

# Can environmental fluctuation prevent competitive exclusion in sympatric flycatchers?

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Ecology has been characterized by a central controversy for decades: namely, whether the distribution and abundance of organisms are determined by species interactions, such as competitive exclusion, or by environmental conditions. In part, this is because competitive exclusion has not been convincingly demonstrated in open, natural systems. In addition, traditional theoretical models cannot predict the outcome of competitive interactions in the presence of environmental variability. In this paper we document the limiting influence of strong interspecific competition on population dynamics and nestling mortality in a mixed population of pied flycatchers (*Ficedula hypoleuca*) and collared flycatchers (*F. albicollis*) in a narrow zone of sympatry. Whereas the former species was limited mainly by interspecific competition, the latter species was limited by the concerted influences of intraspecific competition and climate. The analysis suggests a march towards competitive exclusion of the pied flycatcher during warm periods. However, competitive exclusion is apparently prohibited on a local scale because intraspecific competition among individual collared flycatchers intensifies when they are forced to cope with severe environmental conditions, promoting the temporary and local presence of pied flycatchers.

**Keywords:** *Ficedula albicollis*; *Ficedula hypoleuca*; interspecific competition; intraspecific competition; population dynamics; North Atlantic Oscillation

## 1. INTRODUCTION

The principle of competitive exclusion states that two species cannot coexist within the same habitat in a stable equilibrium when one or both are limited more by interspecific rather than by intraspecific competition (Gause 1934; Volterra 1926; Lotka 1932; Hardin 1960). Accordingly, competitive exclusion has been assumed to be a key predictor of the distribution and abundance of organisms and the structure of communities (see, for example, Hutchinson 1959; MacArthur & Levins 1967). Despite early enthusiasm for these ideas, however, many ecologists have since argued that competition is usually weak or infrequent and thus of little significance, because harsh environmental conditions, stress or density-independent mortality keep population densities low (see, for example, Wiens 1977; Huston 1979; den Boer 1986). On the other hand, recent theoretical investigations have vindicated the importance of both competition and environment in predicting species composition, diversity and niche overlap in ecological communities (Chesson 1990, 1994; Chesson & Huntley 1997). In part, the controversy over the relative importance of competition and environment in population and community ecology is due to a lack of convincing demonstrations of the operation of the process

of competitive exclusion in open, natural systems (see, for example, Begon *et al.* 1996).

Interspecific competition may be particularly likely to influence population dynamics when the interacting species are closely related, because such species may have overlapping ecological requirements. Here we investigate population dynamics of two closely related *Ficedula* flycatcher species in a narrow zone of sympatry, applying time-series analysis.

The distributions of pied and collared flycatchers overlap in central and eastern Europe (Sætre *et al.* 1997, 1999). Yet the main contact zone is narrow, coinciding with topography and climate: collared flycatchers dominate in warm lowland areas whereas pied flycatchers are more common in colder subalpine zones (Sætre *et al.* 1999). The two species show interspecific territoriality in mixed populations, and the collared flycatcher is socially dominant in competitive interactions for the possession of nest sites (Sætre *et al.* 1993; Alatalo *et al.* 1994). However, whether such competitive interactions influence the abundance of the species has not been investigated.

We present analyses of time-series from a mixed population in which both species have been observed breeding in each year of observation (13 years; Sætre *et al.* 1999). The time-series comprised data on annual breeding density for each species, which has been consistently greater for the collared flycatcher than for the declining pied flycatcher throughout the study period (figure 1). Additional data included annual estimates of breeding success of each pair, including identification of the cause of nestling mortality (extrinsic mortality through nest

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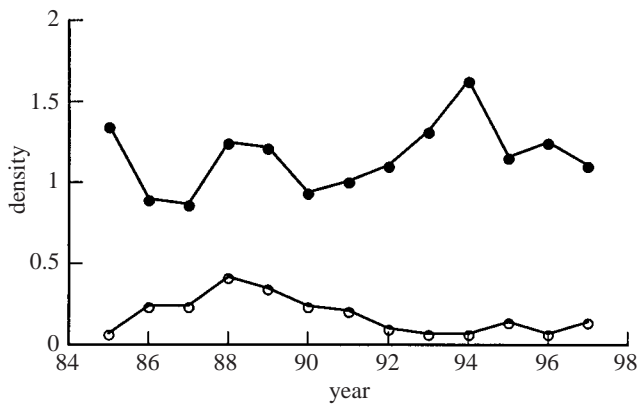


Figure 1. Annual estimates of breeding densities of collared (filled circles) and pied (open circles) flycatchers near Dlouhá Loučka, Czech Republic, 1985–1997. Note that in 1994 no pied flycatcher pairs were observed breeding, although pied flycatcher individuals were present.

predation and adult disappearance; and intrinsic mortality from starvation and/or disease). Our analyses of annual density fluctuations also integrated an index of large-scale climatic variation, the North Atlantic Oscillation (NAO) index. Over large spatial scales, including central Europe where our study was located, the NAO determines variation in winter temperatures (Hurrell & Van Loon 1997), which, in turn, influence the timing of spring flowering by annual plants used by flying insects (Post & Stenseth 1999) as well as breeding phenology and population dynamics of migratory birds (Forchhammer *et al.* 1998). Over the past 130 years, winter temperatures in our study site have covaried positively and relatively strongly with the NAO index (Hurrell & Van Loon 1997).

## 2. METHODS

The analyses in this study are based on long-term observations of the reproductive ecology of collared and pied flycatchers breeding in nest-boxes in a subalpine (300–480 m a.s.l.) mixed deciduous forest near Dlouhá Loučka, Czech Republic (49° 50' N, 17° 15' E). Breeding densities are number of breeding females of each species divided by the size of the area (in hectares) as determined from a map assuming straight lines between the outermost nest sites (Sætre *et al.* 1999). Each nest was followed on a daily basis, or nearly so, to obtain information on phenology and nesting success. Nestlings found dead within the nest were assumed to have died from intrinsic factors (starvation, cold or disease or a combination of these factors). Predation was assumed when nestlings (usually the complete clutch) had disappeared before day 13 after hatching (fledging occurs 15–16 days after hatching in flycatchers; Lundberg & Alatalo 1992; G.-P. Sætre and M. Král, personal observations). Additional marks of predation were usually present: damage to the nest hole (woodpeckers, *Dendrocopos* spp.), muddling of nest material (polecats, *Mustelidae*) or the presence of the predator in the nest-box after preying on the chicks (dormice, *Gliridae*). In some cases nestling mortality was related to disappearance of the parents, possibly caused by predation on one or both adults.

We used forward stepwise multiple regression to analyse inter-annual dynamics of the density (log<sub>e</sub> transformed) of each species. Independent variables included breeding density of each species, fledging success, intrinsic nestling mortality (i.e. starvation and/or

disease), nest predation, adult disappearance, and the NAO index. Each variable was tested at lags of zero and one year to investigate both current and delayed density-dependent and density-independent effects. Models of dynamics of densities of both flycatcher species took the general form

$$X_t = \beta_0 + (1 + \beta_1)X_{t-1} + \sum_d \beta_{t-d}Y_{t-d} + \sum_k \gamma_{t-k}\Pi_{t-k} + \sum_n \omega_{t-n}\text{NAO}_{t-n} + \epsilon_t \quad (1)$$

in which  $X_t$  is  $\ln(\text{density})$  of the species of interest in the current year,  $X_{t-1}$  is the first-order autoregressive term [ $\ln(\text{density})$  in the previous year],  $Y_{t-d}$  is  $\ln(\text{density})$  of the competing species in the current or previous year (including all  $d$  for which  $d \in [0,1]$ ),  $\Pi_{t-k}$  is intrinsic nestling mortality of species  $X$  in the current or previous year (including all  $k$  for which  $k \in [0,1]$ ),  $\text{NAO}_{t-n}$  is the NAO index of the current or previous year (including all  $n$  for which  $n \in [0,1]$ ), and  $\epsilon_t$  is a time-independent error term assumed to be normally distributed with zero mean and constant variance. We used stepwise least-squares multiple regression to estimate significance of coefficients, after confirming homoscedasticity. Significance of the first-order autoregressive term was tested with a two-tailed  $t$ -test as different from 1, because the coefficient includes 1 owing to the log<sub>e</sub> transformation (Forchhammer *et al.* 1998; Post & Stenseth 1999). Variables were checked for autocorrelation and linear trends with time, neither of which was significant.

We analysed the annual mean proportion of nestlings that suffered mortality in each population with stepwise least-squares multiple models that included current and one-year lagged densities (log<sub>e</sub> transformed) of conspecifics and competitors and the NAO index. Proportions were arcsine transformed [ $2\arcsin(\sqrt{p})$ ] to stabilize variance. We present  $r^2$  values adjusted (reduced) for the presence of multiple independent variables (Neter *et al.* 1990).

## 3. RESULTS

Nearly all interannual variation in breeding density of the pied flycatcher ( $r^2=0.86$ ) was explained by inter-specific competition, intraspecific competition and intrinsic nestling mortality (table 1a). Moreover, inter-specific competition had a significantly stronger effect on the population dynamics of the pied flycatcher than did intraspecific competition (figure 2a). The situation was quite different for the collared flycatcher. A substantial proportion of the interannual variation in breeding density of this species ( $r^2=0.60$ ) was explained by intraspecific competition, intrinsic nestling mortality and climatic variation (table 1a). Interspecific competition did not significantly influence the population dynamics of collared flycatchers (partial correlation with pied density in both the previous and current year:  $r^2=0.16$ ,  $p=0.73$ ). For the collared flycatcher, the strength of intraspecific competition was not significantly greater than that of interspecific competition (figure 2a); at the same time, the collared flycatcher was significantly less affected by interspecific competition than was the pied flycatcher ( $t=15.07$ ,  $p<0.001$ ). These results exemplify the classical case where one species (the collared flycatcher) is both more abundant and a stronger interspecific competitor than the other species (the pied flycatcher). According to the competitive exclusion principle, therefore, the pied

Table 1. Density models of flycatchers near Dlouhá Loučka, Czech Republic, 1985–1997

((a) Models of population dynamics of pied flycatchers (*Ficedula hypoleuca*) and collared flycatchers (*F. albicollis*); (b) models of annual intrinsic nestling mortality of pied and collared flycatchers.)

species	variable (lag in years)	coefficient (1 s.e.)	<i>p</i> (two-tailed)
(a)			
pied	pied density (1)	−0.025 (0.16)*	<0.05 <sup>a</sup>
	collared density (1)	−3.24 (0.76)	<0.05
	nestling mortality (0)	1.50 (0.23)	<0.05
collared	collared density (1)	0.013 (0.19)*	<0.05
	nestling mortality (1)	−0.44 (0.10)	<0.05
	NAO (1)	0.032 (0.015)	=0.057
(b)			
pied	pied density (0)	0.12 (0.02)	<0.001
	pied density (1)	0.05 (0.02)	<0.05
	collared density (1)	0.73 (0.07)	<0.001
collared	collared density (1)	0.84 (0.06)	<0.001
	pied density (0)	0.08 (0.02)	<0.01
	pied density (1)	0.18 (0.02)	<0.001

<sup>a</sup>Significance is based on a two-tailed *t*-test of difference from 1 because of the logarithmic scale of the first-order autoregressive term; values less than unity indicate negative direct density dependence (see Post & Stenseth 1999).

flycatcher should not be able to coexist with the collared flycatcher in a stable equilibrium in this habitat.

The density models suggested a link between density and intrinsic nestling mortality in both species. Hence, we analysed the relationship between intrinsic nestling mortality and density of the two species by using multiple regression. In the pied flycatcher, nearly all interannual variation in intrinsic nestling mortality was explained by competition ( $r^2=0.95$ ; table 1b) and interspecific competition was the strongest predictor (figure 2b). In the collared flycatcher, intrinsic nestling mortality was also explained by competition ( $r^2=0.97$ ; table 1b), but in this species intraspecific competition exerted the greater influence (figure 2b).

The potential for coexistence between the species may depend upon the extent to which the dominant competitor is stressed by environmental conditions; for example, as shown above, only the collared flycatcher was significantly affected by the NAO index. We tested this hypothesis by blocking the NAO from entering the density model of the collared flycatcher. As predicted from the competition–climate hypothesis, the coefficient of direct density dependence increased when the influence of the NAO was removed (with NAO:  $b=0.013\pm 0.19$ ; without NAO:  $b=0.081\pm 0.20$ ), whereas the intrinsic rate of increase declined when the positive partial correlation with climate was excluded from the model (with NAO:  $a=0.42\pm 0.09$ ; without NAO:  $a=0.39\pm 0.10$ ). Although the 95% confidence intervals of these coefficients including and excluding the NAO overlap, they suggest an increase in the intensity of density dependence by nearly an order of magnitude, and a reduction in the intrinsic rate of increase by 10%, when the influence of climate is removed. Such differences are likely to be of biological, if not statistical, significance.

#### 4. DISCUSSION

Our results demonstrate that the breeding density of the pied flycatcher was limited mainly by interspecific

competition as it influenced density-dependent nestling mortality. In the collared flycatcher, some density-dependent background nestling mortality was apparently attributable to interspecific competition, but intraspecific competition and climatic variation primarily limited this species. The influence of interspecific competition on population dynamics and nestling mortality of pied flycatchers was very strong, and local extinction would be predicted from the competitive exclusion principle. It is possible that coexistence may be a transitional phenomenon in this locality, or that exclusion may be prohibited, or delayed, by influx of pied flycatchers from more productive areas. As argued below, however, climatic fluctuation appears to oppose competitive exclusion in this zone of distributional overlap, because the dominant competitor is less tolerant of climatic fluctuation than is the subordinate one.

It has previously been shown that the collared flycatcher is socially dominant in competitive interactions for nest sites. Pied flycatchers are often evicted from their territories by collared flycatchers, but not vice versa (Sætre *et al.* 1993; Alatalo *et al.* 1994). As a consequence, pied flycatchers tend to suffer delayed breeding (Lundberg & Alatalo 1992), are forced into marginal territories by the dominant competitor (Sætre *et al.* 1993; Alatalo *et al.* 1994) and possibly even prohibited from breeding. These behavioural observations are thus in accordance with the present results of strong negative interspecific density-dependent effects on nestling mortality and population dynamics of the pied flycatcher.

In a previous paper (Sætre *et al.* 1999), we found that the breeding density and distribution of the collared flycatcher in different populations in central Europe correlated strongly with environmental conditions. That is, its breeding density decreased from warm to colder habitats, and it was absent in higher subalpine and alpine areas. In contrast, breeding densities of the pied flycatcher did not correlate with environmental conditions, but this species was essentially absent in areas

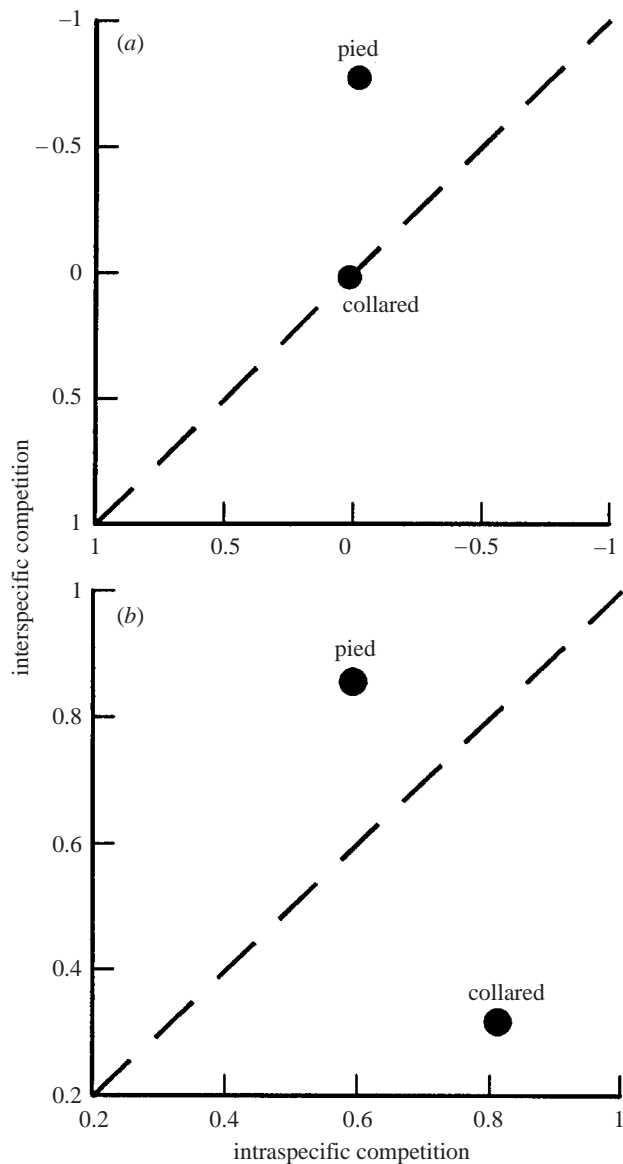


Figure 2. (a) Relative strengths of intraspecific and interspecific competition in population dynamics of collared and pied flycatchers shown as plots of the standardized partial regression coefficients of interspecific versus intraspecific competition for each species from density models. (b) Relative strengths of intraspecific and interspecific competition in intrinsic nestling mortality of collared and pied flycatchers, shown as plots of the standardized partial regression coefficients of interspecific versus intraspecific competition for each species from models of intrinsic nestling mortality. The dashed line represents equality of the two types of competition.

with a high breeding density of the collared flycatcher. In accordance with this description of the biogeography of the species, the analysis presented here demonstrates that the abundance of the collared flycatcher covaried positively with temperature, whereas the pied flycatcher was not significantly affected by climate.

In the light of the present study, we suggest that the distribution of the collared flycatcher is mainly limited by environmental conditions, whereas that of the pied flycatcher is limited primarily by interspecific competition. Coexistence of the two species within the same habitat should thus be restricted to areas and years when

the collared flycatcher is severely stressed by environmental conditions (cf. Chesson 1990). Our analyses suggest that intraspecific competition among individual collared flycatchers in this population intensifies when they are forced to cope with severe environmental conditions, promoting the temporary and local presence of pied flycatchers. Accordingly, the greater density of collared flycatchers in this zone of sympatry may reflect the trend of increasingly warmer winters throughout central Europe during the period of this study (Hurrell & Van Loon 1997), because the relative densities of competing species may be dependent on the influence of climate on the rate of increase of the superior competitor (Andrewartha & Birch 1954). If so, these results imply that patterns of large-scale climatic variation may to some degree influence patterns of spatio-temporal overlap in these closely related species.

Competitive exclusion has been regarded as fundamentally important in multispecies interactions since the dawn of the ecological and evolutionary sciences (Darwin 1859). Surprisingly, however, conclusive evidence for its operation on natural populations is basically absent (den Boer 1986; Begon *et al.* 1996). Even the textbook example of competitive exclusion, on tidal zonation in barnacles (Connell 1961), is not all that conclusive: it may more critically be regarded as an illustration of the result of either amensalism or niche separation rather than the process of competitive exclusion. We suggest that the rarity of conclusive demonstration of competitive exclusion is related to a lack of relevant analyses (cf. Gilpin & Justice 1972) and the inadequacy of the Lotka–Volterra equations to predict the outcomes of interspecific relationships in the presence of environmental variability. Careful analyses of time-series of natural populations involving possible competing species in zones of overlap, incorporating environmental variation, provides an important tool for unravelling possible negative density interactions of the species.

We thank Rolf A. Ims and Nils Chr. Stenseth for comments on an earlier draft of the manuscript. We gratefully acknowledge financial support from the Norwegian Research Council (to G.-P.S.) and the US National Science Foundation (to E.P.).

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