



Within territory abundance of red wood ants *Formica rufa* is associated with the body condition of nestlings in the Eurasian treecreeper *Certhia familiaris*

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Studies on individual reproductive success in relation to interspecific competition between distantly related taxa are scarce. We studied whether the abundance of red wood ants *Formica rufa* -group is related to the breeding habitat selection, fecundity and offspring quality in the Eurasian treecreeper *Certhia familiaris*, an old-growth forest passerine. The nest-box occupancy data were gathered over a five-year study period, whereas the breeding performance analyses were based on a two-year data set. The abundance of wood ants, measured within 50 m around the nest-boxes, was not related to nest-box occupancy rate, fecundity or the physiological stress of nestlings. In contrast, the abundance of wood ants was negatively related to the offspring quality and life-history traits, such as lowered body mass, subcutaneous fat reserves, and tarsus length at fledging. Our results suggest that exploitative competition between distantly related taxa may have considerable and adverse influences on nestling quality as measured by body mass, subcutaneous, fat and tarsus length. Red wood ants may decrease the fitness of treecreepers as the lower body condition of nestlings has the potential to impair recruitment into the breeding population and, additionally, impair the future reproductive effort.

The most intensive examples of interspecific competition in natural populations are principally documented between closely related species with similar niches (Connell 1983; Schoener 1983, Punttila et al. 1994, Confer et al. 2003). Recently, however, competition has been recognized between very dissimilar taxa (Haemig 1996, 1999, Aho et al. 1997). Aho et al. (1997) demonstrated that the Eurasian treecreeper *Certhia familiaris*, which belongs to the bark-foraging guild, can be affected by resource competition with red wood ants, the *Formica rufa* -group.

Competition between species can be defined in two major ways; (1) exploitative competition and (2) interference, i.e., contest competition (Amarasekare 2002, Hawes et al. 2002). Exploitative competition, also called scramble or resource competition, involves indirect negative interactions arising from the use of a common resource by different consumer species (Haemig 1992,

1994). Conversely, interference competition involves direct negative interactions arising from territoriality, overgrowth, undercutting, predation or chemical competition in which one species can negatively alter the foraging behaviour of other species (Haemig 1996).

Exploitative competition between treecreepers and red wood ants for the same food sources has been suggested to have negative effects on the breeding performance of treecreepers (Aho et al. 1997, Aho et al. 1999). In general, the lack of food may lead to chronic physiological stress in nestlings (Nunez-de la Mora et al. 1996, Suorsa et al. 2003).

One crucial component of body mass in birds is the subcutaneous fat reserve. These reserves can change dynamically over a 24 hour period (Cresswell 1998) and they represent the most important source of stored energy in passerines (Blem 1990). An increase in fat reserves during cold weather reduces the risk of

starvation during cold nights and winter storms (e.g. Lahti et al. 1998). In contrast, extremely high fat reserves may reduce manoeuvrability or increase exposure time to predators (Lima 1986, Witter et al. 1994).

Eurasian treecreeper breeds throughout the northern coniferous zone (Kuitunen 1987). Breeding home range size is approximately 10 hectares; a rather large territory for a small passerine (Kuitunen and Törmälä 1983). The first broods are reared in April and May when snow cover and night frosts are still common. About one third of the females laid a second clutch in June or July (Aho et al. 1999). The forest dwelling treecreeper specializes in catching bark-dwelling invertebrates on tree trunks; it does not eat ants. Treecreepers prefer larger tree trunks to forage on (Suhonen and Kuitunen 1991).

In Finland the *Formica rufa* -group includes the ant species *F. aquilonia*, *F. lugubris*, *F. polyctena*, *F. pratensis* and *F. rufa* (Collingwood 1979). Of red wood ants, *F. aquilonia* and *F. polyctena* are the two dominant species in our study area. They are polygynous (multiple queens in a single nest), polydomous (multiple nest coexist in the same area without competition) and exist in large mature forests (Punttila et al. 1994, Punttila 1996). Their dry weighted diet consists of sugars from aphids' honeydew (82%), arthropods (18%) and seeds (2%) (Rosengren and Sundström 1991). The treecreepers and wood ants use similar food sources and thus have the combined potential to significantly reduce the biomass of bark-dwelling invertebrates (Haemig 1994, Jääntti et al. 2001).

In this study we explored the relationship between the abundance of red wood ants and several life-history traits of treecreepers deepening the results of Aho et al. (1997) by providing nest-boxes in forest patches characterized by low to high red wood ant densities. We assessed whether the red wood ant levels are related to: (1) nest-box occupancy rate, (2) fecundity, (3) individual body condition, and (4) individually measured physiological stress in treecreeper chicks.

Methods

The study was conducted around the Konnevesi Research Station and in the rural region of Laukaa in Central Finland (62°37'N, 26°20'E) during the summers of 1999–2003. The study area is mainly coniferous forest dominated by Norway spruce *Picea abies* and Scots pine *Pinus sylvestris*, though two birch species *Betula pendula* and *B. pubescens*, and other hardwood species are present. The remaining area consists of open habitats such as cultivated fields, clear-cuts, roads, lakes and mires. We placed two nest-boxes 30 m apart in the interior of 228 separate

forest patches having a mean age of 52 years (Suorsa et al. 2003). Each forest patch contained two nest-boxes for the first and second breeding attempts respectively (Kuitunen 1987).

Nest-boxes were checked daily to determine the occupancy rate, clutch size, numbers of nestlings, and the nestling mortality rate. Nest-boxes were considered occupied if they contained some nest material and adults were observed within the territory. Morphological measurements of nestlings were collected prior to fledging (ca 14 days of age). Wing length was measured to the nearest 1 mm by the maximum method (Svensson 1992) and body mass was measured to the nearest 0.1 g with Pesola spring balance. Subcutaneous fat in the abdomen and tracheal pit as well as the condition of the pectoral muscle, were recorded on a 0–3 scale (Gosler 1991). Physiological stress was measured already in 9 day-old nestlings with an Amersham radioimmunoassay of plasma corticosterone (RIA) kits (Biotrak rat corticosterone [¹²⁵I], Amersham, UK) in the summer of 2000 (see details in Suorsa et al. 2003).

Of the 228 nest-box pairs, we measured red wood ant abundance around 146. We located all the nest mounds within a radius of 50 m from the treecreepers nest, and measured their basal diameter to the nearest 0.01 m. The total basal area of the nest mounds (Σm^2 varying from 0 to 12.41, mean 1.95 ± 2.74 SD, $n = 146$) were used as an estimate of the red wood ant abundance around the nest-boxes (modified after Klimetzek 1981, Deslippe and Savolainen 1994). The basal area of nest mound has been shown to correlate well with the number of worker ants in *Formica* -species (Breen 1979, Deslippe and Savolainen 1994, Liautard et al. 2003).

First, we studied the association between the abundance of red wood ants and the nest-box occupancy rate using a five-year breeding data set from 1999 to 2003. We ran a generalized linear model (SAS, GENMOD procedure) which allowed for the analysis of the binomial error variance. In this analysis, a nest-box pair was used as the sampling unit ($n = 146$) and the proportion of occupied nests over the five year study (number of occupied breeding seasons/total number of potential breeding seasons) was used as a dependent variable (binomial error term, logit link-function). The abundance of wood ants, as measured by the total area of the nest mounds within a radius of 50 m from the nest, was used as an independent quantitative variable in the analysis.

Second, we analyzed the effects of ants on clutch size and fledgling production using breeding attempt (both first and second clutches from 1999 to 2000) as a sampling unit. The years from 2001 to 2003 were not included since other experimental work done during these years might have affected breeding performances. We also omitted the nests destroyed by nest predators,

to focus explicitly on the effects of wood ants. We used a four-way mixed-model ANOVA design with each breeding attempt as a sampling unit ($n = 183$). Year (1999 vs 2000) and brood (first vs second) were regarded as fixed factors, while territory was treated as a random factor. The continuous abundance of wood ants acted as an independent quantitative variable in the analysis. The presented results were obtained after the deletion of non-significant interaction terms.

The same factorial design was used in five separate four-way mixed-model ANOVAs to explore the effects of wood ants on nestling quality using body mass, fat and muscle indices, and wing and tarsus lengths as dependent variables. In these analyses, individual nestlings were treated as sampling units ($n = 598$) and the data covered the years of 1999–2000.

Finally, we conducted a three-way mixed model ANOVA to study the effects of wood ants on individually measured plasma corticosterone levels. These data were collected in the summer of 2000 and included 243 nestlings. Year was treated as a fixed factor, territory as a random factor and the abundance of wood ants as an independent quantitative variable. The generalized linear model analysis was carried out in SAS 8.2 with procedure GENMOD, and all the other analyses were conducted in SPSS 10.2.

Results

The abundance of red wood ants (within a radius of 50 m from the nest-box) was not associated with the occupancy rate of nest-boxes over the five-year study period (generalized linear model, $\chi^2 = 0.74$, $df = 1$, $P = 0.39$). Similarly, neither the clutch size nor the numbers of fledged chicks were related to the abundance of wood ants during 1999–2000 (Table 1). In contrast, the high wood ant levels were adversely associated with measurements of individual quality such as body mass, subcutaneous fat content, and tarsus length at fledging (Table 2; Fig. 1). The condition of the pectoral muscle seemed to be related to the abundance of wood ants differently during 1999 and 2000 (see significant

Table 1. Results of the mixed-models ANOVAs on the effects of year, brood and abundance of wood ants on the clutch size and the number of fledglings using territory as a random factor.

	Clutch size		Number of fledglings	
Year	$F_{1,59} = 1.67$	$P = 0.20$	$F_{1,58} = 2.68$	$P = 0.11$
Brood	$F_{2,59} = 2.21$	$P = 0.12$	$F_{2,58} = 1.35$	$P = 0.27$
Wood ants	$F_{1,59} = 0.25$	$P = 0.62$	$F_{1,59} = 0.00$	$P = 0.96$
Year \times wood ants	$P > 0.05$		$P > 0.05$	
Brood \times wood ants	$P > 0.05$		$P > 0.05$	

Table 2. Results of the mixed-model ANOVAs on the effects of wood ants on the quality of the 14-d-old treecreeper nestlings using territory as a random factor. The results are shown from the models were insignificant interaction terms were removed. Abbreviation (-) depicts the direction of the effect.

	Year (1999, 2000)		Brood (first, second)		Wood ants (radius of 50 m) (Σ area of nest mounds m^2)		Year \times wood ants		Year \times brood	
Body mass (g)	$F_{1,292.7} = 3.037$	$P = 0.082$	$F_{1,406.5} = 65.020$	$P = 0.001$	$F_{1,62.1} = 6.503$	$P = 0.013$	$P > 0.05$	$P > 0.05$	$P > 0.05$	ns
Fat index (0–4)	$F_{1,401.5} = 79.527$	$P < 0.001$	$F_{1,493.0} = 41.156$	$P < 0.001$	$F_{1,73.4} = 6.283$	$P = 0.014$	$P > 0.05$	$P > 0.05$	$P > 0.05$	ns
Muscle index (0–4)	$F_{1,447.9} = 2.553$	$P = 0.111$	$F_{1,532.2} = 0.261$	$P = 0.610$	$F_{1,79.9} = 1.048$	$P = 0.309$	$F_{1,386.8} = 5.349$	$F_{1,386.8} = 5.349$	$P > 0.05$	$P > 0.05$
Wing length (mm)	$F_{1,418.3} = 20.595$	$P < 0.001$	$F_{1,507.8} = 4.762$	$P = 0.030$	$F_{1,76.3} = 2.646$	$P = 0.108$	$P > 0.05$	$P > 0.05$	$P > 0.05$	$P > 0.05$
Tarsus length (mm)	$F_{1,235.4} = 0.622$	$P = 0.431$	$F_{1,348.7} = 69.328$	$P < 0.001$	$F_{1,66.8} = 6.496$	$P = 0.013$	$P > 0.05$	$P > 0.05$	$P > 0.05$	$P > 0.05$

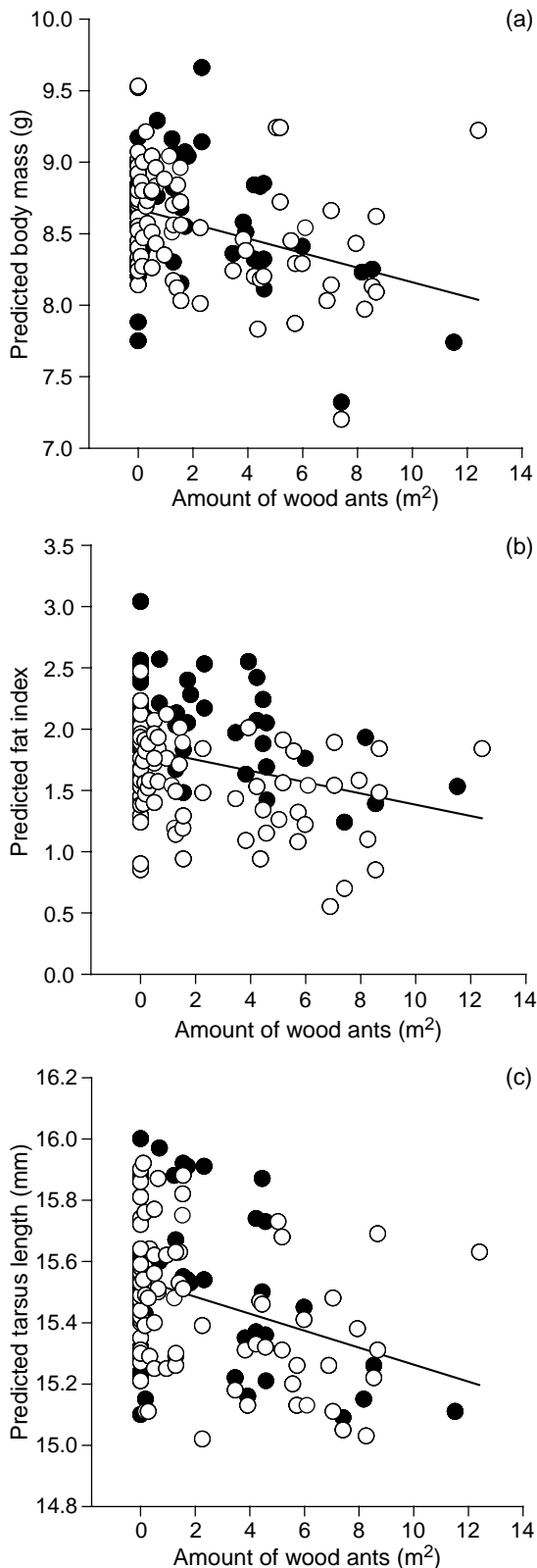


Fig. 1 (Continued)

interaction term in Table 2). Yet, when the years were analysed separately, muscle condition showed no significant effect from wood ants (mixed-model ANOVA $P > 0.18$ for all of the comparisons). Additionally, the wing length (Table 2) and corticosterone levels were not related to wood ant abundance (mixed-model ANOVA: factor brood $F_{2,31.4} = 34.10$, $P = 0.001$; covariate wood ants $F_{1,18.3} = 0.16$, $P = 0.69$; using territory as a random factor).

Discussion

We found evidence that the quality of tree creeper nestlings was adversely associated with the abundance of red wood ants dwelling in the territories. Body mass, subcutaneous fat index and tarsus length of nestlings were all lower when the abundance of red wood ants in territories was high. This result supports the suggestion that tree creepers may be affected by exploitative resource competition with red wood ants (Aho et al. 1999). Haemig (1996) compared the effects of interference competition on the foraging behaviour of distantly-related taxa, specially *Formica aquilonia* and great tits. It was found that tree trunks without ants were visited by great tits more frequently and for longer time periods than those tree trunks containing ants. Furthermore, the biomass of arthropod prey for birds may be greater in trees from which wood ants have been excluded (Skinner and Whittaker 1981, Haemig 1994). The level of arthropod biomass on trees also increases with distance from the ant nest mound (Laine and Niemelä 1980, Aho et al. 1999, Jäntti et al. 2001).

Body mass is partly a measure of the body size and partly a measure of condition, and it seems to be more sensitive than tarsus length to environmental variation (Keller and van Noorwijk 1991). In nestlings, the development of body mass, tarsus length, and fat reserves are known to be good predictors of future survival. In addition to body mass, the tarsus length has been shown to be a good indicator of future success in chicks. In the coal tit *Parus ater*, relative tarsus length was significantly associated with juvenile recruitment and both relative tarsus length and body condition were positively associated with the probability of individuals becoming residents within their native area during the next winter (Brotons and Broggi 2003). This indirectly shows that skeletal size may affect the social status of juveniles during winter, which may further influence survival probabilities.

Fig. 1. Predictions of body mass (a), fat index (b) and tarsus length (c) in relation to the abundance of wood ants within tree creeper territories in 1999 (filled circles) and 2000 (open circles). Predicted values are based on models presented in the Table 2.

Suorsa et al. (2003) found that the concentration of plasma corticosterone in nestlings of treecreepers was higher in a dense, young forest habitat with a poor food supply than in a sparse, old forest with better food resources. In addition, the nestlings in large forest patches had lower corticosterone levels and better body condition than those in small forest patches. In this study, we did not find any association between the abundance of red wood ants in territories and corticosterone levels in nestlings. This suggests that the effect of breeding habitat quality on treecreeper corticosterone levels may be stronger than that of the red wood ants. When treecreepers choose their territories in winter or early spring, they cannot estimate the abundance of red wood ants directly because of deep snow cover. This may also explain that the occupancy rate of nest-boxes was not related to the abundance of red wood ants. However, earliest possible egg laying is one of the most important determinants of reproductive success in birds (e.g. Svensson 1997, Visser and Verboven 1999). In the treecreeper, early breeding could be one way to avoid competition with wood ants since ants are not active in the cold weather during early spring.

We conclude that exploitative competition between distantly related taxa can have considerable and adverse influences on nestling quality as measured by body mass, subcutaneous fat and tarsus length. The lower body condition of nestlings has the potential to impair recruitment into the breeding population and additionally impair the future reproductive effort.

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