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An investigation of demographic and component Allee effects in the Madagascar hissing cockroach

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Abstract

Population density affects the behaviour and population dynamics of insects, but the nature of that effect may depend on the degree of sociality. We experimentally manipulated initial population density of a subsocial insect, the Madagascar hissing cockroach, *Gromphadorhina portentosa* Schaum, 1853 (Blattodea: Blaberidae), to determine its effect on vital rates and population dynamics. In accordance with the predicted Allee effect, we hypothesised that intermediate cockroach population density will increase per capita birth rates and cause a higher population growth rate relative to smaller and larger population densities. After tracking 12 experimental populations (three replicates of four initial population densities) for 15 months, we found evidence of Allee effects in this insect. Per capita birth rates showed a quadratic response, with rates highest at intermediate population densities, suggesting a component Allee effect. Contrary to expectations for a demographic Allee effect, population growth rates showed negative density dependence. The proportion of adult females in the population increased with population density, but the mechanism for this increase is not known. Our findings provide evidence for at least one form of Allee effect in *G. portentosa* and shows a possible connection between subsocial behaviour and population-level responses.

Introduction

An Allee effect occurs when population growth or a measure of individual fitness increases as density increases (Kramer *et al.* 2018). As the response variable increases with density, an Allee effect is a form of positive density dependence (Herrando-Pérez *et al.* 2012). Because population growth and individual fitness typically decrease with density (negative density dependence), Allee effects are considered unusual but potentially important for the population dynamics of the species exhibiting them. For example, Allee effects may increase risk of extinctions for small populations, decrease the probability of establishment of colonising species, and provide a selective pressure on life history evolution, and they may be used to assist management of invasive species (Stephens and Sutherland 1999; Liebhold and Bascompte 2003; Kramer *et al.* 2018). Biologists have exerted considerable effort to detect Allee effects, to determine their causes, and to evaluate their effects on extinction risk (Kramer *et al.* 2009; Angulo *et al.* 2013). Part of the difficulty of evaluating the importance of Allee effects has been attributed to differentiating component and demographic Allee effects (Stephens *et al.* 1999). Component Allee effects are the positive effect of density on per capita vital rates (*e.g.*, birth and death rates), whereas demographic Allee effects are positive effects

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of density on population dynamics (Angulo *et al.* 2018). A component Allee effect does not always lead to a demographic Allee effect but must be present for a demographic Allee effect to exist. For example, the butterfly *Parnassius smintheus* has a component Allee effect attributed to female mating failure at low population densities but not a resulting demographic Allee effect (Matter and Roland 2012), and the bird *Turdoides squamiceps*, a cooperative breeding species, exhibits both component and demographic Allee effects (Keynan and Ridley 2016).

Regardless of the type of Allee effect, the positive effect of conspecifics is crucial. This has led to the assumption that Allee effects are more common in social than solitary species – an assumption that has not been adequately tested (Angulo *et al.* 2018). For example, Luque *et al.* (2013) find three indicators of component Allee effects in the eusocial ant species, *Linepithema humile*. Allee effects were not detected in the less social beetle species, *Tribolium castaneum* (Halliday and Blouin-Demers 2016). As sociality is a complex phenomenon that exists along a continuum, studies that examine the population-level effects of social behaviour along this continuum are useful in exploring the relationship between behaviour and population dynamics.

Cockroaches are an excellent model system to explore population-level consequences of social behaviour. The variety of social systems within this group (Lihoreau *et al.* 2012) allows for an exploration of behaviour–population connections within one order, the Blattodea (Inward *et al.* 2007). For example, *Blattella germanica*, a socially aggregating species, exhibits kin discrimination in mating, but the subsocial species *Nauphoeta cinerea* does not (Bouchebti *et al.* 2016). This behaviour may then affect population dynamics as inbred-mated *N. cinerea* females produce 20% less offspring than outbred-mated females do (Bouchebti *et al.* 2016). Lihoreau and Rivault (2008) reported that nymphs of *B. germanica* develop faster in the presence of conspecifics, whereas nymphs of nonaggregating cockroach species did not show benefits from conspecifics. Similarly, Izutsu *et al.* (1970) detected faster individual growth rates in *B. germanica* nymphs reared in groups than in isolation, and Holbrook *et al.* (2000) reported that female *B. germanica* produce larger oocytes when paired than in isolation. These studies provide evidence for the potential existence of component Allee effects, but they do not provide evidence of demographic Allee effects. We conducted a population-scale experiment explicitly to connect possible component and demographic Allee effects in the subsocial Madagascar hissing cockroach, *Gromphadorhina portentosa* Schaum, 1853 (Blattodea: Blaberidae).

Gromphadorhina portentosa is subsocial according to the Michener–Wilson classification scheme (as reviewed in Costa and Fitzgerald (1996)) because they exhibit neither cooperative brood care nor division of labour but do have parent–offspring aggregation (Bell *et al.* 2007) and overall aggregation (Yoder and Grojean 1997). The sexes differ in the extent of aggregating behaviour. Adult male *G. portentosa* defend territories with distinct hissing and a variety of aggressive physical behaviours (Clark and Moore 1994). Varadinová *et al.* (2010) found no evidence of an aggregation tendency in adult male *G. portentosa* under experimental conditions. Adult female *G. portentosa* are more gregarious and do not show aggressive behaviours to other females (Clark 1998; Varadinová *et al.* 2010). Relatively little is known about their aggregating behaviour in the wild, other than reports that they exist in groups of 10 individuals (Varadinová *et al.* 2010), typically with one territorial male (Laurent-Salazar *et al.* 2021). Even with these sexual differences, *G. portentosa* forms aggregates in laboratory settings. The finding of Yoder and Grojean (1997) of a reduction of individual water loss in same-sex groups of six relative to individuals provides evidence for a benefit of aggregation. Other individual and population consequences of aggregation for this gregarious species may include a more beneficial thermal environment, improved antipredator behaviours, and increased access to nutrition (Laurent-Salazar *et al.* 2021). None of these potential benefits have been confirmed.

Given that *G. portentosa* forms aggregates in the wild and in the laboratory and that evidence exists for a reduction in individual water loss within groups, we hypothesised the species would

exhibit Allee effects. Intermediate population densities would have higher per capita birth rates and survival rates (component Allee effects) and population growth rates (demographic Allee effect) than lower and higher densities would (Stephens *et al.* 1999). We experimentally manipulated the initial population density of *G. portentosa* to test for Allee effects in the short and long term. We expected Allee effects to be most apparent in the first several months of the experiment as the individuals respond to their initial population density and resource availability. As the populations grow over time, and resources such as food, water, and space become more limited, we expected to detect a negative density-dependent response. We also asked if the initial population density affected long-term population dynamics. Lastly, we monitored changes in the adult sex ratio over time to determine if our experimental populations would exhibit the female-biased sex ratio of several cockroach species in the wild (Azoui *et al.* 2016). Although sex ratio is not directly an Allee effect, a biased sex ratio can contribute to mate limitation, which is a possible mechanism for Allee effects (Kramer *et al.* 2009).

Materials and methods

On 18 August 2017, we created 12 experimental populations of *G. portentosa* from our laboratory colony that had been established in December 2015. Each population was housed in a 30 × 30 × 30-cm BugDorm[®] (MegaView Science Co., Ltd., Taichung, Taiwan) cage made of woven mesh (1350- μ m aperture) and polypropylene. Wood chips were provided along with a 10-cm paper roll and one-half paper egg carton as substrates to each cage. Our treatments were two, four, eight, and 16 adult roaches of equal sex ratio per cage, replicated three times. We chose these treatment levels to bracket the group size of 10 documented in the wild (Varadínová *et al.* 2010). Although an unequal sex ratio is apparently more common in the wild (Laurent-Salazar *et al.* 2021), we started with an equal sex ratio to provide consistent availability of mates and to determine if the sex ratio changed over time. As the size of each cage was the same, population size and population density are interchangeable. For simplicity, we always report population size and not density. We determined the initial weight of each experimental population using an analytical balance (Mettler-Toledo LLC, Columbus, Ohio, United States of America). The mean (\pm standard deviation) weight (in grams) of each treatment is as follows: two (14.25 \pm 0.74), four (27.50 \pm 4.69), eight (53.73 \pm 2.25), and 16 (100.20 \pm 1.71). Once per week, we provided each population with 10 g of dry commercial turtle food (Fluker's; Cricket Farm Inc., Port Allen, Louisiana, United States of America; ~40% crude protein; ~10% crude fat, ~5% crude fibre) and a quarter slice (~70 g) of fresh apple, seeds removed. The amount of food provided per week was held constant regardless of population size. We recognise this feeding regime creates greater competition for food as population size increases and is thus likely to cause a negative density-dependent response. We did this to better reflect biological reality as food availability does not generally increase with population size. Collective foraging can enhance food availability for a group in the wild (Laurent-Salazar *et al.* 2021), but it is not relevant to an experimental system. We qualitatively noted how much of the food remained at the end of each week. The only sources of water were the supplied food and a manual spray of water on the sides of each cage immediately after food was supplied. Cages were randomly arranged in the same room in a 12:12-hour light regime, held at 22 °C. The temperature was a consequence of the room being used for multiple purposes but is similar to the 25 °C used by Yoder and Grojean (1997).

To account for fertilisations that may have occurred before establishment of the experimental populations, we removed all nymphs born between 18 August and 7 October 2017. As the gestation period for *G. portentosa* is 60–70 days (Cornwell 1968), females inseminated before 18 August 2017 should have given birth by 7 October 2017. This ensured that all observed population responses resulted from the experimental conditions. This species is ovoviviparous,

with nymphs emerging from an expelled ootheca (Bell *et al.* 2007). The number of nymphs per ootheca is variable but is often 20–30 individuals (Chua *et al.* 2017).

We censused each population every two months from October 2017 until January 2019. At each census, we removed from each cage every individual, assigned it to a size class (1, 2, 3, 4, and 5 cm), and identified sex for those with obvious secondary sex characteristics, such as shape of antenna and presence of pronounced pronotum horns on males. We assumed any individuals greater than 5 cm in length with secondary sex characteristics were sexually mature. Nymphs that were first seen in December 2017 had grown to be larger than 5 cm long by June 2018. These individuals had to be at least six months old and likely were mature because maturity is reached at five months (Chua *et al.* 2017). During each census, we removed all wood chips, faeces, and other debris and provided clean wood chips. All cockroaches were returned to their respective cages at the end of each census.

Data analysis

Component Allee effects. We calculated the per capita birth rate in each population over each two-month period by dividing the number of nymphs in the 1- and 2-cm size classes by the number of adult females at the start of the period. These nymphs were born during and survived the two-month period; therefore, our calculations likely undercounted the number born because we could not account for the nymphs that died before census. We tested if the initial population size affected the initial per capita birth rate (*i.e.*, births from October to December 2017) with a nonparametric Kruskal–Wallis test to account for small sample size, nonnormality of the initial per capita birth rate data, and the categorical nature of the original population sizes (*i.e.*, two, four, eight, and 16 individuals). As population sizes changed over the course of the study, we pooled data across treatments to test the hypothesis that total population size would affect the per capita birth rates. We tested for a linear and quadratic fit for total population size *versus* a natural log-transformed per capita birth rate. Because this transformation excluded 0 values, we added a small value (0.01) to each value before transformation to preserve cases where births did not occur.

We tracked survival of the original stocked cockroaches for six months, after which time we could not differentiate them from new recruits into the adult age class. We conducted a Kaplan–Meier survival analysis with treatment level (initial population size) as the factor, using a log-rank test to determine if adult survival rates differed between treatments. Because an interaction between sex and treatment level may exist, we performed a second Kaplan–Meier survival analysis with sex as the factor and treatment as the strata.

Demographic Allee effects. To test for the effect of population size on per capita growth rate, we calculated the per capita growth rate as $r = \ln(N_{t+1}/N_t)$, where N = population size and $t+1$ is each two-month interval. We first compared the initial per capita growth rate (October to December 2017) between treatment levels (two, four, eight, and 16 individuals) using a Kruskal–Wallis test. Using data from the entirety of the study (15 months), we then evaluated a quadratic and linear relationship of population size at the beginning of each two-month period on the per capita growth rate over that two-month period. We also plotted the population growth curves of each treatment level over time to visually assess long-term differences in the experimental treatments.

Sex ratio. At each census, we determined the proportion of adult females in each population. We excluded the two-cockroach treatment level from this analysis because, with the initial population of only one male and one female, the sex ratio was too constrained. We also limited the analysis to census dates beginning with February 2018 to allow time for the adult sex ratio to change by both births and deaths. The two census periods before February 2018

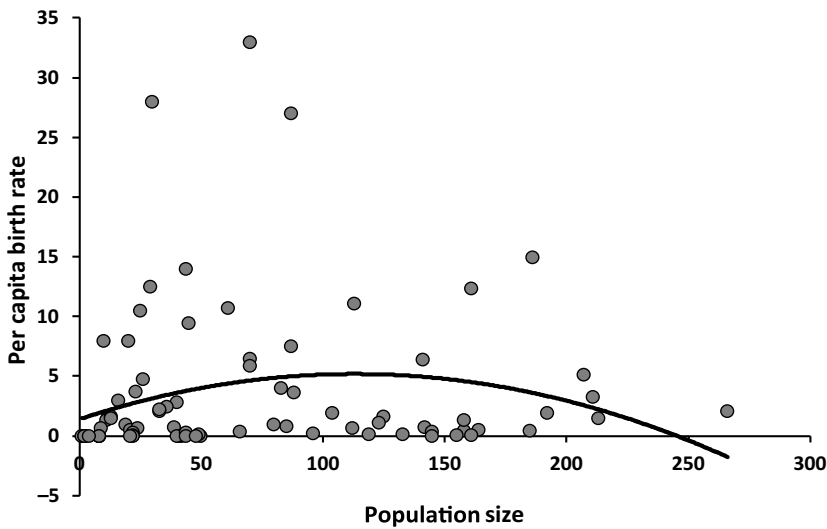


Fig. 1. Quadratic fit of population size of *Gromphadorhina portentosa* on per capita birth rate. A significant quadratic relationship was found between population size and transformed per capita birth rate ($F_{2,85} = 10.492$, $P = 0.00085$, $y = -2.681 + 0.047x - 0.000160x^2$ for $\ln(\text{rate} + 0.01)$).

maintained the initial 1:1 sex ratio in the four-, eight-, and 16-cockroach treatment levels. We used a repeated measures general linear model to determine whether the proportion of adult females changed over time and by treatment. We tested the assumption of sphericity with Mauchly's test and used the Greenhouse–Geisser correction when the assumption was violated.

To test the hypothesis that the proportion of adult females changed with population size, we ran a linear and quadratic regression, excluding the two populations (both of the two-roach treatment level) that did not change over time and thus sex ratio could not change. Because nymphs take several months to mature into adults and potentially change the adult sex ratios, we limited the analysis to dates starting in June 2018. We also compared the total number of females and males recruited during the experiment, pooled across all populations, by means of a chi-square goodness-of-fit test.

We performed all analyses on IBM SPSS (New York, New York, United States of America), version 27, using an alpha level of 0.05. Data are available from the corresponding author upon request.

Results

Component level

For the 15-month duration of the study, we detected a significant quadratic relationship (Fig. 1) between population size and natural log-transformed per capita birth rate ($F_{2,85} = 10.492$, $P = 0.00085$, $y = -2.681 + 0.047x - 0.000160x^2$). Per capita birth rates were highest at intermediate population densities of approximately 100 individuals. Initial population size did not have a significant effect on per capita birth rates ($H_3 = 4.2$, $P = 0.241$) over the initial two-month period. Two replicates in the two-cockroach treatment level had no (zero) and eight nymphs per female, and the third two-cockroach replicate had no adult females to reproduce. The four-cockroach treatment level exhibited the greatest range in birth rates (0, 12.5, and 33 nymphs per female), whereas no births were observed in each of the eight-cockroach populations during the initial two-month period. The 16-cockroach treatment populations had 6.5, 2.9, and 2.1 nymphs per female during the initial two-month period.

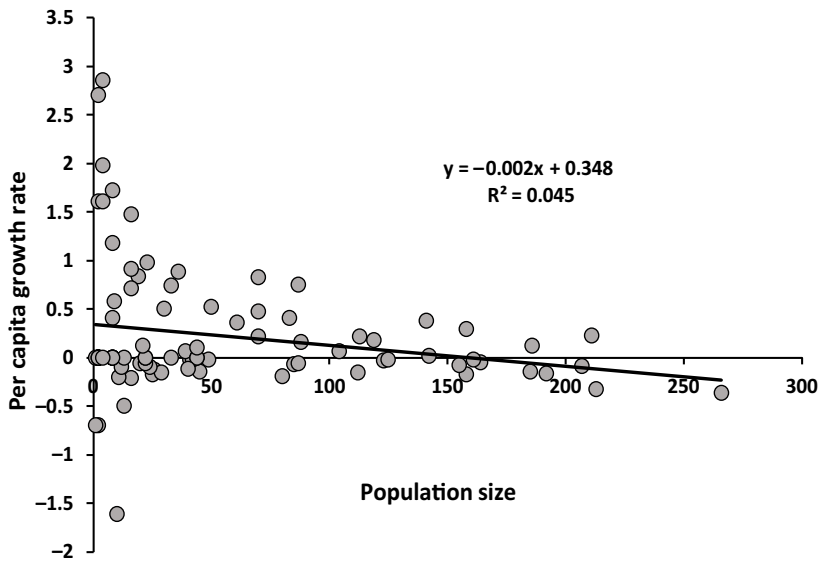


Fig. 2. Linear regression of total population size of *Gromphadorhina portentosa* on per capita population growth rate (r), calculated per two-month period. The slope of the line is significantly different from zero ($P = 0.043$).

Adults in the two-cockroach treatment level had the lowest survival at 66.7%, compared to 91.7%, 91.7%, and 85.4% for the four-, eight-, and 16-cockroach treatment levels, respectively. These differences were not statistically significant, according to the log-rank test ($X^2_3 = 3.297$, $P = 0.348$). A subsequent Kaplan–Meier survival analysis found significant sex difference in the survival at the 16-cockroach treatment level ($X^2_1 = 4.214$, $P = 0.040$) but not for the other three treatments. Of the original 24 adult males (eight in each of three 16-cockroach replicates), six males and one female died within the first six months.

Demographic level

The initial per capita population growth, calculated from the populations from October to December 2017, did not significantly differ among the treatment levels ($H_3 = 4.218$, $P = 0.239$) despite considerable variation in population responses. The replicates in the two-cockroach treatment experienced r values of 0.0, -0.69 , and 1.61 . The replicates in the four-cockroach treatment had both high r (2.86 and 1.98) and low r (0) values. The r value was zero for each of the eight-cockroach replicates. The populations in the 16-cockroach treatments all had positive r values (1.48 , 0.92 , and 0.72). After examining the relationship of population size to per capita growth rate for the entirety of the study, we failed to detect a quadratic relationship. Instead, we found a significant negative linear relationship ($F_{1,89} = 4.214$, $P = 0.043$, $R^2 = 0.045$, $y = -0.002x + 0.348$; Fig. 2).

The variation in initial demographic responses to density persisted for the duration of the study (Fig. 3). The three populations that started with an initial population size of 16 cockroaches grew to a mean of $214.3 (\pm 41.7$ standard deviation) individuals before declining to a mean of $146.3 (\pm 11.5$ standard deviation) by the end of the study. The eight-cockroach treatment level grew to a mean of $55.5 (\pm 41.7$ standard deviation), achieving only 25% of the population size of the 16-cockroach treatment. The four-cockroach treatment level grew to a mean of $71.3 (\pm 53.2$ standard deviation), slightly outproducing the eight-cockroach treatment. The two-cockroach treatment level exhibited the greatest variation in population size. The adult female in one of the two-cockroach populations died by December 2017, less than

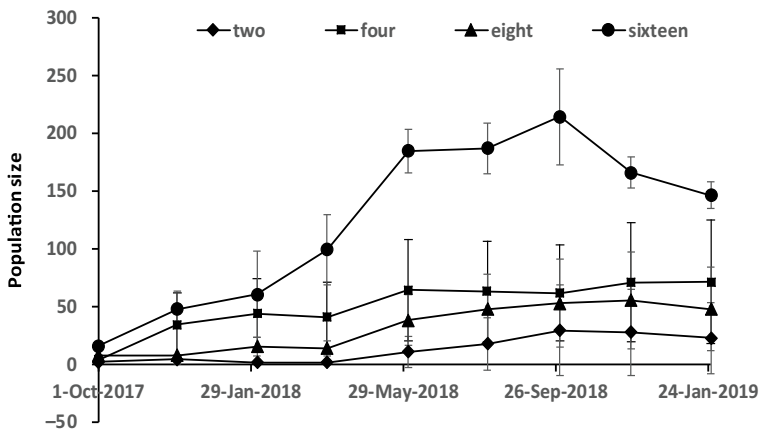


Fig. 3. Mean total population size (\pm standard deviation) of *Gromphadorhina portentosa* for each treatment level (two, four, eight, and 16 initial population size) for the duration of the study.

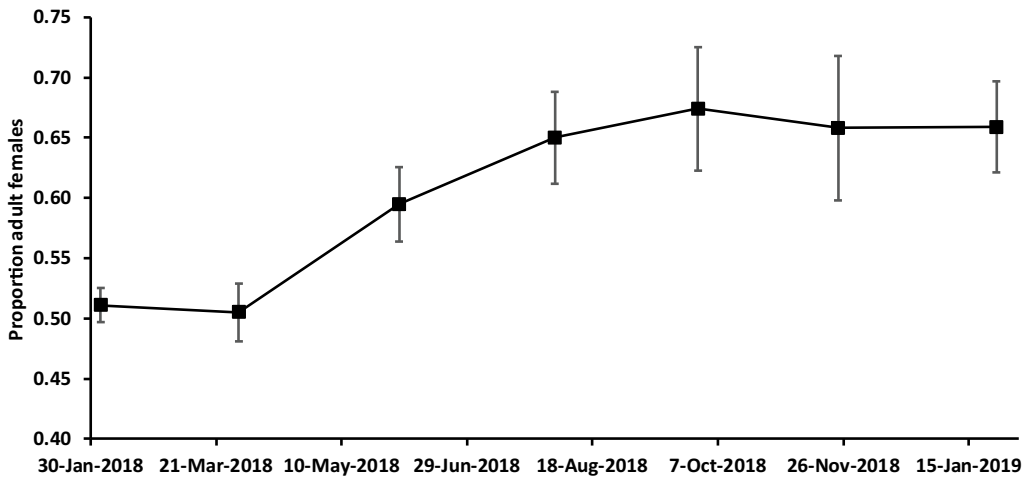


Fig. 4. The mean proportion (\pm standard error) of adult female *Gromphadorhina portentosa* in all populations significantly changed over time ($F_{6,36} = 5.120$, $P = 0.001$).

two months into the study. The second population in this treatment maintained the two roaches until January 2019, when the adult male was found dead. No reproduction had occurred in this replicate. The population in the remaining two-cockroach replicate grew to 85 individuals before lowering to 66 individuals at the end of the study.

Sex ratio. The proportion of adult females significantly increased over time ($F_{6,36} = 5.120$, $P = 0.001$; Fig. 4) and did not vary by treatment level ($F_{12,36} = 0.956$, $P = 0.506$). By August 2018, the proportion of adult females rose to 0.65 and remained at or above that level for the remainder of the study. This increase in adult females is evident in significantly more females (439) being recruited into the 5-cm size class than males (147) were over the entirety of the study, pooled across all populations ($X^2_1 = 145.50$, $P < 0.00001$). We failed to detect either a significant quadratic relationship between proportion of adult females and total population size ($F_{2,47} = 1.384$, $P = 0.261$) or a linear one ($F_{1,48} = 2.569$, $P = 0.116$).

Discussion

The benefits of conspecifics on individuals have been clearly documented in several species of cockroaches. These benefits include increased female feeding rate (Holbrook *et al.* 2000), accelerated oocyte development (Holbrook *et al.* 2000; Lihoreau and Rivault 2008), increased individual growth rates in nymphs (Izutsu *et al.* 1970; Lihoreau and Rivault 2008), enhanced discrimination of resource quality (Canonge *et al.* 2011), and reduced water loss (Yoder and Grojean 1997). Missing from the literature is an explicit linking of these individual benefits of conspecifics to component Allee effects and to possible population-level consequences *via* demographic Allee effects. We experimentally manipulated initial population size starting with a 1:1 adult sex ratio of *G. portentosa* to determine if this subsocial insect species exhibits component and demographic Allee effects.

We found evidence of a component Allee effect for per capita birth rates. We detected a statistically significant quadratic relationship between per capita birth rates and population size using data over the entirety of the study. Per capita birth rates were highest at intermediate population sizes of near 100 individuals. At low population sizes, per capita birth rates were lower, indicating a component Allee effect. We do not know the cause of this effect, but our experimental design precludes the possibility of mate limitation or mechanisms associated with predation (*e.g.*, predator satiation and cooperative defence). Given the relatively low air temperature and limited water availability of our study system, the most likely mechanisms are the reduction of water loss (Yoder and Grojean 1997) and an increase in ambient temperature as more individuals give off metabolic heat (Laurent-Salazar *et al.* 2021). A slight increase in temperatures can increase development in cockroaches (Xu *et al.* 2017). As *G. portentosa* is ovoviviparous, the developing embryos obtain water from the female (Bell *et al.* 2007). The ability of the female to conserve water thus could affect reproductive output. At high population sizes, birth rates decreased, in keeping with common negative density dependence. We assume this was a response of limited food availability because the weekly rations of dry food and apple were completely consumed at population sizes near 100 individuals. Reduced reproduction in food-limited cockroaches such as *B. germanica* has been documented (Holbrook *et al.* 2000). Larger population sizes could also decrease birth rates if the ootheca is damaged during extrusion. Female *G. portentosa* extrude and then retract the ootheca to be internally incubated in the brood sac (Bell *et al.* 2007). When extruded, the ootheca is vulnerable and may be damaged by conspecifics. Presumably, this risk of damage increases with population size, but the form of this relationship is not known. We did observe several incidences of detached ootheca, but we neither witnessed the cause of the detachment nor collected data to correlate incidence with population density.

Our failure to detect an effect of initial population size (two, four, eight, and 16) on per capita birth rates can be attributed to our low sample size and those population sizes being too narrow to differentially affect birth rates. The same is likely true for our failure to detect differences in adult survival among our four treatment levels. For the six months over which survival was measured, the population sizes did not affect survival. The one caveat to this is the lower, but not statistically significant, survival in the two-cockroach treatment. Of the six cockroaches across the three replicates in this treatment, two individuals died within the first six months. With our small sample size and because we did not account for the age or other physiological state of the stocked adults, we cannot tell if older individuals died, if mortality was random, or if the small population size contributed to these deaths (a component Allee effect). Greater replication of each treatment and improved information on the age of the individuals could help differentiate among these possible causes.

For a demographic Allee effect, the per capita population growth rate should peak at a critical intermediate population size before decreasing at higher abundances (Stephens *et al.* 1999). Our data do not support the presence of a demographic Allee effect in our study populations

of *G. portentosa* – either at the initial treatment sizes or as the population sizes changed over time. As population sizes changed over time, we detected a significant negative linear relationship between per capita population growth rate (r) and population size using all data. This linear negative relationship was not consistent with a demographic Allee effect because we expected growth rate to be low at small and large populations. Instead, the per capita population growth rate decreased with increasing population size, in keeping with negative density dependence.

This lack of detection of a demographic Allee effect contrasts with our detection of a component Allee effect. Finding a component but not a demographic Allee effect is common among published reports (Gregory *et al.* 2010; Matter and Roland 2012). This disconnect can be attributed to the interplay of positive and negative density dependence acting at the component level, which collectively gives rise to the demographic response (Stephens *et al.* 1999). For example, the reduced mating success – a component Allee effect – observed in the butterfly *P. smintheus* did not cause a demographic Allee effect, possibly because variation in mating success did not produce a large enough effect to be detected at the population level (Matter and Roland 2012). Our detected component Allee effect of increased per capita birth rates at intermediate population sizes is a weak effect and may thus be counteracted by possible stronger negative density-dependent factors, such as mortality of nymphs, that we could not measure. Our limited sample size also makes the detection of a demographic Allee effect more difficult.

Our only evidence suggesting a demographic Allee effect in *G. portentosa* is the more consistent population response at the 16-cockroach treatment level compared to the other treatments over the duration of the study. The populations starting with 16 individuals more consistently reached higher population sizes than the other treatments did. This could be interpreted as a demographic Allee effect because the overall population performance was greater with the highest initial population size. An alternative explanation involves demographic stochasticity (Stephens *et al.* 1999). Random variation in demographic performance has a larger impact on smaller populations than on larger ones, contributing to the enhanced extinction risk of small populations (Liebhold and Bascombe 2003). Random deaths in smaller populations have a larger impact than they do in larger populations. In our study, the death of the only male in one of the two-cockroach treatments and the female in another early in the study depressed the ability of those populations to grow. With our study design, we cannot differentiate demographic stochasticity from Allee effects in mortality.

As each population grew, the proportion of adult females also increased. This finding agrees with published reports of female-biased sex ratios in wild populations of several cockroach species (Azoui *et al.* 2016). Although we do have modest evidence that adult males suffered greater rates of mortality than did adult females, perhaps because of the negative effects of male aggression (Clark and Moore 1994), we think it is unlikely that differential mortality during young age classes caused the skewed adult sex ratio. Male aggressive behaviour is an adult attribute (Clark and Moore 1994), and it is unlikely to cause greater mortality in immature individuals. We think a more likely explanation for the greater numbers of females being recruited into the 5-cm size class is that more females than males were born. Several possible mechanisms could explain this skewed primary sex ratio. Parthenogenesis is widespread in cockroach species and always produces female offspring (Bell *et al.* 2007). The ability of *G. portentosa* to perform parthenogenesis is not known. *Wolbachia*, an intracellular bacterium common in insects, can alter sex ratio through male killing (Charlat *et al.* 2003; Pan *et al.* 2020). *Wolbachia* is found in many cockroach species, but to our knowledge, its presence in *G. portentosa* has not yet been investigated.

Our study provides evidence that an Allee effect is present in the subsocial insect *G. portentosa*. A component Allee effect was detected in per capita birth rates, and a possible demographic Allee effect was suggested in the population response of the replicates with the largest initial population size. To our knowledge, our study is the first to experimentally investigate component and demographic Allee effects among cockroaches. Thus, we cannot assess if our findings are widely applicable to the range of social systems exhibited in this order and in other insect taxa. Many behavioural and physiological studies of cockroaches show the benefits of groups and thus provide ample justification for the expectation of component Allee effects. More research is needed to extend our collective understanding of behaviour and physiology to how they affect population processes. Allee effects provide a strong theoretical foundation on which to base that extension. Our findings suggest potential productive areas of future research include detecting the Allee threshold transition zone between positive and negative density dependence (Gregory *et al.* 2010), differentiating Allee effects and demographic stochasticity, ascertaining the mechanisms of observed Allee effects, and discovering the causes of female-biased sex ratios.

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Competing interests. The authors declare none.

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