Ecological Entomology

Ecological Entomology (2021), **46**, 1205–1214 DOI: 10.1111/een.13068

Mechanisms driving component Allee effects during invasions: using a biological control agent as model invader

HESTER E. WILLIAMS,[1] ECKEHARD G. BROCKERHOFF,[2,3] ANDREW M. LIEBHOLD[4,5] and DARREN F. WARD[1,6] [1]School of Biological Sciences, University of Auckland, Auckland, New Zealand [2]Scion (New Zealand Forest Research Institute), Christchurch, New Zealand, [3]Swiss Federal Research Institute WSL, Birmensdorf, Switzerland, [4]USDA Forest Service Northern Research Station, Morgantown, West Virginia, USA, [5]Faculty of Forestry and Wood Sciences, Czech University of Life Sciences Prague, Praha, Czech Republic and [6]New Zealand Arthropod Collection, Landcare Research, Auckland, New Zealand

Abstract. 1. A demographic Allee effect refers to increasing per capita population growth with increasing abundance. It arises from component Allee effects, which exist when some component of individual fitness has a positive relationship with density. Newly arrived populations tend to be small, and their establishment success is influenced by various factors, including demographic Allee effects. Identifying mechanisms driving the Allee effect is of relevance for understanding establishment failure, developing strategies for improving biological control and conservation, and for managing biological invasions.

2. We utilised an invasive plant biocontrol agent, *Neolema ogloblini*, as model to study Allee effects experienced by invading populations. We investigated mating failure and predator satiation as two component Allee effects that could potentially drive a demographic Allee effect in *N. ogloblini* populations.

3. We released unmated adults onto isolated host patches using five release sizes and evaluated the mating status of females after 3 weeks in the field. The probability of being mated increased as number of males recovered increased, suggesting the presence of a mating-failure component Allee effect in very small populations of *N. ogloblini*. Exclosures were used to evaluate survival of immatures of *N. ogloblini* developing in small group sizes, either in the presence or absence of generalist predators. Results revealed high levels of predation, but a positive relationship between larval survival and group size in the presence of generalist predators could not be verified.

4. Our study identified relevant life-history traits contributing to establishment failure in *N. ogloblini* and demonstrates the value of biocontrol agents as models to study mechanisms of species invasion.

Key words. Density dependence, generalist predation, invasion, mating failure, *Neolema ogloblini*, *Tradescantia*.

Introduction

When arriving in a novel region, small populations of non-native species, whether deliberately or accidentally introduced, face challenges that can influence their survival, reproduction, and ultimately their establishment. One of these challenges is the Allee effect, which refers to positive density-dependence, that is, individual fitness increasing as population size increases (Stephens *et al.*, 1999).

Stephens *et al.* (1999) distinguish between component and demographic Allee effects. When a population experiences a component Allee effect, some component of individual fitness has a positive relationship with density (e.g. individual

Correspondence: Hester E. Williams, School of Biological Sciences, University of Auckland, PB 92019, Auckland, New Zealand. E-mail: hester.williams@yahoo.ca

survival or reproduction is reduced at low density) (Stephens *et al.*, 1999). In some cases, a component Allee effect leads to a demographic Allee effect for which per capita growth rate is reduced at lower population densities, potentially leading to negative growth and local extinction (Stephens *et al.*, 1999). A component Allee effect does not always give rise to a demographic Allee effect, as the negative influence of density on one component of fitness may be offset by the positive influence on others (Angulo *et al.*, 2007; Berec *et al.*, 2007; Gregory & Courchamp, 2010). Allee effects are caused by mechanisms such as mate-finding failure, insufficient cooperative behaviours (e.g. cooperative feeding or defence), lack of predator satiation, and reduced foraging efficiency, and have been found in a wide range of taxa (Kramer *et al.*, 2009).

Mate-finding failure is one of the most frequently reported causes of a component Allee effect (Gascoigne *et al.*, 2009; Kramer *et al.*, 2009; Yamanaka & Liebhold, 2009a; Fauvergue, 2013; Shaw *et al.*, 2018) and can arise for a variety of reasons. Firstly, in small or low-density populations, mating failure may result simply from low adult density. Secondly, temporal mismatch between the emergence pattern of males or females (protandry or protogyny) can result in mating failure. For example, Rhainds (2013) found that males of the bagworm *Thyridopteryx ephemeraeformis* (Haworth) emerged earlier than females in the season and caused a lower ratio of males per female late in the season. The ensuing decline in female mating probability later in the season due to protandry provided indirect evidence for a component Allee effect resulting in local extinction of populations (Rhainds, 2013). Thirdly, spatial mismatches in reproductive activity between males and females may influence the ability to find mates. Walter *et al.* (2015) found that spatial heterogeneity in temperature resulted in heterogeneity in developmental time, and the resulting reproductive asynchrony reduced population growth of invading gypsy moth (*Lymantria dispar* (L.)) populations. Lastly, in small or low-density populations, mating failure may result simply due to the low probability of random encounters between males and females (or their sexual communication signals) (Gascoigne *et al.*, 2009; Fauvergue, 2013). For example, Régnière *et al.* (2013) found a component mate-finding Allee effect in the eastern spruce budworm (*Choristoneura fumiferana* (Clemens)) with increasing mating success correlated with increasing population density. No study has yet clearly demonstrated a causal relationship between mating failure and lower rates of population growth (Fauvergue, 2013), even though such mechanisms are likely to be important in many species (Contarini *et al.*, 2009; Tobin *et al.*, 2013). In *L. dispar*, most data suggest that mating failure at low density is the most likely explanation for a demographic Allee effect in this moth species (Liebhold & Bascompte, 2003; Tobin *et al.*, 2009), but other processes cannot be entirely ruled out (Fauvergue, 2013). However, the high measurement error that typically occurs when sampling low-density populations greatly constrains our ability to detect Alee effects (Kramer *et al.*, 2009).

More recently, there has been increased interest in the potential for predator–prey interactions to produce a component Allee effect as a result of a Type II predator functional response (Gascoigne & Lipcius, 2004; Kramer & Drake, 2010). With a Type II functional response, predators do not actively search for prey but encounter them randomly; thus, the predator consumption rate decreases with increasing prey density as a result of predator satiation. This pattern is especially true for predation by generalist predators (Pavlová & Berec, 2012). In these circumstances, an Allee effect may emerge in the prey population at low densities; the lower the prey density, the lower the probability of each individual escaping predation (Gascoigne & Lipcius, 2004; Berec *et al.*, 2007; Gregory & Courchamp, 2010). Since predation is a fundamental ecological mechanism, and a Type II functional response in predators is the most frequent type of functional responses observed in nature (Pavlová & Berec, 2012), a predator-driven Allee effect can potentially impact the establishment of many newly arrived, small populations of non-native species, irrespective of their life history (Gascoigne & Lipcius, 2004; Kramer & Drake, 2010). However, there has been limited evidence for a predator-driven demographic Allee effect in invertebrates when compared with vertebrates, and Kramer *et al.* (2009) speculated this was either the result of study bias or a real difference between taxonomic groups, thus identifying a need for further research. Nonetheless, predation by larvae of two midge species in the genus *Chaoborus* can cause extinction of small populations of a water flea *Daphnia magna* Straus via a predator-driven demographic Allee effect (Kramer & Drake, 2010). The gypsy moth has been a prominent exemplar for studies on the Allee effect, and although a generalist predator *Peromyscus* spp., a deer mouse, is regarded as one of the most important predators of low-density gypsy moth populations (Tobin *et al.*, 2009; Larsen *et al.*, 2018), the role of natural enemies in causing or contributing to the demographic Allee effect in gypsy moth populations is still unclear (Tobin *et al.*, 2009; Walter *et al.*, 2015).

The outcomes of weed biological control introductions could potentially provide indirect evidence of predator-driven Allee effects causing declining population growth and establishment failure. It has been reported that native natural enemies may interfere with the initial establishment of weed biocontrol agents or their subsequent population build-up, spread, and impact (Sebolt & Landis, 2004; Ding & Blossey, 2005; Ghosheh, 2005; Downey *et al.*, 2007; Crider, 2011). However, evidence for the importance of predation in limiting biocontrol agent populations is largely anecdotal (Dávalos & Blossey 2010), but since predators have to be 'caught in the act', predation is likely under-reported (Paynter *et al.*, 2018). In their study on the impact of predation by a mirid bug *Plagiognathus politis* Uhler on the leaf beetle *Galerucella calmariensis* (L.), a biocontrol agent against *Lythrum salicaria* L. in North America, Hunt-Joshi *et al.* (2005) found evidence that suggested there may be a population threshold above which the beetle may escape the limiting influence of mirid predation. In New Zealand, predation is considered to significantly reduce the establishment and impact of at least four agents on their target weeds, with the potential of more unsuccessful agents being added to the list in future surveys investigating predation levels (Paynter *et al.*, 2018).

Releases of biological control agents provide opportunities to experimentally study ecological and evolutionary

processes associated with invasion success (Ehler, 1998; Fagan *et al.*, 2002; Marsico *et al.*, 2010; Fauvergue *et al.*, 2012; Schulz *et al.*, 2021). Non-native species and biological control agents face similar obstacles throughout the invasion process, though success may likely be greater for biocontrol introductions, which are typically conducted under conditions favourable for establishment. In this study, we used a leaf beetle *Neolema ogloblini* (Monrós) (Coleoptera: Chrysomelidae), a biocontrol agent released against *Tradescantia fluminensis* Vell. (Commelinaceae) in New Zealand, as a model species to improve our understanding of the source and influence of component Allee effects experienced by incipient populations of non-native species. Results of a companion study indicated the presence of a demographic Allee effect in small populations of this beetle species (Williams *et al.*, 2020). Here, we focused on two mechanisms as candidate component Allee effects that could potentially drive the demographic Allee effect in small populations of *N. ogloblini*. The first is mate-finding failure and was chosen on the premise that all sexually reproducing organisms are potentially vulnerable to this mechanism (Fauvergue, 2013). The second mechanism evaluated was predation of immature life-stages, which was motivated by observations of high rates of larval disappearance in previous field experiments (Williams *et al.*, 2020).

It was expected that (i) the existence of a mate-finding component Allee effect will cause more unmated females to be found in smaller releases, and (ii) the presence of a predator-driven component Allee effect will cause survival of larvae to be lower in smaller groups.

Materials and methods

Study system

Neolema ogloblini is a specialist leaf-feeding chrysomelid beetle utilising both *T. fluminensis* and *T. mundula* Kunth as hosts (Fowler *et al.*, 2013). A colony of *N. ogloblini* was obtained from beetles reared by Landcare Research (Lincoln, New Zealand) for the biocontrol programme against *T. fluminensis* in New Zealand, originally imported from Brazil (Lages and Curitiba). A population of beetles was maintained year-round in a glasshouse environment on caged, potted plants of *T. fluminensis* (hereafter referred to as the 'general population'). Temperatures in the glasshouse varied between 15 and 25 °C in winter and 15 and 30 °C in summer.

Tradescantia fluminensis and *T. mundula* are native to south-east Brazil and northern Argentina, *T. fluminensis* has escaped cultivation in New Zealand and is now considered as one of New Zealand's worst invasive forest weeds (Syrett, 2002). Plants used in this study were grown from cuttings in plant trays under greenhouse summer conditions, using a well-draining, compost-rich potting medium. Cuttings were obtained from *T. fluminensis* and *T. mundula* stock plants maintained at Landcare Research.

Experiment 1: impact of male density on the mating status of Neolema ogloblini *females.*

This experiment was conducted at 24 sites in the Selwyn district of Canterbury, New Zealand, in the southern hemisphere summer of 2017/2018 and again in late summer 2019. All sites were located in an area classified as the Canterbury-Otago tussock grasslands ecoregion (McEwan, 1987). *Tradescantia mundula* and *T. fluminensis* are not widespread in the district, but even so, care was taken to ensure sites were not close to naturalised patches of either species. This prevented beetle populations emigrating from unknown host patches in the surrounding landscape and contaminating experimental plots. As both the beetle species and its host plant prefer shady conditions, all sites were situated under trees, with no access by livestock and a minimum distance of 500 m between sites to prevent cross-over dispersal. Adults *of N. ogloblini* rarely disperse over substantial distances without host patches as stepping-stones (in a mark-release-recapture study, only 1% (N = 1200) of adults were able to locate an unoccupied host patch 60 m away (H. Williams, unpublished data)), and a distance of 500 m was deemed as sufficient isolation between sites.

At each site, potted plants were arranged to form a rectangular patch size with a leaf-cover of *ca.* 1 m^2. As a ground-cover species, the *T. mundula* foliage filled the entire area of the plant trays they were grown in, and therefore, patch size was determined by the area of adjoining trays. The potted plants were placed on weed-mat to prevent rooting and minimise the likelihood of the plants becoming established. Plants were watered on a regular basis to ensure plants stayed in a healthy growing condition. The use of patches of potted host plants grown in a shade house enabled control of confounding factors such as host quality, patch size, stem density, nitrogen content, plant physiological stage, and soil type and drainage.

The experiment was run for a period of 3 weeks. We assumed that a 3-week period would be long enough to give an indication of the potential for a mate-finding Allee effect in small populations of the beetle, because under laboratory conditions adults of *N. ogloblini* commence mating after completing a pre-oviposition period of approximately 6 days.

In the first summer (2017/18), the influence of release size on female mating success was evaluated for release sizes consisting of 2, 8, and 16 unmated adults, and in the second summer (early 2019) for release sizes consisting of 8, 16, 32, and 64 unmated adults. There were six replicates for all release sizes in each summer (thus, in total, six replicates each for release sizes 2, 32, and 64 adults, and 12 replicates each for 8, and 16 adults). Replicates were placed out into the field in groups as availability of newly-eclosed adults allowed, with these groups staggered in time (hereafter called 'group-in-time'). In total, there were seven 'groups-in-time'. For summer of 2017/18, replicate groups were staggered over the period from November 2017 to March 2018, and for summer 2019, staggered from March 2019 to April 2019.

To obtain unmated adults of similar ages for the field releases, eggs were collected from the general population and reared on *T. fluminensis* leaves in ventilated plastic containers (30 × 15 × 15 cm) under laboratory conditions (25:18 °C temperature regime, 14 L:8D photoperiod). The day before release, the required number of newly emerged, unmated adults was collected and confined in small mesh bags on cut leaves of *T. mundula* to settle and feed. For release sizes of 32 and 64

adults, individuals were chosen at random, while equal numbers of each sex were used for release sizes of ≤16 adults. The leaves with adults were then gently released in a single location in the host plant patches the next morning when temperatures were cooler, in order to reduce the likelihood of immediate dispersal.

After 3 weeks, the plants were bagged in sealed plastic bags and brought back to the laboratory, carefully searched, and the presence of each life stage noted. Adults were collected and placed individually into small containers with *T. mundula* foliage. Each container was monitored for up to 14 days to determine: (i) the gender of the adult–containers with eggs were assumed to be female, while those without eggs were assumed to be male (females laid eggs irrespective of being mated, though at a lower rate); and ii) the mating status of the females–by determining if any eggs laid were fertilised and hatched into larvae. Foliage was replaced as needed. Any females that did not lay fertilised eggs were then exposed to two males from the general population and any resulting eggs monitored to ensure that she was capable of mating and laying fertilised eggs. Females that laid fertilised eggs only after being exposed to males from the general population indicated that they were unmated when collected from the field and signify mate-finding failure.

Experiment 2: impact of generalist predation on survival of immature stages of Neolema ogloblini. Enclosure experiments to investigate the influence of predation on the survival of *N. ogloblini* immatures at different group densities were conducted in the summer of 2018 (March–April) and again in 2019 (Jan–Feb). The trials were carried out on the grounds of the Lincoln Landcare Research facilities. In 2018, larval survival was measured in groups initiated with 20 or 50 eggs, and with or without predator access. However, low survival observed in both these group sizes prompted additional trials with larger group sizes in 2019, using groups started with 50, 100, and 200 eggs.

Potted plants of *T. mundula*, equal in size and age, were used for the experiments. Following a factorial design, each plant was randomly assigned to one of two levels of predation (exposed or not exposed), and three levels of egg group size (50, 100, or 200 eggs) (only two levels in 2018 with 20 or 50 eggs). To obtain desired initial egg densities, adults were released onto individual potted plants and allowed to oviposit for 2 days. After removing adults, excess eggs were removed to achieve each target group size. Plants were then randomly placed outside under trees with a minimum spacing distance of at least 4 m. To exclude predators, selected plants were enclosed in fine white mesh bags tied closed at the top, but which could be opened to inspect the plant inside. Plants allocated to allow predator access were not enclosed. Larvae are not very mobile and do not normally disperse from suitable host plants, so dispersal from uncaged plants would not be the cause for any differences in density that arose during the experiments. It is acknowledged that the mesh bags may have influenced plant growth and microclimate, which may affect larval performance and thereby contribute to differences in resultant densities. The plants were left in the field for approximately 4 weeks to allow development to the pupal stage. At the end of this period, plants were carefully searched, and the number of pupae recorded. There were three replicates for each group size in 2018 and nine for each group size in 2019.

Statistical analysis

All analyses were conducted in R (R Core Team, 2017). Mixed effects models were implemented using the 'glmer' function in package 'lme4' (version 1.1-21) (Bates *et al.*, 2015) and model fits checked using diagnostic plots generated by the 'DHARMa' package (version 0.4.0) (Hartig, 2018). Predicted probability plots were created using the 'ggpredict' function of the 'ggeffects' package (version 1.0.2) (Lüdecke, 2018).

Experiment 1: impact of male density on the mating status of Neolema ogloblini *females.*

Dispersal propensity of adults. To determine whether adults stayed in their host patches within the 3-week period, or disappeared (due to dispersal, predation, or natural death), the relationship between initial release size (fixed effect variable–as factor with five levels (2, 8, 16, 32, and 64 adults)) and the proportion of adults recovered (dependent variable) was examined using a logistic mixed effects model. Replicates were performed in groups at different times during the summer season (more details provided in Materials and Methods, Experiment 1) with potentially varying conditions such as temperature and weather events. As these conditions may influence activity levels of adults, replicate group-in-time was included as a random effect to capture seasonal variation. An observation-level random effect was added to account for overdispersion.

Mating status of females. To evaluate the factors influencing female mating success, data on the mating status of each recovered individual female ($n = 270$ females pooled from all release sizes and across years) were analysed using a logistic mixed effects regression model. The number of males recovered (continuous covariate accounting for variation in actual number of males present as caused by immediate dispersal and mortality factors) was included as a fixed factor. Because conditions such as temperature and weather events may influence activity levels of adults, and these conditions may vary at different times in the season, a random effect of the seasonal timing of each replicate (group-in-time) was included in the model.

Experiment 2: impact of generalist predation on the survival of immature stages of Neolema ogloblini. Experiments for each year were analysed separately because the design changed slightly. To determine how generalist predation impacts the survival of larvae under field conditions, data on the proportion of immatures that successfully developed from eggs to pupae were analysed by maximum likelihood estimation using a generalised linear model with binomial errors. The explanatory variables included access by generalist predators (or not), group size, and their interactions. Backwards model simplification with likelihood ratio tests was used to estimate the significance of variables in the model.

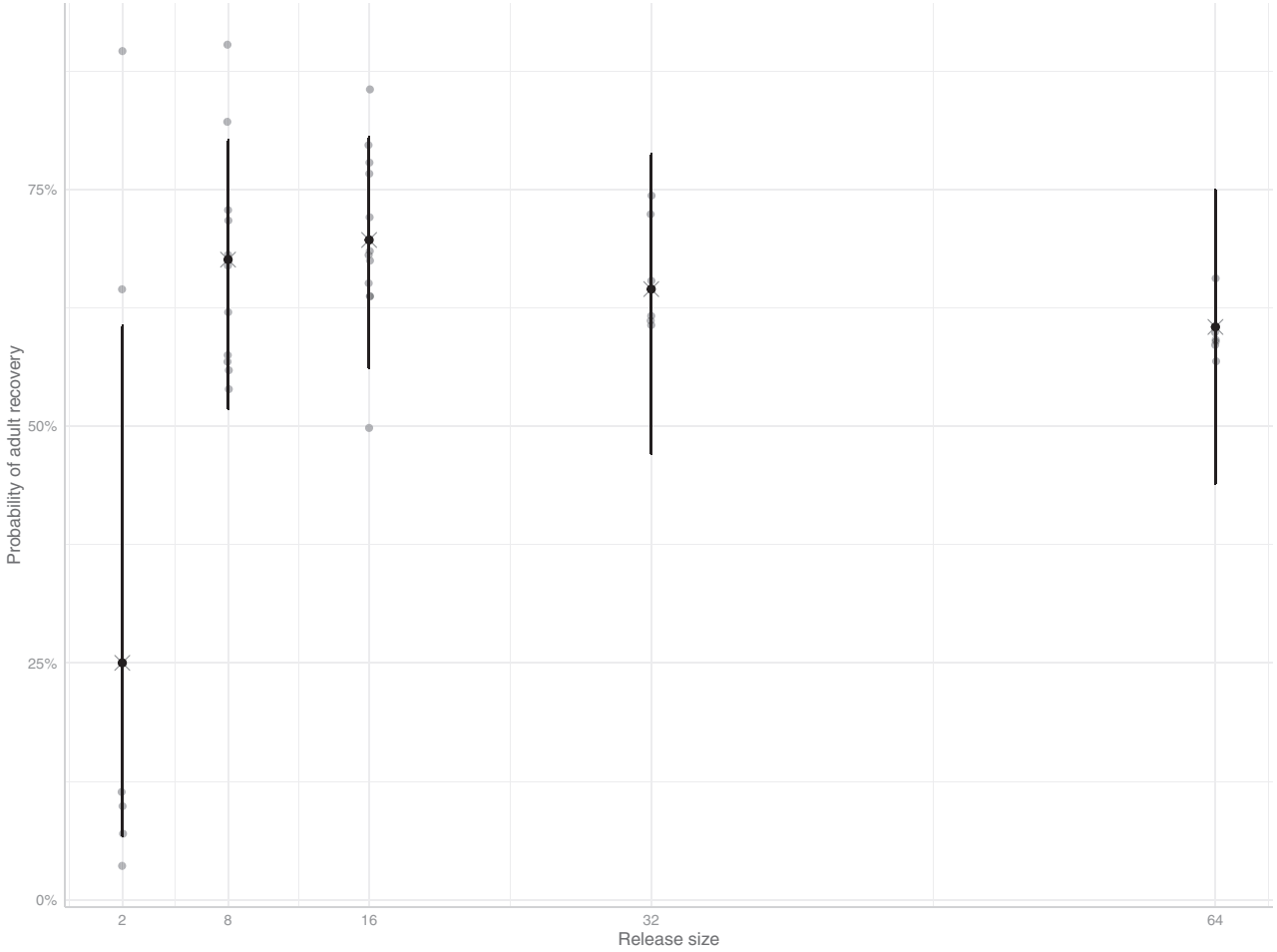

Fig. 1. The influence of initial release size on the proportion of *Neolema ogloblini* adults recovered after 3 weeks in the field. Crosses represent predicted values (logistic mixed effects regression). The bars represent 95% confidence intervals and dots are residuals.

Results

Experiment 1: impact of male density on the mating status of Neolema ogloblini *females*

Dispersal propensity of adults. Out of the total of 876 adults introduced in different release sizes, 346 (39%) were not recovered at the end of the 3-week monitoring period. Initial release size significantly influenced the proportion of adults recovered ($\chi^2_{(2,7)} = 37.775$; $P < 0.001$). The mean proportions recovered were relatively similar among all release sizes (8 adults: 0.64 ± 0.06 (mean $\pm$ SE); 16 adults: 0.66 ± 0.06; 32 adults: 0.61 ± 0.10; 64 adults: 0.58 ± 0.07; $P = 0.069$; Fig. 1). The lowest recovery was for the smallest release size (2 adults: 0.25 ± 0.17), which was significantly lower compared with the release sizes of 8 ($P = 0.024$), 16 ($P = 0.015$), and 32 adults ($P = 0.045$) (Fig. 1).

Mating status of females. Across all years and releases, 530 (61%) out of the 876 adults released were recovered at the end of the experiment. Of these, 270 were female, of which 17 (6.3%) were unmated. A logistic mixed effects regression model indicated that the probability of females being mated was significantly associated with male density (total number of males recovered) ($\chi^2_{(2,3)} = 5.356$; $P = 0.021$), increasing as the number of males recovered increased (Fig. 2). Though the relationship was significant, overall, the effect of male density on mating success was weak. The model predicted a mating success probability of 86% in the presence of no males, with an increase in female mating success of 12% between the minimum observed male density (zero males – males either dispersed away or died before mating) and maximum male density (25 males) (Fig. 2). At maximum male density, the model predicted a mating success probability of 98% (Fig. 2).

Experiment 2: impact of generalist predation on the survival of immature stages of Neolema ogloblini

Predation by generalist predators had a profound influence on the survival of immatures to the pupal stage. Throughout the experiment, predation by several spider species, lacewing larvae, and predatory mites were frequently observed preying on

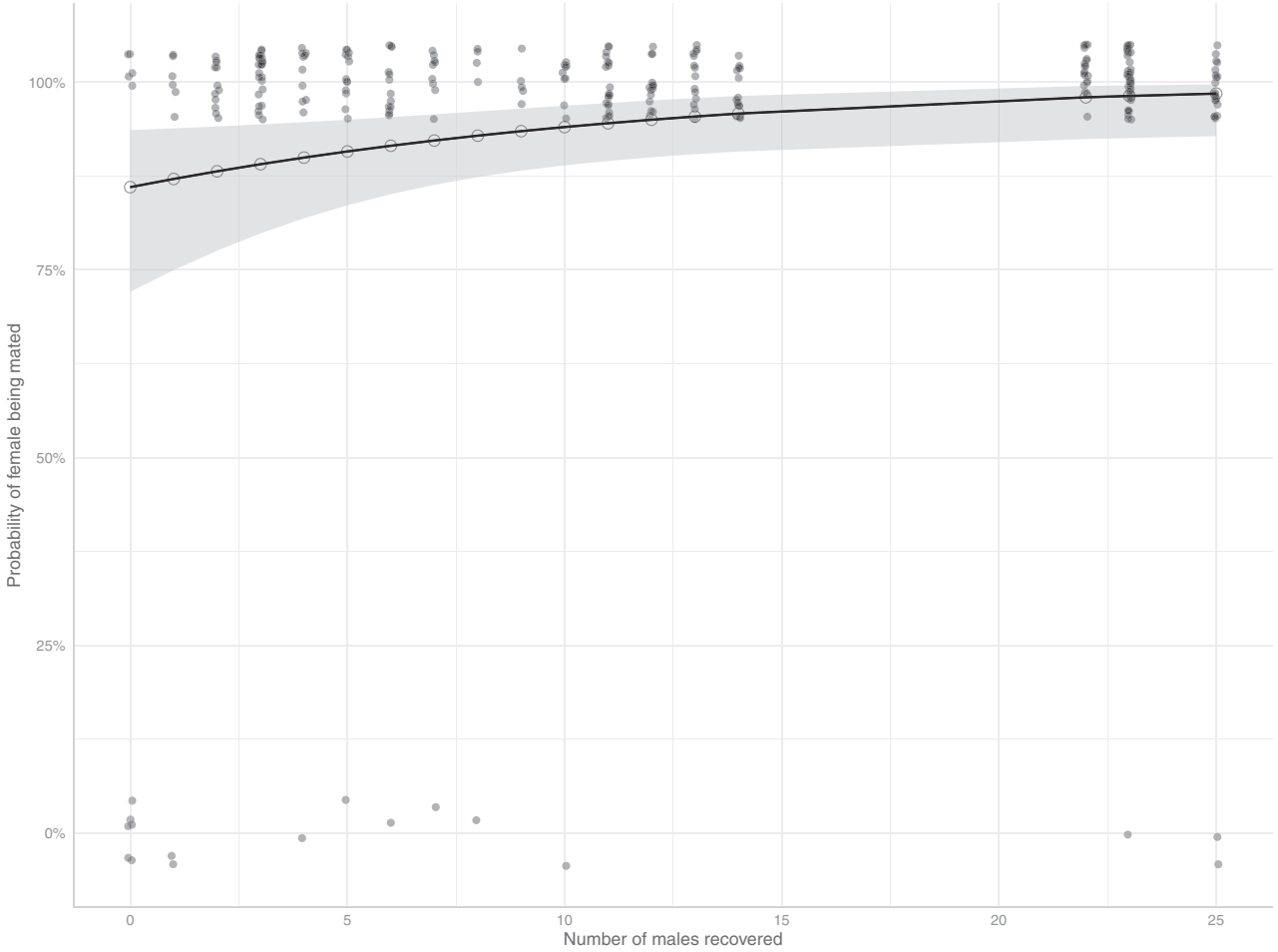

Fig. 2. Influence of male density (number of males recovered) on *Neolema ogloblini* mating success. The circles connected by the solid black line represent predicted values (logistic fixed effect regression). The shaded area is a 95% confidence band and dots are residuals.

N. ogloblini larvae, especially on smaller instars. At the conclusion of the experiment, remains of larvae (dried husks typically left by predatory mites and/or remain tangled in spider web threads) were often found on leaves near larval feeding marks.

Experiments in 2018 used group sizes of 20 (low) and 50 (high) eggs per host patch; predator exclusion ($F_{(10,9)} = 86.610$; $P < 0.0001$), but not group size ($F_{(11,10)} = 0.010$; $P = 0.922$), significantly influenced immature survival to the pupal stage. There was no significant interaction between group size and predator exclusion ($F_{(8,9)} = 0.769$; $P = 0.406$). Larval survival to pupal stage was very low on plants where predators had access, with a mean proportion of 0.01 (±0.01) larvae surviving in the high group size and no larvae surviving in the low group size (Fig. 3a). On plants protected from predator access, larval survival to the pupal stage was significantly higher ($P = 0.001$), with a mean proportion of 0.51 (±0.09) larvae surviving in the high group size and a mean proportion of 0.53 (±0.03) larvae surviving in the low group size (Fig. 3a).

In 2019, in an attempt to find a larger initial group size where the number of larvae present would satiate predation, initial groups of 50 (low), 100 (medium), and 200 (high) eggs per patch were deployed. Once again, predator exclusion ($F_{(50,49)} = 984.307$; $P < 0.0001$), but not group size ($F_{(52,50)} = 0.289$; $P = 0.750$) significantly influenced immature survival to the pupal stage. There was no significant interaction between group size and predator exclusion ($F_{(47,49)} = 1.134$; $P = 0.331$). Larval survival to the pupal stage was very low on plants where predators had access, with no larvae surviving in the high group size, a mean proportion of 0.01 (±0.01) larvae surviving in the medium group size, and a mean proportion of 0.02 (±0.01) larvae surviving in the low group size (Fig. 3b). Larval survival was significantly higher on plants protected from predator access ($P < 0.0001$), with a mean proportion of 0.72 (±0.03) larvae surviving in the high group size, a mean proportion of 0.71 (±0.03) larvae surviving in the medium group size, and a mean proportion of 0.81 (±0.03) larvae surviving in the low group size (Fig. 3b).

Discussion

In this study, we used a biocontrol agent, *N. ogloblini*, as a model species to improve our understanding of the source and

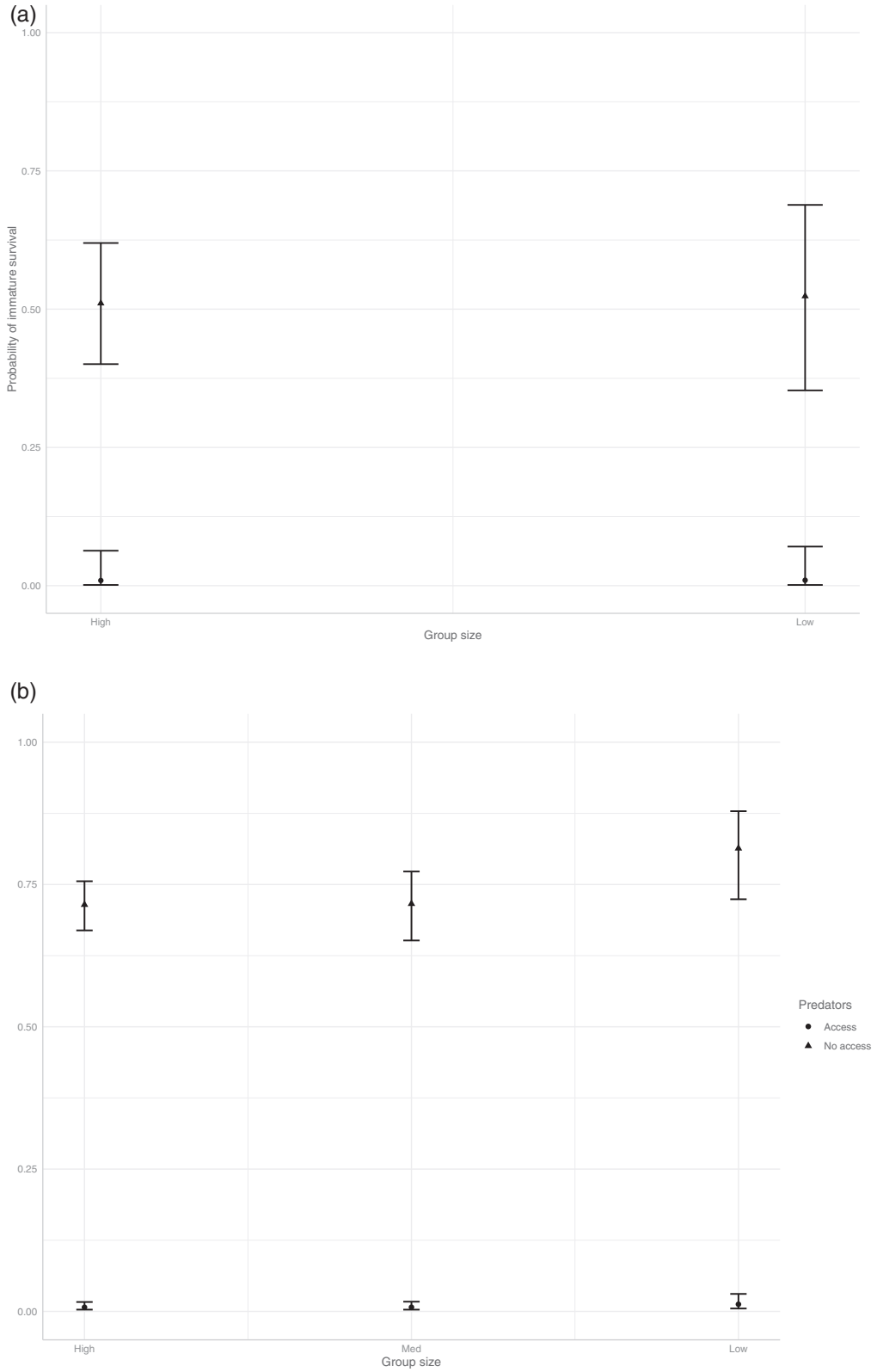

Fig. 3. The effect of predator exclusion treatment and population size on *Neolema ogloblini* immature survival to the pupal stage in (a) 2018 (groups initiated with: 50 eggs (High), 20 eggs (Low)), and (b) 2019 (groups initiated with: 200 eggs (High), 100 eggs (Medium), 50 eggs (Low)). Error bars represent 95% CI.

influence of component Allee effects experienced by incipient populations of non-native species. The results from our experiments indicated that, in the first 3 weeks after introduction, mate-finding failure caused a component Allee effect in releases of *N. ogloblini* where lower numbers of males were recovered (Fig. 2). This suggests that very small populations of *N. ogloblini* may suffer from this component Allee effect under natural field conditions. Although generalist predators caused very high levels of mortality in *N. ogloblini* larvae living in small groups (survival was 51–81% greater on control plants than on plants with predator access), a positive relationship between larval survival and group size (indicating a component Allee effect) was not verified.

It is expected that the mating-failure component Allee effect would be relatively weak and may not be the main driving force behind a demographic Allee effect, for several reasons. Firstly, the increase in mating success from the lowest to highest numbers of males recovered was only 12%, with the largest changes in mating success happening when male density was very low (e.g. between 0 and 6 males the probability of being mated increased by 6%, while between the larger jump in males from 6 to the maximum of 25 males, the probability also just increased by 6%) (Fig. 2). Secondly, adults of *N. ogloblini* can live up to 5 months in captivity (personal observation) and have been noted to partake in multiple mating events. Models of Yamanaka and Liebhold (2009b) predicted that for insect species with long-lived adults that are capable of multiple mating events, Allee effects arising from mate-finding failure should be relatively weak. It is thus likely that the mating-failure component Allee effect present in the first 3 weeks of adulthood in small releases of *N. ogloblini* would be offset over time (by multiple mating and being long-lived). During the mating experiment, adults dispersed or disappeared more frequently from the smallest release size [average proportion recovered was 0.25 (Fig. 1)]. This suggests that in very small populations adults may disappear or disperse away, preventing the mating-failure Allee effect from being offset over time. Thirdly, the proportions of adults recovered were relatively similar for intermediate release sizes, and slightly reduced in the largest release size (though not significantly so). These results suggest an absence of inter-specific competition at intermediate release sizes, although it may be present in the largest release size (hence the lower recovery rate). In the absence of intra-specific competition, adults of *N. ogloblini* showed little tendency to disperse, thereby potentially offsetting the strength of a mate-finding component Allee effect.

Larvae of *N. ogloblini* display well-known anti-predator behaviours (e.g. food-regurgitation, and retaining faeces and skin moults as a shield over their bodies (Morton & Vencl, 1998; Bacher & Luder, 2005)), but they are also slow-moving and relatively sessile and therefore highly susceptible to predation (Eubanks & Denno, 2000). Since its introduction as a biocontrol agent in 2011 in New Zealand, no parasitoids have been found attacking *N. ogloblini* populations in the field, but instances of generalist predation by spiders, predatory mites, lacewing larvae, skinks, and wasps have been reported (Q. Paynter, personal communication, June 2019). Allocation of predation to individual predator species is difficult as predation generally must be directly observed or their prey items detected using molecular techniques (e.g. Ward & Ramón-Laca, 2013).

Direct evidence for a predator-driven component Allee effect can only be demonstrated if a positive relationship is found between the proportion prey killed and prey density (i.e., the mortality rate is highest at low prey density and decreases as prey density levels increases). Unless this relationship has been quantified, the incidence of predation in low-density populations is not always indicative of predator-driven Allee effects. This was clearly demonstrated in the case of the bone-seed leaf roller (*Tortrix* s.l. sp. '*chrysanthemoides*') released against the invasive plant *Chrysanthemoides monilifera* (L.) Norl. subsp. *monilifera* in New Zealand. Paynter *et al.* (2012) found establishment of the bone-seed leaf roller was significantly lower in the presence of predatory ant species. But, contrary to the expectation that establishment success should increase with increasing release size, over half of the establishment failures were associated with the highest (>500 moths) release sizes (Paynter *et al.*, 2012). It thus seems that although predation contributed to establishment failure, a predator-driven Allee effect did not appear to play a role. One possible explanation for such a deviation is a type III predator response where the predator has multiple prey and can switch between prey (Holling, 1959). In the case of the ant and bone-seed leaf roller interaction, the ants were also attracted to honey-dew producing scale insects that occupied the same habitat as the bone-seed leaf roller (Paynter *et al.*, 2012). The ants thus had multiple prey (for protein vs. carbohydrate resources) and could potentially switch between prey when one resource became scarce. According to Gascoigne and Lipcius (2004), a type III predator response arising from 'prey switching' can keep prey (bone-seed leaf roller) at a low stable equilibrium, sometimes called a 'predator pit'. This functional response does not have the potential to create an Allee effect, and could potentially counteract an Allee effect in some other component of fitness (Gascoigne & Lipcius, 2004).

In our study, results from the predator exclusion trials indicated that in the presence of generalist predation, immature survival was virtually zero across all of the initial larval group sizes tested (Fig. 3a,b). However, we cannot rule out the existence of a predator-driven component Allee effect in this system, and a controlled experiment where both predator and immature levels are manipulated, would be needed to further evaluate whether this exists. Furthermore, it may be worthwhile to consider additional mechanisms, for example, reduced defence or reduced vigilance in smaller population sizes, as potential drivers of a predator-driven component Allee effect in *N. ogloblini*. Even if predation does not cause a component Allee effect in this or other systems, it could still influence the establishment probability of small populations via its reduction of growth rates. As an ubiquitous ecological interaction, generalist predation could reduce population densities and interact with other component Allee effects as well as stochasticity, thereby enhancing the extinction risk of small populations.

Conclusions

Neolema ogloblini is an arthropod species characterised by life-history traits such as long-lived adults, multiple mating

events, and low daily reproductive rates. At very low population levels, the combination of low mating success with low daily reproductive rates and high levels of predation on immature stages may lead to low population growth rates and ultimately the failure of small populations to establish. We suggest that the existence of a component Allee effect arising from mating failure at low male densities, and potentially contributing to a demographic Allee effect in very small populations of *N. ogloblini*, is a phenomenon that is likely to exist in other arthropod species with similar life-history traits. Our study emphasises the substantial overlap that exists between the research fields of biological control and invasion ecology, and demonstrates how biocontrol agent species can serve as effective models to study the mechanisms of species invasion.

Acknowledgements

This study was funded by a joint Ministry for Primary Industries and the University of Auckland PhD scholarship. Additional funding was received from MBIE (contract C04X1501). AML was supported by the USDA Forest Service and by grant EVA4.0, No. CZ.02.1.01/0.0/0.0/16_019/0000803 financed by Czech Operational Programme Science, Research and Education. We are grateful to the researchers and staff of Manaaki Whenua–Landcare Research for advice and logistical support. We thank Laureline Rossignaud and Anouchka Perret-Gentil for their assistance during the different stages of the study. We would like to acknowledge two anonymous reviewers whose constructive comments greatly improved an earlier version of this manuscript.

The authors declare that there is no conflict of interest.

Author contributions

Research was conceived and designed by all authors; HEW performed research and analysed data; and HEW wrote the manuscript with input from all authors.

Data availability

The data that support the findings of this study are openly available in Figshare (www.figshare.com) with the identifier DOI: https://doi.org/10.17608/k6.auckland.13868564.

References

Agulo, E., Roemer, G.W., Berec, L., Gascoigne, J. & Courchamp, F. (2007) Double Allee effects and extinction in the Island Fox. *Conservation Biology*, **21**, 1082–1091.

Bacher, S. & Luder, S. (2005) Picky predators and the function of the faecal shield of a cassidine larva. *Functional Ecology*, **19**, 263–272.

Bates, D., Machler, M., Bolker, B. & Walker, S. (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, **67**. https://doi.org/10.18637/jss.v067.i01.

Berec, L., Angulo, E. & Courchamp, F. (2007) Multiple Allee effects and population management. *Trends in Ecology & Evolution*, **22**, 185–191.

Contarini, M., Onufrieva, K.S., Thorpe, K.W., Raffa, K.F. & Tobin, P.C. (2009) Mate-finding failure as an important cause of Allee effects along the leading edge of an invading insect population. *Entomologia Experimentalis et Applicata*, **133**, 307–314.

Crider, K.K. (2011) Predator interference with the Cinnabar Moth (*Tyria jacobaeae*) for the biological control of Tansy Ragwort (*Senecio jacobaea*). *Invasive Plant Science and Management*, **4**, 332–340.

Davalos, A. & Blossey, B. (2010) The effects of flooding, plant traits, and predation on purple loosestrife leaf-beetles. *Entomologia Experimentalis et Applicata*, **135**, 85–95.

Ding, J. & Blossey, B. (2005) Invertebrate predation on the water lily beetle, *Galerucella nymphaeae* (Coleoptera: Chrysomelidae), and its implications for potential biological control of water chestnut, *Trapa natans*. *Biological Control*, **35**, 17–26.

Downey, P.O., Holtkamp, R.H., Ireson, J.E., Kwong, R.M. & Swirepik, A.E. (2007) A review of the *Chrysanthemoides monilifera* biological control program in Australia: 1987-2005. *Plant Protection Quarterly*, **22**, 24–32.

Ehler, L.E. (1998) Invasion biology and biological control. *Biological Control*, **13**, 127–133.

Eubanks, M.D. & Denno, R.F. (2000) Health food versus fast food: the effects of prey quality and mobility on prey selection by a generalist predator and indirect interactions among prey species. *Ecological Entomology*, **25**, 140–146.

Fagan, W.F., Lewis, M.A., Neubert, M.G. & van den Driessche, P. (2002) Invasion theory and biological control. *Ecology Letters*, **5**, 148–157.

Fauvergue, X. (2013) A review of mate-finding Allee effects in insects: from individual behavior to population management. *Entomologia Experimentalis et Applicata*, **146**, 79–92.

Fauvergue, X., Vercken, E., Malausa, T. & Hufbauer, R.A. (2012) The biology of small, introduced populations, with special reference to biological control. *Evolutionary Applications*, **5**, 424–443.

Fowler, S.V., Barreto, R., Dodd, S., Macedo, D.M., Paynter, Q., Pedrosa-Macedo, J.H. *et al*. (2013) Tradescantia fluminensis, an exotic weed affecting native forest regeneration in New Zealand: ecological surveys, safety tests and releases of four biocontrol agents from Brazil. *Biological Control*, **64**, 323–329.

Gascoigne, J.C. & Lipcius, R.N. (2004) Allee effects driven by predation. *Journal of Applied Ecology*, **41**, 801–810.

Gascoigne, J., Berec, L., Gregory, S. & Courchamp, F. (2009) Dangerously few liaisons: a review of mate-finding Allee effects. *Population Ecology*, **51**, 355–372.

Ghosheh, H.Z. (2005) Constraints in implementing biological weed control: a review. *Weed Biology and Management*, **5**, 83–92.

Gregory, S.D. & Courchamp, F. (2010) Safety in numbers: extinction arising from predator-driven Allee effects. *Journal of Animal Ecology*, **79**, 511–514.

Hartig, F. (2018) DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models. [WWW Document]. R package version 0.2.0. https://cran.r‐project.org/package=DHARMa (accessed 2018).

Holling, C.S. (1959) Some characteristics of simple types of predation and parasitism. *The Canadian Entomologist*, **91**, 385–398.

Hunt-Joshi, T.R., Root, R.B. & Blossey, B. (2005) Disruption of weed biological control by an opportunistic mirid predator. *Ecological Applications*, **15**, 861–870.

Kramer, A.M. & Drake, J.M. (2010) Experimental demonstration of populationextinction due to a predator-driven Allee effect. *Journal of Animal Ecology*, **79**, 633–639.

Kramer, A.M., Dennis, B., Liebhold, A.M. & Drake, J.M. (2009) The evidence for Allee effects. *Population Ecology*, **51**, 341–354.

Larsen, A.L., Jacquot, J.J., Keenlance, P.W. & Keough, H.L. (2018) Mechanical thinning to restore oak savanna promoted predator assemblages of gypsy moth pupae in Michigan. *Agricultural and Forest Entomology*, **20**, 531–540.

Liebhold, A.M. & Bascompte, J. (2003) The Allee effect, stochastic dynamics and the eradication of alien species. *Ecology Letters*, **6**, 133–140.

Ludecke, D. (2018) Ggeffects: tidy data frames of marginal effects from regression models. *Journal of Open Source Software*, **3**, 772.

Marsico, T.D., Burt, J.W., Espeland, E.K., Gilchrist, G.W., Jamieson, M.A., Lindstrom, L. *et al*. (2010) PERSPECTIVE: underutilized resources for studying the evolution of invasive species during their introduction, establishment, and lag phases. *Evolutionary Applications*, **3**, 203–219.

McEwan, W.M. (1987) Eastern northland and islands ecoregion. *Ecological Regions and Districts of New Zealand*, 2nd edn (ed. by W. M. McEwen), p. 30. Department of Conservation, Wellington.

Morton, T.C. & Vencl, F.V. (1998) Larval beetles form a defense from recycled host-plant chemicals discharged as fecal wastes. *Journal of Chemical Ecology*, **24**, 765–785.

Pavlova, V. & Berec, L. (2012) Impacts of predation on dynamics of age-structured prey: Allee effects and multi-stability. *Theoretical Ecology*, **5**, 533–544.

Paynter, Q., Forgie, S.A., Winks, C.J., Peterson, P.G., Ward, D.F., Nicholson, L. *et al*. (2012) Biotic resistance: Facilitation between invasive Homoptera and invasive ants limits the establishment of an introduced weed biocontrol agent in New Zealand. *Biological Control*, **63**, 188–194.

Paynter, Q., Fowler, S.V. & Groenteman, R. (2018) Making weed biological control predictable, safer and more effective: perspectives from New Zealand. *BioControl*, **63**, 427–436.

R Core Team (2017) *R: A Language and Environment for Statistical Computing*. R Core Team.

Regniere, J., Delisle, J., Pureswaran, D.S. & Trudel, R. (2013) Mate-finding allee effect in spruce budworm population dynamics. *Entomologia Experimentalis et Applicata*, **146**, 112–122.

Rhainds, M. (2013) Spatio-temporal variation in mating success of female bagworms. *Entomologia Experimentalis et Applicata*, **146**, 123–129.

Schulz, A.N., Lucardi, R.D. & Marsico, T.D. (2021) Strengthening the ties that bind: an evaluation of cross-disciplinary communication between invasion ecologists and biological control researchers in entomology. *Annals of the Entomological Society of America*, **114**, 163–174.

Sebolt, D.C. & Landis, D.A. (2004) Arthropod predators of *Galerucella calmariensis* L. (Coleoptera: Chrysomelidae): an assessment of biotic interference. *Environmental Entomology*, **33**, 356–361.

Shaw, A.K., Kokko, H. & Neubert, M.G. (2018) Sex difference and Allee effects shape the dynamics of sex-structured invasions. *Journal of Animal Ecology*, **87**, 36–46.

Stephens, P.A., Sutherland, W.J. & Freckleton, R.P. (1999) What is the Allee effect? *Oikos*, **87**, 185.

Syrett, P. (2002) *Biological Control of Weeds on Conservation Land: Priorities for the Department of Conservation. DOC Science Internal Series 82*. Department of Conservation, Wellington, New Zealand. https://www.doc.govt.nz/documents/science‐and‐technical/dsis82.pdf.

Tobin, P.C., Robinet, C., Johnson, D.M., Whitmire, S.L., Bjornstad, O.N. & Liebhold, A.M. (2009) The role of Allee effects in gypsy moth, Lymantria dispar (L.), invasions. *Population Ecology*, **51**, 373–384.

Tobin, P.C., Onufrieva, K.S. & Thorpe, K.W. (2013) The relationship between male moth density and female mating success in invading populations ofLymantria dispar. *Entomologia Experimentalis et Applicata*, **146**, 103–111.

Walter, J.A., Meixler, M.S., Mueller, T., Fagan, W.F., Tobin, P.C. & Haynes, K.J. (2015) How topography induces reproductive asynchrony and alters gypsy moth invasion dynamics. *Journal of Animal Ecology*, **84**, 188–198.

Ward, D.F. & Ramon-Laca, A. (2013) Molecular identification of the prey range of the invasive Asian paper wasp. *Ecology and Evolution*, **3**, 4408–4414.

Williams, H.E., Brockerhoff, E.G., Liebhold, A.M. & Ward, D.F. (2021) Probing the role of propagule pressure, stochasticity, and Allee effects on invasion success using experimental introductions of a biological control agent. *Ecological Entomology*, **46**, 383–393.

Yamanaka, T. & Liebhold, A.M. (2009a) Mate-location failure, the Allee effect, and the establishment of invading populations. *Population Ecology*, **51**, 337–340.

Yamanaka, T. & Liebhold, A.M. (2009b) Spatially implicit approaches to understand the manipulation of mating success for insect invasion management. *Population Ecology*, **51**, 427–444.

Accepted 21 June 2021
First published online 14 July 2021
Associate Editor: Julia Ferrari