

## Winter Territoriality and Irruptive Behavior in the Paridae

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Irruptions are irregular mass movements performed outside the main breeding area of a species (Svårdson 1957, Bock and Lepthien 1976). These movements commonly involve juveniles or individuals with poor competitive ability (Smith and Nilsson 1987) and often are attributed to large-scale variation in food supplies or weather conditions that lead to population booms (Bock and Lepthien 1976, Perrins 1979). Irruptions may be produced after years of good food production followed by a successful breeding season (Ulfstrand 1963, Bejer and Rudemo 1987, Hussell 1996). However, anomalous seed-crop production may be interpreted only as the proximate cause for the irruptive behavior of parids (Ulfstrand 1962) and fringillids (Jenni 1987). Large seed crops increase resource availability and may lead to high population densities, which in turn may force some individuals to make long movements (Ulfstrand et al. 1974). However, some related species of parids with similar foraging behavior and habitat selection (e.g. Great Tit [*Parus major*] and Marsh Tit [*P. palustris*], or Coal Tit [*P. ater*] and Crested Tit [*P. cristatus*]; Cramp and Perrins 1993) show very different responses to variation in food-crop size, resulting in specific irruptive tendencies.

Few studies have been conducted on mechanisms of irruptive behavior (but see Bock and Lepthien 1976). In this study, I used comparative methods to examine possible links between winter territoriality and irruptive behavior in parids. Differences in nonbreeding social systems (i.e. degree of winter territoriality) can affect spacing mechanisms of individuals (Matthysen 1990). Therefore, an increase in the degree of winter territoriality likely would reduce the benefits of irruptive behavior. I also assessed the relative importance of annual fecundity in the predicted relationship between winter territoriality and irruptive behavior, because high fecundity favors offspring production and therefore may lead to irruptive episodes.

*Methods.*—I gathered data from the literature on winter territoriality and irruptive tendency for 13 species of parids and the White-breasted Nuthatch (*Sitta carolinensis*), which I used as an outgroup (see Appendix). Whether a species was considered to be irruptive was based on information in Cramp and Perrins (1993) and Harrap and Quinn (1996). Al-

though some degree of geographic variation in irruptive behavior exists in parids, my coarse-grained classification allowed high confidence that the data were representative of the true tendency for each species. Within parids, similar observations on territorial behavior have been interpreted in different ways (Desrochers and Hannon 1989, Matthysen 1990). I interpreted winter territoriality as the exclusive use and/or active defense of home ranges by the base units of winter social groups (after Matthysen 1990). Because nonbreeding social organization may vary among populations according to local environmental conditions (Smith and van Buskirk 1988), I took into account information available for any species included in the study. I chose only studies conducted on color-banded populations that were not located in the extremes of a species' geographic distribution. As an index of winter territoriality for each species, I calculated the proportion of population studies in which individuals occupied exclusive territories, often in groups of stable membership (after Matthysen 1990). Data were insufficient for most species to allow me to control for possible latitudinal variation in territoriality. However, most studies of nonbreeding social organization have been conducted in optimal (i.e. high-density) habitats, so I presumed that estimates of winter territoriality also were representative of the tendency for each species.

I used population-based studies for each species to obtain comparable data on clutch size and the proportion of pairs that attempted a second brood. Data on clutch size were obtained from Mönkkönen and Orell (1997), whose estimates were from populations in optimal habitats. Most of the studies included in Mönkkönen and Orell (1997) corresponded to those used in the index of winter territoriality. Clutch sizes obtained with this method agree with those used by Martin and Clobert (1996) in a subsample of 11 species of parids for which data were also based on population estimates ( $r = 0.93$ ,  $F = 57.3$ ,  $df = 3$  and  $9$ ,  $P < 0.001$ ). In parids, clutch size is not related to body size (Mönkkönen and Orell 1997), so I did not include body size as a covariate in subsequent analyses. The proportion of second broods within species varies considerably among different populations (Verboven 1997). Thus, I used two approaches to calculate this parameter. First, I used the proportion of second broods based on the sample of populations in Mönkkönen and Orell (1997). Second, I used the proportion of populations within species in which more

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TABLE 1. ANCOVA comparing winter territoriality (main effect) between irruptive and non-irruptive species, with annual fecundity as a covariate. Critical values for *F*-statistics and associated significance levels are presented from conventional tables, which would be appropriate if all species radiated instantaneously from a common ancestor, and based on analyses of data simulated on the phylogeny of Gill et al. (1989) under different models of character change. Significant effects occur when the *F*-value is larger than the critical value from computer simulations.

Source	SS	df	MS	<i>F</i>	Conventional		Brownian <sup>a</sup>		Punctuated equilibrium	
					Critical value	<i>P</i>	Critical value	<i>P</i>	Critical value	<i>P</i>
Main effect	0.02	1	0.02	0.02	4.84	>0.50	4.62	>0.50	4.48	>0.50
Covariate	2.28	1	2.28	21.92	4.84	<0.01	5.81	<0.01	6.74	<0.01
Explained	3.45	2	2.40	23.17	3.98	<0.01	4.04	<0.01	5.16	<0.01
Error	1.14	11	0.10	—	—	—	—	—	—	—
Total	4.85	13	—	—	—	—	—	—	—	—

<sup>a</sup> Results were the same for gradual and speciation (not shown) Brownian models.

than 5% of the pairs laid second clutches. The data sets obtained by these two methods were positively correlated ( $r = 0.79$ ,  $F = 19.65$ ,  $df = 1$  and  $12$ ,  $P < 0.01$ ); therefore, only results from the first method were used in later analyses. To obtain an estimate of annual reproductive effort for each species, I calculated a new variable as the product of clutch size and the proportion of second clutches laid plus 1 (hereafter, annual fecundity).

Because of the hierarchical nature of phylogenetic descent, species may not represent statistically independent data points, degrees of freedom may be inflated, and significance levels derived from conventional tests cannot be trusted (Garland et al. 1993). Therefore, I used a comparative method to study the relationship between irruptive behavior and nonbreeding territoriality in parids. I adopted the phylogeny provided by Gill et al. (1989), which is based on protein relationships among parids. Other phylogenies are available for parids, such as Kvist et al. (1996) based on mitochondrial DNA, and Slikas et al. (1996) based on DNA-DNA hybridization. More recent phylogenies (Slikas et al. 1996) supported Gill et al.'s (1989) main results of branching relationships. I chose Gill et al. (1989) because the other studies included some species for which few ecological data were available to suit my purpose.

To test whether irruptive species differed from non-irruptive ones in the degree of winter territoriality, I used the phylogenetic approach of Garland et al. (1993). I conducted a conventional ANCOVA that disregarded phylogenetic effects by comparing the *F*-statistic obtained with a null distribution from computer simulations of characters evolving up the phylogenetic tree, instead of using conventional tabular values from statistical textbooks. These empirical null distributions allow one to set critical values for hypothesis testing that account for nonindependence owing to specified phylogenetic topologies, branch lengths, and models of evolutionary change.

I repeated computer simulations 1,000 times for each trait using PDSIMUL software described by Garland et al. (1993). Simulations were conducted under Brownian and punctuated evolutionary models (see Table 1), setting upper and lower limits with the replace option that were equivalent to the largest and smallest values, respectively, that were recorded for the species included in the study. Average trait values and their variances were based on the empirical data analyzed here. Data on degree of winter territoriality were arcsine transformed and on annual fecundity were log transformed to meet requirements of parametric analyses.

I also used logistic regression to identify the relative importance of factors in influencing the probability of a species being irruptive. To override phylogenetic effects in this approach, I included the genus for each species of Paridae considered in this study (*Poecile*, *Baeolophus*, and *Parus*) as a categorical factor (Harvey and Pagel 1991). Then, I used a backward-removal procedure to select only the significant factors associated with the irruptive habit in parids (Crawley 1993).

**Results.**—Winter territoriality tended to be less common in irruptive species ( $\bar{x} = 0.13 \pm \text{SE of } 0.43$ ,  $n = 7$ ) than in non-irruptive species ( $\bar{x} = 0.93 \pm 0.12$ ,  $n = 7$ ;  $F = 4.97$ ,  $df = 1$  and  $12$ ,  $P < 0.05$  under the three models of evolutionary character change). However, a high reproductive effort also might favor the irruptive habit, and in fact, the index of annual fecundity was significantly higher in irruptive species ( $\bar{x} = 11.28 \pm 1.37$ ,  $n = 7$ ) than in non-irruptive ones ( $\bar{x} = 6.59 \pm 1.40$ ,  $n = 7$ ;  $F = 6.75$ ,  $df = 1$  and  $12$ ,  $P < 0.05$  under the three models of evolutionary character change). Therefore, I took this effect into consideration by including it as covariate when analyzing the effect of winter territoriality on irruptive habit in the ANCOVA. After the phylogeny was taken into account, the correlation between winter territoriality and annual fecundity was highly signifi-

cant under both models of evolutionary change (covariate; Table 1); that is, the  $F$ -value obtained from a typical ANCOVA procedure was always significant when compared with the  $F$ -values obtained from the computer simulations that included the phylogenetic information about the evolution of characters. The analysis that included fecundity as a covariate showed that irruptive and non-irruptive species did not differ in the degree of winter territoriality (main effect; Table 1).

Logistic regression analysis revealed that the probability of a species being irruptive was independent of genus ( $\chi^2 = 3.57$ ,  $df = 2$ ,  $P > 0.10$ ). The best final model explaining variation in irruptive tendencies removed the factor territoriality ( $\chi^2 = 0.02$ ,  $df = 1$ ,  $P > 0.80$ ) and included the index of annual fecundity of a species as the only significant factor ( $\chi^2 = 7.21$ ,  $df = 1$ ,  $P < 0.01$ ). Therefore, my results suggest that irruptive behavior in parids is not directly related to winter social organization of a species and is indirectly associated with higher fecundity of less-territorial species.

*Discussion.*—My results do not support the hypotheses that the nonbreeding social system and degree of winter territoriality are directly linked to the tendency for irruption in parids. Rather, irruptive behavior of less-territorial species may be indirectly favored through their higher fecundity. Of course, interspecific comparisons cannot determine causation, but the correlations potentially can provide insight into causes and may highlight potential evolutionary influences that would not be covered by intraspecific tests.

High fecundity should lead to higher variation in population density and, in good years with high survival of young, to a surplus of juveniles that are the main component of irruptive movements (Ulfstrand 1963, Smith and Nilsson 1987). In this context, large crops of pine or beech seeds are the proximate mechanisms leading to high overwinter survival and probably to higher breeding densities in the next season (Bejer and Rudemo 1985). In such situations, if breeding is successful, the production of many fledglings would force extensive movements of juveniles in autumn and winter. However, large seed-crop production by itself would not lead to irruptions if the production of many offspring does not occur for a particular species. For example, the Coal Tit and the Crested Tit inhabit coniferous forests in most of Europe, where both feed on pine seeds and hoard food during autumn and winter (Cramp and Perrins 1993, Brotons and Haftorn 1999). Whereas Coal Tits frequently are involved in irruptions, Crested Tits almost never have been reported to undergo extensive movements from breeding areas (Scherrer 1972, Cramp and Perrins 1993). Variation in seed-crop production is present for both species and should affect both to a similar degree. Higher reproductive output of Coal Tits would favor larger breeding populations after large seed-crop production through

higher survival, leading to irruptive episodes. Differences in the life-history strategies of these two species and differential spacing patterns during winter can explain the differences observed in their reproductive output (Ekman and Askenmo 1986, Cramp and Perrins 1993, this study). The Crested Tit often is dominant over the Coal Tit. Therefore, the Coal Tit may have a greater tendency for irruptive movements because it would perceive a hypothetical food shortage earlier than would the Crested Tit. However, competition in the Paridae seems to be involved only secondarily in the tendency to irrupt, because other irruptive species such as Great Tits clearly are dominant over the rest of the species in the group (Perrins 1979).

One risk when examining life-history traits is that any correlation between traits could emerge because both are related to a third trait. Life-history theory suggests that a relationship occurs between reproductive effort and adult survival during the nonbreeding season (Stearns 1992, Martin 1995). Large investments in reproduction may increase winter mortality, but winter mortality also may be related to other factors such as social organization. Perhaps the pattern in irruptive tendencies that I found for parids is related to adult winter survival and not to annual fecundity. Although winter survival data for most species included in this study are scarce, available estimates imply that this trait does not differ to a great extent in species differing in their social systems, although intraspecific variation is wide (Clobert et al. 1988, Cramp and Perrins 1993). For example, survival estimates in nonterritorial species range from 0.60 to 0.65 for the Coal Tit (L. Brotons unpubl. data) to 0.40 to 0.93 for the Blue Tit (Blondel et al. 1992). Similar estimates in more-territorial species range from 0.50 to 0.71 for the Willow Tit (*Parus montanus*; Orell et al. 1994) to 0.69 for the Gray-headed Chickadee (*Poecile cincta*; Orell et al. 1999). Furthermore, in a detailed study, Blondel et al. (1992) explicitly tested the hypotheses of a negative correlation between fecundity and adult survival in the Blue Tit. Their results run counter to the idea of higher survival in low-fecundity populations, suggesting that the tradeoff between reproduction and adult survival may involve many more life-history traits than the number of fledglings per pair and adult survival.

My study supports the view that irruptive behavior is a characteristic associated with the fecundity of a given species rather than with its nonbreeding social system. Large variation in food abundance would be only a proximate cause of the survival of large numbers of individuals needed for an irruption to take place. The association between life-history traits of species and their irruptive tendencies suggests that some species are indeed more likely than others to be involved in invasion episodes. Further investigations of irruptive behavior should involve closely related species, or populations within species, that have similar ecological habits and different

irruptive tendencies to identify the exact role of various life-history traits in this behavior.

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APPENDIX. Data on winter territoriality, mean clutch size, proportion of second clutches, and irruptive status for 13 parids and the White-breasted Nuthatch.

Species	Winter territoriality <sup>a</sup>	Clutch size	Second clutch	Irruptive?	Source <sup>b</sup>
Black-capped Chickadee ( <i>Parus atricapilla</i> )	0.75 (6/8)	6.6	0.05	Yes	1, 2, 19
Mountain Chickadee ( <i>Parus gambeli</i> )	1.00 (3/3)	7.2	0.10	Yes	2, 5, 4, 19
Boreal Chickadee ( <i>Parus hudsonica</i> )	1.00 (2/2)	6.5	0.00	Yes	2, 5, 19
Chestnut-backed Chickadee ( <i>Parus rufescens</i> )	1.00 (1/1)	6.1	0.00	No	2, 4, 19
Carolina Chickadee ( <i>Parus carolinensis</i> )	1.00 (3/3)	6.1	0.00	No	2, 6, 7, 19
Marsh Tit ( <i>Parus palustris</i> )	0.80 (4/5)	7.2	0.05	No	2, 8, 9, 10, 19
Willow Tit ( <i>Parus montanus</i> )	0.80 (4/5)	7.8	0.00	Yes	2, 8, 9, 11, 19
Crested Tit ( <i>Parus cristatus</i> )	1.00 (3/3)	6.3	0.11	No	2, 8, 9, 12, 19
Coal Tit ( <i>Parus ater</i> )	0.25 (1/4)	8.9	0.67	Yes	2, 8, 9, 13, 19
Great Tit ( <i>Parus major</i> )	0.00 (0/6)	9.4	0.20	Yes	2, 8, 9, 14, 15, 19
Blue Tit ( <i>Parus caeruleus</i> )	0.00 (0/2)	10.5	0.38	Yes	2, 8, 9, 16, 19
Tufted Titmouse ( <i>Baeolophus bicolor</i> )	0.75 (3/4)	5.7	0.00	No	2, 8, 17, 19
"Plain" Titmouse ( <i>Baeolophus inornatus/ridgwaji</i> )	1.00 (2/2)	5.4	0.00	No	2, 8, 4, 19
White-breasted Nuthatch ( <i>Sitta carolinensis</i> )	1.00 (2/2)	7.3	0.00	No	18, 19

<sup>a</sup> Number of territorial populations / number of populations surveyed.  
<sup>b</sup> (1) Smith 1991; (2) Mathysen 1990; (3) Dahlsten and Cooper 1979; (4) D. Dahlsten unpubl. data; (5) McLaren 1975; (6) Tanner 1952; (7) Brewer 1963; (8) Ekman 1989; (9) Cramp and Perrins 1993; (10) Ludescher 1973; (11) Orell and Ojanen 1983a; (12) Lohrl 1991; (13) L. Brotons unpubl. data; (14) Verboven 1997; (15) Orell and Ojanen 1983b; (16) Delmee et al. 1972; (17) Grubb and Pravosudov 1994; (18) Pravosudov and Grubb 1993; (19) Hara and Quinn (1996).