

Exclusion of the native bog bush-cricket *Metrioptera brachyptera* by the currently invading Roesel's bush-cricket *Metrioptera roeseli*

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Berggren, Å. & Low, M.: Exclusion of the native bush-cricket *Metrioptera brachyptera* by the currently invading bush-cricket *Metrioptera roeseli*. [**Den inhemska ljungvårtbitaren *Metrioptera brachyptera* trängs undan av den invaderande cikadavårtbitaren *Metrioptera roeseli***]. – Entomologisk Tidskrift 125 (3): 125-132. Uppsala, Sweden 2004. ISSN 0013-886x.

Roesel's bush cricket *Metrioptera roeseli* is currently expanding its distribution mainly in southern Sweden. To investigate its impact on a related native species, we censused twenty-five successfully colonised introduction sites of Roesel's bush-cricket and matched control areas for the presence and density of males of the bog bush-cricket *Metrioptera brachyptera*. We found a significant difference in the presence and numbers of *M. brachyptera* males between sites with introduced *M. roeseli* and matched control sites without *M. roeseli*. *Metrioptera brachyptera* was absent from 40% of the introduction sites compared to 2% of the control sites and, when present, was significantly more abundant in the control sites. As food appears superabundant, other resources such as acoustic and olfactory space might produce the observed distribution pattern. If the displacement of *M. brachyptera* as seen in this study is ubiquitous and continues, the two species' distributions will shift, resulting in *M. roeseli* dominating grassland habitats and *M. brachyptera* being forced into drier, less preferred habitat in heath lands and forest edges.

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Species will naturally colonise new areas, but in recent history the rate of colonisation has increased with human movement and associated environmental modification (di Castri 1989). While most introductions fail (Simberloff 1981), when they succeed the new species can have profound effects on the community in which it establishes. Although the effects can be positive or neutral (Walser *et al.* 2000), many are negative and their impacts range from minor changes in population dynamics to species extinction (Atkinson 1989). The negative effects an introduced species can have on the community can be multiple and include new forms of competition (Byers 2000). This may occur through competition for food, reproduction sites and living space (Atkin-

son 1989). The resulting impact of this may manifest as one or both of the species decreasing in number, or altering their feeding, reproductive or other behaviours to escape the pressure of competition. One consequence of this being an increased likelihood of the local extinction of one species (Bengtsson 1989). The form of competition and its impact may be difficult to determine because of confounding variables. Commonly, the community or species is not studied before an introduction is undertaken and thus there are no "control" communities to compare with afterwards.

Interspecific competition has been shown to be an important variable in grasshopper population dynamics and distribution (Belovsky 1986,



Figure 1. A male of Roesel's bush cricket *Metrioptera roeseli*. The body colour of this species is variable, with it ranging from brown to bright green. Photo: Åsa Berggren

En hane av ciakdavårtbitaren, *Metrioptera roeseli*. Individerna är oftast bruna till gröna, men vissa exemplar starkt ljusgröna.

Beckerman 2000). The underlying mechanisms are not always clear and these studies have been concerned with already existing communities where the aim has been to understand interspecific relationships already present. While studies into interspecific competition are often concerned with resources such as food (Ritchie & Tilman 1993), it is important to understand that other forms of resource limitation may have an impact on species distribution. During stridulation, a form of acoustic signalling competition in orthopterans, one limiting resource is acoustic space. Male orthopterans have been found to mask each other's call and thus make it hard for competitors to attract females. One result of this is that acoustically masked individuals have to move to new sites (Bailey & Morris 1986, Beckerman 2000).

We investigated the impact of an introduced orthopteran on a related native species in the agricultural landscape in south-eastern Sweden. In this region Roesel's bush-cricket *Metrioptera roeseli* was experimentally introduced into 70 habitat islands previously uninhabited by this species (Berggren 2001). Twenty-five successfully colonised sites were censused for the presence and density of the bog bush-cricket *Metrioptera brachyptera*, a species previously shown to be displaced by *M. roeseli* under laboratory conditions (McHugh 1971). These sites were

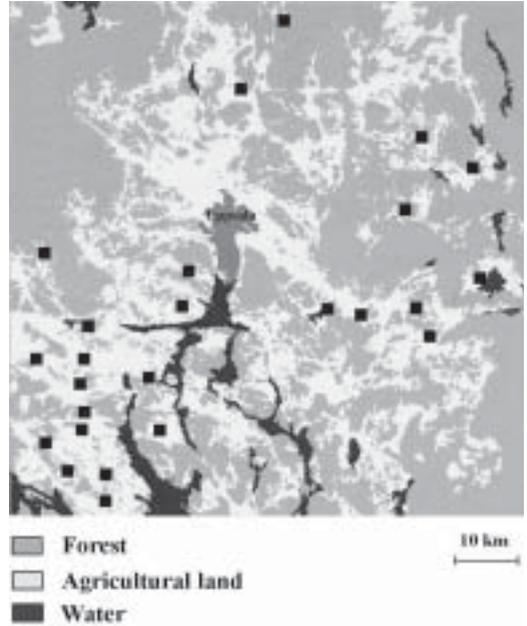


Figure 2. Map of study sites (black squares) in the agricultural landscape around Uppsala town in southeastern Sweden.

Karta över lokalerna i studien (svarta kvadrater) i odlingslandskapet runt Uppsala i sydöstra Sverige

then compared with nearby control sites in the same habitat where *M. roeseli* has yet to colonise.

Materials and Methods

The species

Metrioptera roeseli (Fig. 1) is a medium sized bush-cricket species, 13-26 mm in length and is common in south and central Europe, Finland and Latvia (Marshall & Haes 1988). In Sweden the species is generally restricted to the south-east around Lake Mälaren, with the population core being close to the harbour of Västerås (de Jong & Kindvall 1991). The combination of the location of the core population and the recorded expansion from this point (Pettersson 1996), suggests this species was introduced via cargo ships and is now invading the country. The species' preferred habitat is moist ungrazed tall-grass areas where they feed on grass, grass seeds and small insects.

Metrioptera brachyptera is also a medium sized bush-cricket, 11-21 mm in length. This species is palaeartic, naturally occurring in Sweden and also across central and northern Europe from the Pyrenees, through northern Italy, Yugoslavia and Romania across Russia to Siberia (Marshall & Haes 1988). It is common in different types of grass vegetation, both dry and wet. Nymphs of both species hatch in May and progress through six instar phases before becoming adults (Marshall & Haes 1988). Adult males stridulate from July to October and if the weather is warm or sunny they will stridulate almost continuously during the day at this time. Each species' song is characteristic, making the males of the species easy to census. A variable proportion of the population of both species are macropterous (winged), but these numbers are low and in *M. roeseli* less than 1% (Vickery 1965).

The introduction experiment and censuses

Propagules of *M. roeseli* were introduced onto 70 habitat islands, in parts of the country previously uninhabited by the species in a large-scale experiment in 1994-1995 (Berggren 2001). The habitat islands used were situated at a minimum distance of 17 km from the edge of the species' current distribution range and were expected to be incorporated in the species distribution range within 10 years due to the species spreading behaviour. The islands were of ungrazed seminatural grasslands and the minimum distance between the introduction sites was 2 km. The experimental areas were situated in the agricultural landscapes in the counties of Uppland and Stockholm, located in south-eastern Sweden. *Metrioptera roeseli*'s current restriction to well-defined areas in the south-east of Sweden, its documented range expansion and its conservation status, make it an ideal model species and an excellent candidate for introduction experiments. Moving it from areas where it occurs abundantly to areas where it has yet to colonise meant that individuals later found at the introduction sites were either the originally introduced individuals (if found the same year) or their descendants. This ensured that there would be no confusion with already existing individuals and allowed easy interpretation of the species'



Figure 3. Road verges, like the ones examined in this study, and other linear elements in the landscape facilitate the dispersal and the spread of the species. Photo: Åsa Berggren

Dikesrenar, som de som inventerades i denna studie, och andra linjära landskapselement underlättar spridningen av vårtbitare i landet.

ability to establish and expand in the landscape (see Berggren 2001 for more details).

Populations with numbers of *M. roeseli* of over 25 males in the latest census (1999) were used in this study, producing a total of 25 introduction sites (Fig. 2). Censuses were carried out by listening for stridulating males of both species during the reproductive seasons of 2001 and 2002. Because of the grass composition of road verges, these areas are preferred habitats for both species and provided the focal point for all censuses. A 50 m stretch of road verge (Fig. 3) was searched in each area where *M. roeseli* had colonised. Within these areas, every individual male of the two species was recorded. Control sites for the study were located within a few hundred metres from the edge of distribution of each of these introduced populations, and consisted of the same dimensions of road verge (length, width and depth) and vegetation type. The control sites were censused on the same occasion for individuals of *M. brachyptera* and in the same way as the area in the introduction site. The censuses were only made during sunny days, with a temperature over 18°C to ensure that the bush-cricket were stridulating and could be detected. Numbers of individual males of the two species from each introduction and control site were then compared. As the distribution of *M. roeseli* expanded slightly between the

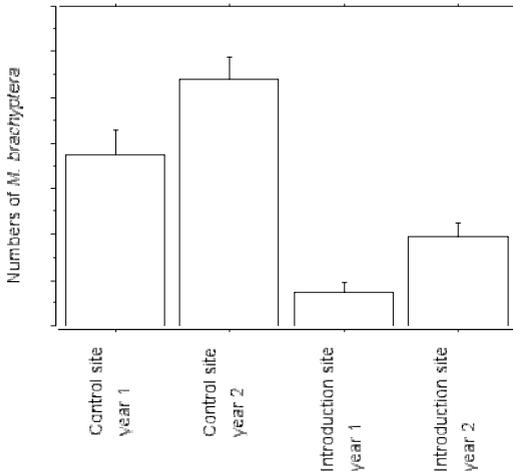


Figure 4. Mean numbers \pm SE of *M. brachyptera* for year one and year two in sites where *M. roeseli* is present compared to the control sites where *M. roeseli* has not yet invaded.

Medelantal \pm SE av *M. brachyptera* första och andra studie året på lokaler där *M. roeseli* introducerats jämfört med kontrollområden där *M. roeseli* ännu inte finns.

seasons the control sites used were not the same for both seasons.

Statistical Analyses

The distribution of the variables and residuals were tested for normality by using a Shapiro-Wilk W test and were found not to be normal (all $p < 0.05$). The variables were then transformed by using $Y \oplus \sqrt{Y} + \sqrt{Y+1}$ (Freeman & Tukey 1950), which resulted in normal to near normal distribution of both the variables and the residuals. An ANOVA (analysis of variance) was used to investigate if there was an interaction effect between years and type of site (introduction sites and control sites) that could influence analyses combining the two years. An ANOVA was also used to examine if there was a difference in number of *M. roeseli* between years. An ANCOVA (analysis of covariance) with the type of site (with or without *M. roeseli*) used as a covariate, were used to examine if there were differences between years and the number of *M. brachyptera*. To compare the presence of *M. brachyptera* between sites with and without introduced *M. roeseli* a chi-square test was used. To investigate if there was a relationship

Table 1. Numbers (mean \pm SE) of *M. brachyptera* and *M. roeseli* within a 50 m road-verge habitat during the study years at the different sites.

Antal (medel \pm SE) av *M. brachyptera* (ljung-) och *M. roeseli* (cikadavårtbitare) längs 50 m habitat sträcka i de olika typerna av lokaler under de två studieåren.

Site	Study year	<i>M. brachypt.</i> (mean \pm SE)	<i>M. roeseli</i> (mean \pm SE)
Introduction site	1	0.72 \pm 0.23	8.52 \pm 0.70
	2	1.96 \pm 0.29	10.72 \pm 0.74
Control site	1	3.76 \pm 0.52	-
	2	5.40 \pm 0.47	-

between the number of *M. brachyptera* in sites with and without *M. roeseli* an ANCOVA with years as a covariate was used. A Pearson product-moment correlation tested if there was a correlation between numbers of male *M. brachyptera* and *M. roeseli*.

Results

There was no interaction effect between year and type of site (introduction sites and control sites) (ANOVA, $n=100$, $F=0.39$, $p=0.53$). *Metrioptera roeseli* was a more abundant species (number of individuals per 50 m) than *M. brachyptera*, and both species' abundances changed between the years. Both the numbers of *M. brachyptera* and *M. roeseli* were higher the second year than the first (Table 1, *M. brachyptera*: ANCOVA, $n=100$, $F=12.75$, $p=0.0006$; *M. roeseli*: ANOVA, $n=50$, $F=4.67$, $p=0.036$).

There was a difference between the introduction and control sites in the presence of *M. brachyptera*. Combining the two years, 20 of the 50 introduction sites (40%) were without a single male of *M. brachyptera* while only 2 of the 50 control sites (4%) were without a male *M. brachyptera*. Numbers of *M. brachyptera* were higher in sites without *M. roeseli* (ANCOVA, $n=100$, $F=65.05$, $p < 0.0001$) (Fig. 4). In the introduction sites the numbers of *M. brachyptera* were not correlated with the numbers of *M. roeseli* the first ($n=25$, $r=0.045$, $p=0.83$) or the second year ($n=25$, $r=0.138$, $p=0.609$) (Fig. 5a, b).

Discussion

This study showed that 18 more introduction than control sites were without a single *M. brachyptera* male, which represents a 90% de-

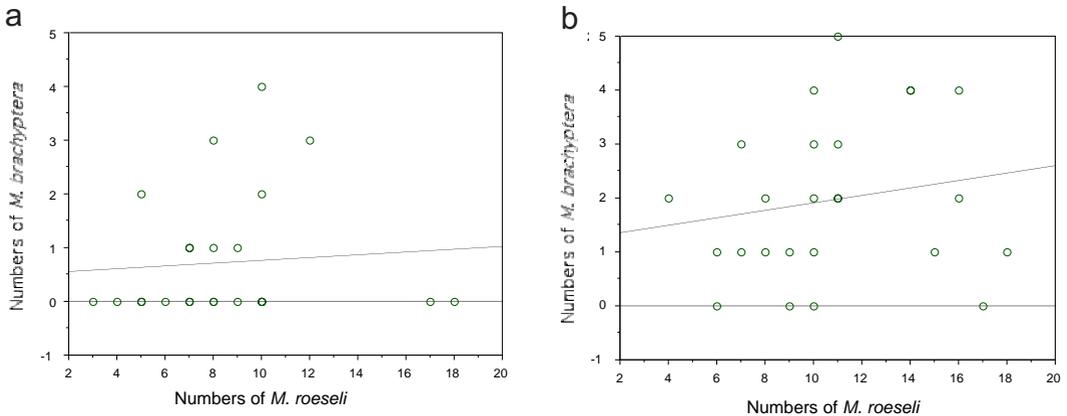


Figure 5. The relationship between numbers of *M. brachyptera* and *M. roeseli* study year one (a) and two (b) in sites where *M. roeseli* had been introduced.

Förhållande mellan antal ljungvårbitare (*M. brachyptera*) och cikadavårbitare (*M. roeseli*) studieår ett (a) och studieår två (b) i områden där cikadavårbitaren hade introducerats.

crease in sites with *M. brachyptera*. Even if *M. brachyptera* females were left in these areas, no males remained for them to mate with. In introduction sites where *M. brachyptera* males were still present (though fewer), mating opportunities for females still existed and reproduction was likely to occur. Unfortunately, because of their smaller effective population size in these areas, this would increase the extinction risk associated with small populations (Richter-Dyn & Goel 1972). Varying abundances between years did not alter the fact that the presence of *M. roeseli* affected the presence of *M. brachyptera* males in a negative way. Thirty-six percent of sites where *M. roeseli* was introduced and had established a population, had no *M. brachyptera* despite the matched control area containing *M. brachyptera*. In sites where *M. brachyptera* coexisted with *M. roeseli*, the density was always lower than in the control sites. It appears that the presence rather than the actual number of *M. roeseli* is the major determining factor affecting the presence of *M. brachyptera*.

No data was collected on the abundance of *M. brachyptera* males at the introduction sites prior to *M. roeseli* establishing. Despite this, there is nothing in the distribution pattern of the sites to explain the effect seen in this study other than the presence or absence of *M. roeseli*. The 25 sites differ significantly in landscape characters

such as the type and amount of different landscape elements, farm practices and local climate. Several of the introduction sites are tens of kilometres apart (Berggren *et al.* 2001). Therefore, it is reasonable to assume that *M. brachyptera* existed at a similar density as the matched control sites in all introduction areas before *M. roeseli* was introduced. Because of this, we believe that *M. brachyptera* has declined in these areas as a direct result of the presence of *M. roeseli*. The mechanism behind this decline is unclear, with there being several possibilities such as limitation of: food, olfactory space and acoustic space; these are discussed below.

Food limitation

Food resources (grass and grass seeds) in the study areas appear to be superabundant. The road verges are un-cut and ungrazed by during the study animals' life-times, leaving the vegetation high and dense. Due to the habitat structure there is a moisture gradient within it, which is important for keeping the vegetation growing throughout the season and making it a good habitat for both species (Berggren *et al.* 2001). An average road verge width of 1.1 m in this study produces a density of 0.17 individuals of *M. roeseli* per m² and 0.08 individuals of *M. brachyptera* per m². These densities are almost two orders of magnitude lower than the lowest densities

found to have a food limitation effect (Joern & Klucas 1993). Thus, food competition is unlikely to be responsible for the differences seen in our study.

Limitation of olfactory space

A means of communication between some species of orthopterans are chemical cues produced from hydrocarbons in the individual's cuticula (Nagel & Cade 1982). These pheromones are responsible for the well-known aggregation behaviour seen in locusts (Obeng-Ofori *et al.* 1994). For some orthopteran species, pheromones make it possible for individuals to gain information about other individuals' age and sex (Tregenza & Wedell 1997, Ochieng & Handsson 1999). While pheromones have been shown to have an effect on male stridulation in the field cricket *Gryllus bimaculatus* (Tregenza & Wedell 1997), we do not know of any study investigating pheromones in *M. roeseli* or *M. brachyptera* or any related species. Thus we cannot rule-out the possibility that these two species are using chemical signalling and are competing for olfactory space.

Limitation of acoustic space

A large part of the energy expenditure for the males of both species during summer is their almost continuous stridulation - calling for females by rubbing their wings together (Hoback & Wagner 1997). The male's mating success is at least partly determined by females hearing his stridulation. In addition to microclimatic and vegetation interference effects, an important factor determining how females perceive a male's stridulation, is the calling of other males. Males from the same or different species can mask each other's songs, so pieces or larger parts of the song become inaudible to females (Bailey & Morris 1986). Masking and modifying songs has been observed in several species, i.e. *Metrioptera bicolor* mask the call of *Psorodonotus illyricus* (Keuper *et al.* 1986), *Platycleis albopunctata* is inhibited by the *M. roeseli* song (Latimer 1981) and in the presence of *Megalopsis marki* the song of *Hemisaga denticulata* is suppressed (Römer *et al.* 1989).

In this study, populations of *M. roeseli* had higher population densities in both years (mean

9.62 males per 50 m) than *M. brachyptera* (mean 4.58 males per 50 m in control sites). If we assume that the equal body size and habitat choice indicate that the area needed for optimal foraging should be similar, then the difference in density may be an effect of the *M. brachyptera* males increasing inter-male distances to reduce acoustic interference. Where acoustic competition occurs, males will maximise their chances of being evaluated by females by providing enough distance between them and other males to enable females to discover the individual callers, but also be close enough to other males to attract females by the concentration of numbers (Arak *et al.* 1990). Another potential problem for *M. brachyptera* is that the exaggerated song of *M. roeseli* may not only mask their call but also attract *M. brachyptera* females through a combination of conspecific scarcity, mistakes in mate recognition and supernormal stimuli (Arak *et al.* 1990, Randler 2002).

Acoustic competition may cause species to exhibit temporary or permanent shifts in calling behaviour (frequency or pulse rate) or shifts in habitat use. Because the calls of *M. roeseli* and *M. brachyptera* are within the same frequency range, it is likely that a *M. roeseli* male calling close to a *M. brachyptera* male will mask some of its song (Latimer & Broughton 1984). Where the possibility for call variation to minimise acoustic competition does not exist, a species will need to move out of a habitat to prevent being out-competed. Active spacing behaviour between males has been seen between *P. albopunctata* and *M. roeseli* (Latimer 1981), between *M. bicolor* and *M. roeseli* (McHugh 1971) and between the species *Platycleis affinis* and *P. intermedia* (Samways, 1977a). Thus while it is often assumed that differences in distribution reflect particular habitat needs, it may simply be a result of competitive exclusion (Beckerman 2000). As *M. roeseli* and *M. brachyptera* have not co-existed before in Sweden, there has not been time for evolution to act to separate permanent types of calls and create specific calling niches for the two species. Instead, it may be that the dominant caller (*M. roeseli*) is affecting *M. brachyptera* numbers through the natural acoustic competitive avoidance reaction of the subordinate species, producing the pattern seen in the introduction sites.

Implications for conservation

In this study we did not monitor the number of females of the two species mainly for methodological reasons. Females are difficult to accurately and consistently locate as they do not stridulate and both species are cryptically coloured. The drawback of not having data on female abundance is that we do not know to what frequency females were present in the introduction and control sites. However, regardless of female abundance, we can see that males of one orthopteran species can negatively affect the presence of males of a closely related species. While the lack of data on females prevents us from generalising to the whole population, it is likely that the change seen in male densities reflects a significant shift in population dynamics and potentially an increased local extinction risk for *M. brachyptera*. While competition is likely to be the cause of *M. brachyptera*'s decline, the mechanisms behind it are not clear and require further study.

The findings of this study provide an important clue that in some species, habitat selection may be a function of competition as one or both species escape a disadvantageous situation. If the displacement of *M. brachyptera* is ubiquitous and continues, the two species' distributions will shift resulting in *M. roeseli* dominating grassland habitats and *M. brachyptera* being forced into drier, less preferred habitat in heath lands and forest edges. Being pushed into marginal habitats may increase the mortality of individuals and thereby increase the extinction risk of sub-populations. One of the primary threats to species conservation today is human activity causing deterioration and fragmentation of habitats (Fahrig 1997). This can force species together (native/native or native/exotic) that otherwise would have been able to escape competition through dispersal to new patches or utilise other resources in a heterogenous environment (Samways 1977b, Kiensecker *et al.* 2001). Increased competition created by fragmentation will be compounded by ongoing undesirable species introductions. The combined effect of habitat fragmentation and novel species' competition currently presents a major biodiversity conservation challenge.

Acknowledgements

We are thankful to Oskar Kindvall, Mattias Jonsson, Bengt Gunnarsson and Mats Jonsell for valuable comments on earlier drafts of the manuscript.

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Sammanfattning

Cikadavårtbitaren *Metrioptera roeseli* utbredningsområde ökar främst i södra Sverige. Det är möjligt att detta kan påverka inhemska arter förekomst negativt. Vi undersökte hur den närbesläktade ljungvårtbitarens (*Metrioptera brachyptera*) antal påverkas av cikadavårtbitarens närvaro. Tjugofem områden som cikadavårtbitaren hade koloniserat jämfördes med tjugofem matchade kontrollområden där cikadavårtbitaren saknades. Vi noterade förekomst och antal av hannar av ljungvårtbitare på dessa lokaler. Ljungvårtbitare saknades på 40% av områdena med cikadavårtbitare jämfört med 2% av kontrollområdena och fanns i statistiskt signifikant större antal i kontrollområdena. Då förekomst av föda verkar vara riklig, är det antagligen konkurrens om andra resurser som ljud- och luktutrymme som leder till det funna mönstret. Om undanträngandet av ljungvårtbitaren som vi sett i denna studie är ett generellt mönster och fortsätter, kan de två arternas utbredning komma att ändras i framtiden. Cikadavårtbitaren kan komma att dominera i gräsmarker medan *M. brachyptera* kan bli tillbakaträngd till torrare och mindre föredragna habitat såsom hedlandskap och skogskanter.