SHORT COMMUNICATION

Evidence for mate-encounter Allee effect in an invasive longhorn beetle (Coleoptera: Cerambycidae)

MARC RHAINDS,[1] STEPHEN B. HEARD,[2] CORY HUGHES,[1]
WAYNE MACKINNON,[1] KEVIN PORTER,[1] JON SWEENEY,[1]
PETER SILK,[1] IAN DEMERCHANT,[1] SARAH MCLEAN[1]
and GARRETT BRODERSEN[1] [1]Natural Resources Canada, Canadian Forest Service - Atlantic Forestry
Centre, Fredericton, New Brunswick, Canada and [2]Department of Biology, University of New Brunswick, Fredericton, New
Brunswick, Canada

Abstract. 1. Limited empirical support is available for mate-encounter Allee effects in invasive insects due to the logistical challenges of studying demographic trends in low-density populations.

2. Traps baited with pheromone and spruce volatiles were used to monitor the abundance of female *Tetropium fuscum* F. (Coleoptera: Cerambycidae) at multiple sites in Nova Scotia in 2011 and 2012. Each female was dissected to determine the presence or absence of sperm in its spermatheca (mated or virgin female, respectively).

3. Both male and total *T. fuscum* abundance declined with increasing distance to the focal point of *T. fuscum*'s invasion. Female mating probability declined with male abundance and with distance from the invasion focus, and mating probabilities were very low at the most peripheral sites. Difficulty in encountering mates may thus contribute to limiting the spread of *T. fuscum*.

4. The approach outlined here could be integrated into existing surveys of wood borers using traps baited with semiochemicals to improve our understanding of the role of the mate-encounter Allee effect in invasion dynamics.

Key words. Female mating failure, geographical range boundary, invasion pinning.

Introduction

Allee effects (reduced individual fitness at a low population density) are believed to be widespread in nature, although the difficulty in studying sparse populations means that well-documented cases remain uncommon (Drake & Kramer, 2011). Allee effects have been proposed as a general principle of ecology (Berryman, 2003), with implications for population dynamics, biogeography, and evolution. While Allee effects may arise from a variety of mechanisms, one of the most common is the individual's difficulty locating mates when local population densities are low (Gascoigne *et al.*, 2009; 'mate-encounter' Allee effect).

Mate-encounter Allee effects may have especially important consequences for biological invasions, because of their potential to modulate the rate of invasion spread and 'pin' invasion boundaries, suppressing further spread (Keitt *et al.,* 2001; Tobin *et al.*, 2011). The persistence of insect populations may be particularly sensitive to mate-encounter Allee effects (Kramer *et al.*, 2009), and insects account for the majority of invasive animal species (Pyšek *et al.*, 2008). Surprisingly, however, empirical support for mate-encounter Allee effects among insects is limited (Gascoigne *et al.*, 2009; Fauvergue, 2013). In the context of invasions, for example, the existence of mate-encounter Allee effects has thus far been demonstrated unequivocally only for the gypsy moth, *Lymantria dispar* L. (Lepidoptera: Lymantriidae) (Contarini *et al.*, 2009; Tobin *et al.*, 2013).

The brown spruce longhorn beetle, *Tetropium fuscum* F. (Coleoptera: Cerambycidae) (BSLB), is a Palearctic woodborer that feeds on *Picea* species. It was introduced to Halifax, Nova Scotia, with the earliest detected specimens from 1990 (Smith & Hurley, 2000). The invasion range of BSLB has expanded slowly and may be 'pinned' geographically approximately 80 km from its point of introduction (Rhainds *et al.*, 2011).

The slow spread of BSLB may have several causes. Anthropogenic spread of BSLB through the movement of infested wood appears minor compared with other invasive wood-boring insects (Tobin *et al.*, 2010), in part as a result of regulatory measures that have restricted the movement of potentially infested spruce logs. The natural dispersal of BSLB is only by adults (larvae complete development within the subcortical tissue of their hosts), and females emerge sexually mature and reproduce within hours (Juutinen, 1955), often very near their emergence site and presumably on their natal host trees. Laboratory experiments using flight mills reveal that adult BSLB are capable of lengthy flights (as much as 14 km, and on average nearly 2 km in 24 h; J. Sweeney, unpublished), but the incidence of long-distance dispersal in nature remains unclear.

A mate-encounter Allee effect in low-density peripheral populations is a potential alternative explanation for the limited spread of BSLB. Under this scenario, high rates of mating failure at the margins of the invasion range reduce population growth and could lead to local extinction events. We tested this hypothesis for BSLB by assessing the mating status (mated or virgin) of BSLB females captured in semiochemical-baited traps deployed throughout its invasion range.

Materials and methods

We trapped BSLB at sites in Nova Scotia in 2011 (29 sites) and 2012 (37 sites, of which 22 were repeated from 2011; Fig. 1). Each site consisted of a forest stand with red or white spruce [*Picea rubens* Sarg. and *P. glauca* (Moench) Voss, respectively] as dominant or co-dominant trees. At each site, we deployed 3–20 black panel traps (AlphaScents, Bridgeport, New York), each baited with the male-produced pheromone (E)-6,10-dimethyl-5,9-undecadien-2-ol (fuscumol) and host volatiles (monoterpenes and ethanol). For a detailed description of semiochemicals and release rates, see Sweeney *et al.* (2010) and Rhainds *et al.* (2011). Trapping was conducted at each site over the entire flight period from mid-May to late August. In BSLB, both sexes are attracted to the male-produced pheromone, and host volatiles synergize attraction (Silk *et al.*, 2007; Sweeney *et al.*, 2010). We report and analyse data only for sites where at least one female was captured.

We collected beetles from the traps every other week and stored them in 70% ethanol for subsequent identification and sexing. We placed each female, ventral side up, in a glass dish with a thin layer of distilled water under a stereoscope. We removed the two terminal abdominal segments with dissection scissors, then removed the spermatheca (a tan coloured, comma-shaped structure) using fine-tipped forceps, rinsed it, and mounted it in a drop of glycerol on a glass micro slide. Slides were examined under a compound microscope to determine the presence or absence of sperm in the spermatheca. We calculated the proportion of mated females (vs. total females) for each site.

We asked whether log-transformed male and total densities (beetles/trap) declined with distance from the invasion focus, using linear regression. For count data, log transformations yield a better-controlled type I error than generalized linear models assuming a Poisson distribution (Ives, 2015). We began by modelling density as a function of distance, year, and the
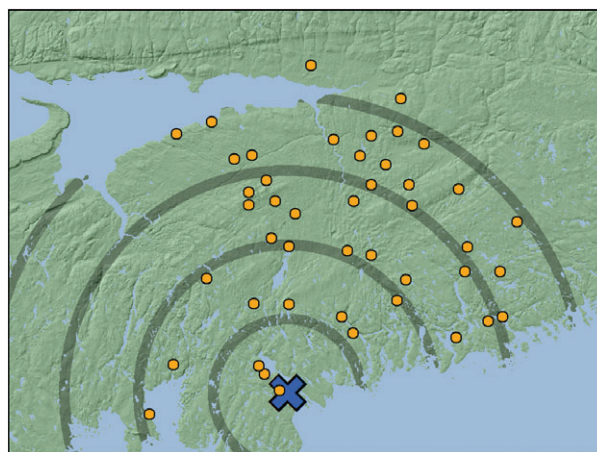
Fig. 1. *Tetropium fuscum* trapping sites (for 2011 and 2012) in Nova Scotia, Canada. The cross indicates the focal point of *T. fuscum*'s introduction, near Halifax, and arcs show distances from the focal point in 20-km increments.

distance × year interaction, but then deleted the interaction and the year effect in turn when neither approached significance. To examine effects on mating success, we used a generalised linear model assuming a binomial distribution (logistic regression). This model included male density, distance, and year; we added male density first and asked whether distance (and then a year) explained further variance after accounting for male density. Finally, we fitted mating success to male density using the 'mechanistic Allee effect' function (e.g. McCarthy, 1997): $P(\text{mated}) = 1 - \exp(-M/\alpha)$, where M is male density and α measures the strength of the Allee effect. All analyses were conducted in R 3.1.1 (R Core Team, 2014).

Results

Male density declined with distance to the invasion focus in both years ($R^2 = 0.32$, $F_{1,64} = 30.5$, $P = 6.6 \times 10^{-7}$; effects for year and distance × year interaction both $P > 0.45$). The same was true for total density ($R^2 = 0.57$, $F_{1,64} = 85.0$, $P = 2.3 \times 10^{-13}$; effects for year and distance × year interaction both $P > 0.13$). The proportion of mated females was higher in 2011 than 2012, but in both years increased significantly with male density and declined with distance from the invasion focus (Table 1, Fig. 2; analysis using total density rather than male density yielded similar results). We trapped no mated females at any site > 80 km from the invasion focus.

The fit to the mechanistic Allee effect function yielded $\alpha = 4.01 \pm 0.96$ (SE) ($P = 9.7 \times 10^{-5}$), but the fit was poor (Fig. 2a, dotted line), with mating underestimated at low male densities and overestimated at high male densities.

Discussion

Densities (captures per trap) declined with distance from the invasion focus for males only and total captures. Traps baited with spruce volatiles and fuscumol catch ~1.4 times as many

Table 1. Effects of male density, distance, and year on *Tetropium fuscum* mating probabilities (analysis of deviance from a generalised linear model).

Effect	Direction	d.f.	Deviance	Residual d.f.	Residual deviance	P
(Intercept)	–	–	–	65	222.8	–
Male density	Positive	1	82.0	64	140.8	2×10^{-16}
Distance	Negative	1	30.7	63	110.0	3×10^{-8}
Year	2011 > 2012	1	16.4	62	93.6	5×10^{-5}
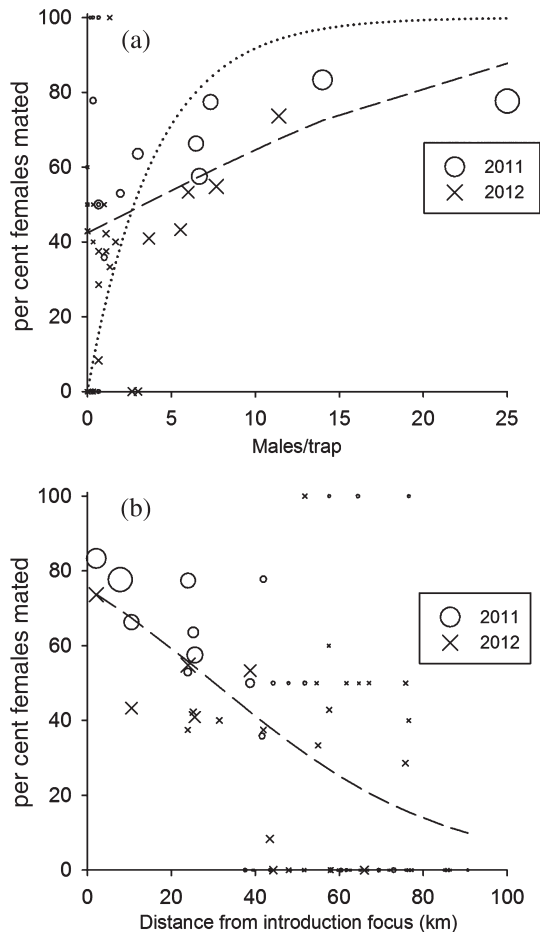
Fig. 2. Female mating percentages for each site as a function of (a) male density and (b) distance from the invasion focus. Symbol area is proportional to a site's total beetle captures. Fit lines for separate logistic regressions on male density or distance are shown (dashed) for illustrative purposes only; we interpret the full model as reported in Table 1. Dotted line in panel (a) is for the alternative 'mechanistic Allee effect' fit.

females as males (Sweeney *et al.*, 2010); thus we cannot directly measure the sex ratio. However, because this effect applies equally to all traps, patterns in male densities can be interpreted with confidence.

We observed a low mating success of females at sites with low male densities, consistent with a mate-encounter Allee effect (although, without experimental manipulation of male density, we cannot unequivocally point to causation). Low-density sites were, in general, distant from the invasion focus; however, distance explained significant deviance in mating probability even after accounting for male density. This distance effect could arise because distance is correlated with unknown factors influencing mating probability, such as climate suitability or habitat quality. Alternatively, distance (which we can measure precisely) may be a better proxy for local beetle density than our trap captures (which will be imperfectly correlated with actual density). Because mating probabilities were very low for the most peripheral sites, mate-encounter Allee effects could be playing an important role in limiting the spread of BSLB.

An alternative approach fitting our data to the mechanistic Allee effect function yielded a poor fit. This is not surprising, for two reasons. First, that function as commonly used (e.g., McCarthy, 1997) does not allow mating probability to plateau below 100%; in our data, at least 17% of females remained unmated at every site. Second, the mechanistic function assumes undirected search by males for randomly distributed females, whereas in BSLB both males and females are attracted to male-released pheromone. Nevertheless, we report fitted values to facilitate comparison with literature results.

Our results are significant in light of the limited empirical support for the mate-encounter Allee effect in invasive insects. The major challenge in documenting Allee effects is rooted in the logistical difficulty of studying demographic processes in low-density populations (Gascoigne *et al.*, 2009). These challenges are amplified early in the invasion process, and for cryptic species such as BSLB. For cerambycids, semiochemical baiting has become a major tool for monitoring (relative) local densities over large areas (Brockerhoff *et al.*, 2006), and the captured specimens can be assessed relatively easily for mating history. All this makes BSLB, and invasive cerambycids in general, promising model systems for understanding mate-encounter Allee effects and their role in controlling invasion spread and geographical range limits.

Acknowledgements

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