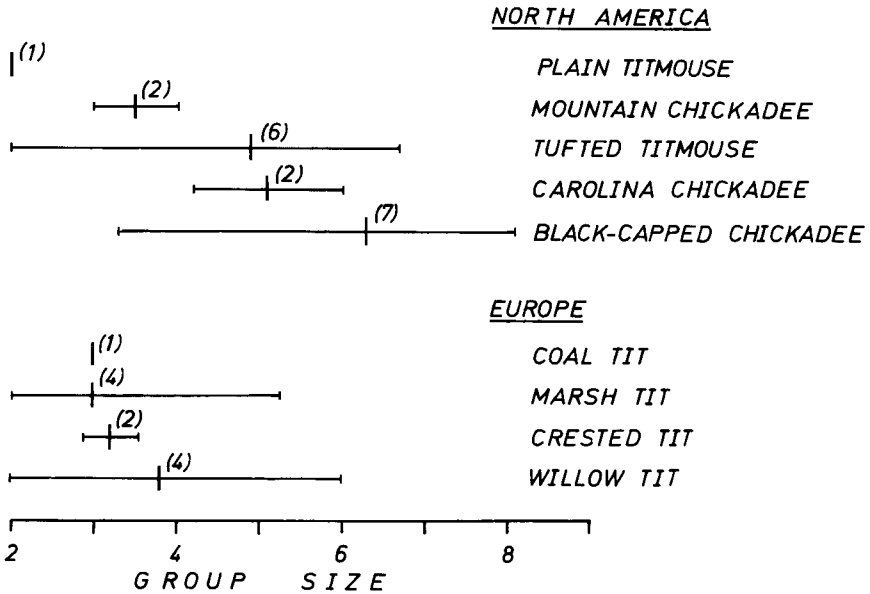
NORTH AMERICA

|$^{(1)}$ PLAIN TITMOUSE

├──┼──$^{(2)}$ MOUNTAIN CHICKADEE

├────────────┼──$^{(6)}$──────┤   TUFTED TITMOUSE

├──────┼──$^{(2)}$────┤   CAROLINA CHICKADEE

├────────────┼──$^{(7)}$──────────┤ BLACK-CAPPED CHICKADEE

EUROPE

|$^{(1)}$ COAL TIT

├──┼──$^{(4)}$─────────┤   MARSH TIT

├┼──$^{(2)}$┤   CRESTED TIT

├──────┼──$^{(4)}$─────┤   WILLOW TIT

2   4   6   8
        G R O U P   S I Z E

Fig. 2. Group size of European and North American parids. Grand mean of means (from Table 1) and their range. Significantly larger group size for temperate North American parids (excluding the Plain Titmouse; $P < 0.05$, Mann-Whitney test).

granivorous in winter, a diet where information transfer can be used. The beech mast that Great Tits largely feed on in winter occurs in local clumps that are sufficiently rich to be shared. Yet, it has only been verified that Great Tits respond to information conveyed by flock mates about the location of food. If social foraging is to be considered a selective advantage of sociality, adjustments of flock size are required as the social strategy minimizing starvation risk changes with food abundance (Caraco 1981; Pulliam and Millikan 1982; Clark and Mangel 1984, 1986; Ekman and Rosander 1987). Some empirical evidence suggest that such diverse animals as finches and spiders actually are able to make these adjustments (Ekman and Hake 1988, Uetz 1988).

OPEN OR CLOSED SYSTEM?

Characteristics. —Enhanced predator protection and food-finding efficiency are factors making sociality beneficial but whether individuals will coalesce into social units also depends upon the options available. The decision animals face then differs according to whether there is a limit on the number of social units or not, corresponding to closed and open

systems in the terminology of Cohen (1971). In closed systems there is a limit to the number of social units an area can accommodate, while there is no such limit in open systems. Once all social units have been established in a closed system, the only alternative option to leaving the habitat for unestablished individuals will be to settle within already existing units. Formation of social units in an open system is a matter of whether it brings any additional benefits, as the individual still has access to the habitat, while membership in a social unit within a closed system may serve as a "ticket" to enter the habitat.

Implicit in the concept of a closed system is that dominants can enforce its priority of access to resources on subordinates. Individuals of low social rank may then be forced to accept a fitness loss relative to being the solitary owner of an area, if their only option is to leave for a habitat of inferior quality. The free access to habitat in open systems does not necessarily exclude aggressive interaction over resources, but they must not result in exclusion of individuals or unequal access to resources. In open systems solitary individuals are able to impose themselves upon existing flocks, and the evolutionary stable size will therefore be larger than optimal (Sibly 1983, Pulliam and Caraco 1984).

Field data. — Members of Great Tit and Blue Tit flocks with their looser organization, appear to have access to their habitat as assumed for open systems (Colquhoun 1942, Saitou 1978, Drent 1983). Site-dependent dominance (Brian 1949, de Laet 1984) also reconciles aggressive behavior with equal access to resources if each member has its own area of dominance. Individuals then do not fight over exclusive right to an area but merely priority to resources within it (Drent 1983).

Discrete and coherent groups residing within territories, which appears to be the prevalent pattern among temperate zone parids, match the requirements of a closed system. Removal experiments have confirmed that established groups within such systems prevent new groups from being formed and new members from joining in at least the Crested Tit, the Tufted Titmouse, and the Willow Tit (Samson and Lewis 1979, Ekman et al. 1981). The lack of replacements in the Black-capped Chickadee, as reported by Samson and Lewis (1979), does not exclude a closed system. The lack of replacements, except by local birds, only shows that there are no floaters around to fill vacancies within flocks. Still, not only floaters but also flock subordinates could be prevented from taking up territories of their own in a closed system. This was the case in a Crested Tit population where removal of flocks resulted in splitting of neighboring groups with subsequent emigration to the vacated area by subordinates (Fig. 3). A similar experiment with Willow Tits confirms that it is subordinates which depart (Ekman, in press). Such replacement not only
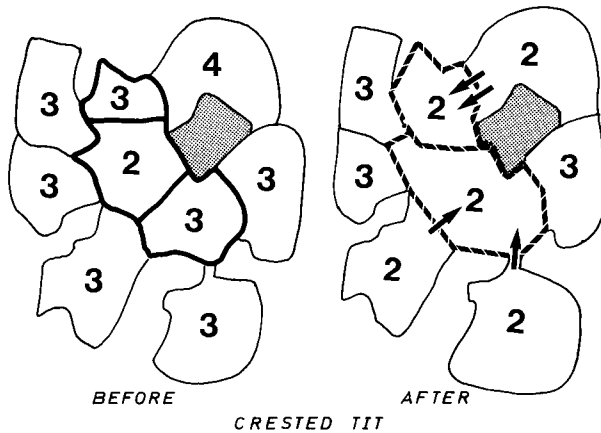
FIG. 3. Redistribution of group members in a Crested Tit population after an autumn removal (Ekman et al. 1981). Bold lines = borders of vacated territories, stippled bold lines = borders after replacement, arrows = the origin of immigrant birds, shaded = lake, figures give group size before removal and after replacement. Territory size around 20 ha.

shows a limit to the number of groups but also that group membership could be a second-rate choice to subordinates. Subordinate Willow Tits not only choose to depart, but their survival also improved after the break-up of groups (Ekman et al. 1981). Hence, the long-term costs of increased local competition within groups obviously outweighs short-term benefits of gregariousness, for instance predator vigilance (Ekman 1987).

Subordinate options. — Parid societies organized in discrete flocks living within territories are dominance-structured, and hierarchies are as a rule linear and stable. The ecological and evolutionary consequences of this dominance structure are poorly known. Survival is better for high-ranked flock members among Black-capped Chickadees (Smith 1984) and Willow Tits (Ekman and Askenmo 1984, Koivula and Orell 1988), the only parids with data available for individuals of known rank. A problem plaguing attempts to relate social rank to survival is that individuals rise within the dominance hierarchy as they come of age, and rank will, therefore, be correlated with age and experience. A comparison of the recruitment probability of juvenile Willow Tits shows that the probability of being recruited as a breeder is higher for more dominant individuals (Ekman, in press). Such age-specific comparisons avoid the risk that survival effects are due to differences in age or experience. The rank effect on survival is at least partly the effect of rank-related differences in tree use (Ekman and Askenmo 1984, Hogstad 1987c) where dominants have priority to more protected sites (Ekman 1987). Individual differences in habitat use are

known also among Black-capped Chickadees (Glase 1973), although their ecological consequences have not been studied.

The information is too meager for generalizations, but available data suggest that subordinates do less well than dominants within the parid group system. Data for more species are needed to determine whether this is a general pattern. Metabolic costs of maintaining a high rank (Røskaft et al. 1986, Hogstad 1987b) are apparently not sufficient to outweigh benefits of resource priority for dominant Willow Tits, and rank does not appear to be maintained in a frequency-dependent balance as a mixed ESS. As subordinates within parid groups consistently appear to be younger individuals (Dixon 1963, 1965; Glase 1973; Brawn and Samson 1983; Hogstad 1987a), all present evidence suggests that they are "hopeful dominants" (West Eberhard 1975) suffering a transient fitness loss. As subordinates rise in rank with age, it is perfectly conceivable that in a long-term perspective the *expected* lifetime fitness is equal for all members in a group, although at present the possibility cannot be excluded that among those which die as subordinate juveniles, there are poorer phenotypes that had a reduced probability of ever becoming dominants.

When to settle. — The rapid establishment of groups after independence (Nilsson and Smith 1988, Ekman, in press) is one characteristic of the parid group system. How long do dispersing juveniles wait until they finally settle? One good reason for them to settle as early as possible might be the benefit of being able to hoard for a long time. There is no point in hoarding other than in areas the individual expects to use later on. Still, the benefit of becoming a permanent member of a group early leaves us with the problem of explaining individual differences in the time of establishment in a group as some juveniles apparently defer to become members. Are such individuals precluded from groups or do they refrain from settling? Early establishment may also have its cost in a dominance-structured society, as the individual then runs a risk of forgoing the opportunity of finding an even better position. As higher rank positions fill up, the value of becoming established declines, as high-rank positions will then only become available as group members die. Assume that the probability for a flock member of rank i to survive is P. The probability for a vacancy of rank i is then $1 - P$, which also represents the probability for an established individual of rank i + 1 to take this rank position. Now assume that juveniles have the option of remaining as floaters rather than settling with rank i + 1 (lower i means higher rank). If we assume that there are N groups available per floater, their corresponding probability of finding a vacancy becomes $1 - P^N$. When will it pay to wait rather than to settle immediately? The survival probability, P(S), of a group member of rank i for time t is

$$P_i(S(t)) = \exp(-\Phi_i t) \tag{1}$$

assuming that the mortality rate, Φ_i, depends on social rank (f will be used for floaters) in line with the empirical evidence. In a continuous time model the probability for a vacancy of rank i to become available in time t (=waiting time) is:

$$P(\text{vacancy }(t)) = 1 - \exp(-N\Phi_i t) \tag{2}$$

where $N = 1$ for the special case of established group members. I assume that established subordinates can advance only within their own group. We can see from this expression that the probability of finding a vacancy increases with time, N and mortality risk.

We can now compare survival of individuals which settle as permanent flock members with those that remain floaters. To do this, we first assume that there is a time horizon T, in this case up to the next breeding season, available for settling. An individual gains from remaining a floater for time t only if

$$P_f(S(t))P(\text{vacancy }(t))P_i(S(T - t)) > P_{i+1}(S(t))P(\text{vacancy}(t))P_i(S(T - t)) \tag{3}$$

After rearranging this expression and substituting equations 1 and 2 for the P:s we obtain

$$\frac{1-\exp(-N\Phi_i t)}{1-\exp(-(\Phi_i t)} > \frac{\exp(-\Phi_{i+1}t)}{\exp(-\Phi_f t)}. \tag{4}$$

Now assume there is a survival cost to being a floater. As the mortality risk in the lowest rank position available (Φ_{i+1}) increases towards that of floaters, this inequality can be satisfied. The penalty of being a floater may then eventually become so small that it is outweighed by the enhanced survival value from better prospects of finding a vacancy of higher rank as a floater. If there is no survival cost of being a floater, it is trivial that floaters always do better because of their possibility of finding a better position of higher rank, and we would expect no subordinates to settle as permanent flock members.

From the left side of equation 4, we see that the compensation for costs of being a floater comes from being able to inspect more flocks to find out whether a vacancy of a dominant position has emerged. The more juveniles that settle, the more groups there will be available per floater with a higher probability of finding a vacancy of higher rank. The value of being a floater is, therefore, frequency-dependent. To compensate

for larger survival costs of being a floater, the probability of finding a high rank vacancy must increase, which requires a shift in the balance towards fewer floaters in the population. Notice that the actual value of the vacancy does not affect this decision. One consequence of this frequency-dependence is that group size may not be limited in the sense that floaters are actively precluded from becoming flock members. A rank-related access to resource as verified for Willow Tits (Ekman 1987) may be sufficient for the alternatives to benefit the bird.

The frequency-dependence in the payoff from being a floater does not necessarily imply a mixed ESS where group membership and being a floater are two routes of becoming recruited with equal success. A mixed ESS argument requires that floaters do not become recruited from the bottom of dominance hierarchies. Otherwise, floaters will never do better than existing subordinates, and will not be able to compensate later for their poor present survival by finding vacancies of high rank. Floaters recruited from the bottom will always be at a disadvantage compared to established members, as these have priority to higher rank positions that may become open. The evidence for this pattern is conflicting. Recruitment from the bottom of rank orders occurs in the Black-capped Chickadee (Hartzler 1970). A strong prior occupancy overriding both age and size has further been confirmed for the Marsh Tit (Nilsson and Smith 1988), and rank appears to be the effect of seniority in a number of parids (Dixon 1963, 1965; Glase 1973; Smith 1976; Brawn and Samson 1983). Prior occupancy implies that already established birds have priority for emerging vacancies and that floaters are recruited from the bottom of the rank order and that they can never expect the fitness of established subordinates. The generality of prior occupancy has been questioned by observations among Black-capped Chickadees (Smith 1984, 1987) and Carolina Chickadees (Mostrom pers. comm.), suggesting that floaters can be recruited to intermediate rank positions.

Presumably the parameters affecting the decision between taking a low-ranking position in a group and remaining a floater change during the season. Such seasonal dynamics could account for the eventual settling of floaters (Ekman et al. 1981, Nilsson and Smith 1988). For instance, the penalty for not having stored food is likely to increase as energy stress becomes more severe towards winter.

Group size in a closed system. —Subordination appears to entail a penalty in parids, judging by the limited data from the Black-capped Chickadee and especially from the Willow Tit. Then why do subordinates accept remaining as group members when they, like the Willow Tit, would do better in their own territories? One possibility is that the option for sub-

ordinates is not to be a dominant owner of a territory within a closed system, but to leave for a habitat of inferior quality. Flocking may be treated as a habitat selection game where crowding in the optimal habitat is traded against low competitor density in suboptimal habitat (Pulliam and Caraco 1984). Subordinates in dominance-structured population may then choose to stay for lack of good alternatives (Ekman 1989). Subordinates should be more willing to stay and accept the cost of low rank the steeper the gradient in habitat quality. Studies of performance in different habitats could thus be important to our understanding of the social system in parids. In the Plain Titmouse subordinates spend the winter in suboptimal habitat (Dixon 1949). Conceivably, the small social units (pairs) in the Plain Titmouse could be due to a gently sloping habitat gradient. In the Willow Tit, subordinates never venture into open farmland, which is the only alternative to coniferous forest (Ekman 1979). An abrupt habitat transition may then be a basic factor behind flock formation in this species (Ekman, in press).

The importance of social dominance was realized early in studies of parid sociality (Hamerstrom 1942, Odum 1942). Studies of the social organization of parids during the non-breeding season have shown that to understand sociality within dominance-structured populations it is not sufficient to focus on the evolutionary benefits of gregariousness. It is also crucial to understand the constraints imposed by the system itself and the options open to different individuals. The social system is part of the environment within which traits operate and are selected. Whether a *Parus* species is a hoarder or not generates different conditions affecting group size. The explanation of group formation among parids through habitat constraints has its counterpart for cooperative breeders (Koenig and Pitelka 1981, Emlen 1982). Then why do more parid species not have kingroups? The habitat saturation leading to juvenile retention and group formation in many species depends on both demography and habitat structure. Juvenile dispersal should only be postponed under conditions of high adult survival when the probability of finding a vacancy is poor. Survival among temperate parids may, however, be low enough for sufficient numbers of vacancies to emerge for juvenile dispersal to be adaptive (Ekman, in press). Even if the habitat is not sufficiently saturated after breeding for juvenile retention to evolve, this fact is perfectly conceivable with a habitat saturated with winter territories as a *consequence* of juvenile dispersal. A shortage of space for territories in the optimal habitat may result in an overflow of unestablished individuals into alternative habitats, but a steep gradient in the quality of habitat at the habitat transition will increase the benefits of remaining in the saturated habitat. Such steep

habitat gradients, in combination with saturation of optimal habitats, could be a requirement for group formation in parid species when subordination has a cost.

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