

RESEARCH ARTICLE

Propagule size and sex ratio influence colonisation dynamics after introduction of a non-native lizard

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Abstract

1. The composition of founding populations plays an important role in colonisation dynamics and can influence population growth during early stages of biological invasion. Specifically, founding populations with small propagules (i.e. low number of founders) are vulnerable to the Allee effect and have reduced likelihood of establishment compared to those with large propagules. The founding sex ratio can also impact establishment via its influence on mating success and offspring production.
2. Our goal was to test the effects of propagule size and sex ratio on offspring production and annual population growth following introductions of a non-native lizard species (*Anolis sagrei*). We manipulated propagule composition on nine small islands, then examined offspring production, population growth and survival rate of founders and their descendants encompassing three generations.
3. By the third reproductive season, per capita offspring production was higher on islands seeded with a relatively large propagule size, but population growth was not associated with propagule size. Propagule sex ratio did not affect offspring production, but populations with a female-biased propagule had positive growth, whereas those with a male-biased propagule had negative growth in the first year. Populations were not affected by propagule sex ratio in subsequent years, possibly due to rapid shifts towards balanced (or slightly female biased) population sex ratios.
4. Overall, we show that different components of population fitness have different responses to propagule size and sex ratio in ways that could affect early stages of biological invasion. Despite these effects, the short life span and high fecundity of *A. sagrei* likely helped small populations to overcome Allee effects and enabled all populations to successfully establish.

5. Our rare experimental manipulation of propagule size and sex ratio can inform predictions of colonisation dynamics in response to different compositions of founding populations, which is critical in the context of population ecology and invasion dynamics.

KEYWORDS

Allee effect, *Anolis sagrei*, biological invasion, invasive species, population establishment, population estimation, population growth

1 | INTRODUCTION

Biological invasions threaten biodiversity, alter ecosystems, and have major economic costs (Lockwood et al., 2013). Introductions of non-native species occur frequently, but why some introductions lead to rapid population growth whereas others grow slowly or fail to establish can depend on numerous factors. Indeed, establishment success is often positively related to the number of founders or introduction events, and can be influenced by several other factors related to population demographics (e.g. sex ratio, mortality, birth rates; Bessa-Gomes et al., 2004; Capellini et al., 2015), genetic and environmental factors (e.g. inbreeding, genetic drift, environmental stochasticity; Allendorf & Lundquist, 2003; Simberloff, 2009) and organismal biology (e.g. physiological tolerances, life-history characteristics; Tabak et al., 2018). Additionally, barriers during different stages of the invasion process (introduction, establishment and spread) may affect the dynamics of newly introduced organisms (Blackburn et al., 2011). For example, newly introduced populations are typically characterised by an unstable stage structure, which may be a barrier to establishment, particularly in small populations. This unstable stage structure can lead to highly fluctuating population sizes over a short term (referred to as transient dynamics) before achieving a more stable structure over a longer term (Iles et al., 2016; Stott et al., 2011); this demographic stochasticity can increase the risk of establishment failure.

Propagule pressure, which consists of the number of introduced individuals (propagule size) and the number of introduction events (propagule number), is an important determinant of establishment success of invasive species (Britton & Gozlan, 2013; Simberloff, 2009). These two components of propagule pressure are often positively associated with establishment success and population growth (Simberloff, 2009). Small propagules are vulnerable to the Allee effect, defined as a positive relationship between components of individual fitness and either numbers or density of conspecifics (Stephens et al., 1999). Under the Allee effect, small populations may have a low or even negative growth rate and an increased probability of extinction due to genetic inbreeding, demographic stochasticity or reduction of social interactions (Stephens & Sutherland, 1999). The Allee effect has been documented in many species and often varies with life-history characteristics (Courchamp et al., 1999). Importantly, the Allee effect can decrease invasion success for small propagules.

For example, populations of the invasive moth *Lymantria dispar* have a high probability of extinction when the number of individuals detected (an index of population size) is below a critical threshold (Liebhold & Bascompte, 2003; Tobin et al., 2009). A large propagule number (e.g. repeated colonisation events) may overcome the negative effects of small propagule sizes (Britton & Gozlan, 2013; Simberloff, 2009) as more immigrants over time may reduce the risk of some individuals encountering unfavourable conditions in heterogeneous environments and/or favour genetic admixture (Rius & Darling, 2014). However, repeated introductions may also result in outbreeding depression (but see Colautti et al., 2017) or may be so infrequent that introduced populations go extinct before a subsequent introduction occurs (Lockwood et al., 2013).

The sex ratio of founding populations can also influence invasion success in many ways. Indeed, this aspect of propagule composition can influence population growth or spread (empirical: Miller & Inouye, 2011; modelling: Lee et al., 2011; Rankin & Kokko, 2007), and affect vulnerability to the Allee effect through demographic stochasticity (modelling: Bessa-Gomes et al., 2004; Lee et al., 2011). For example, female-biased propagules could positively affect population growth because the number of female gametes is positively related to offspring production (Dewsbury, 2005; Trivers, 1972). Alternatively, a female-biased population might be sperm limited and suffer reduced population-wide female mating success that could hinder population persistence by reducing fecundity and population growth (reviewed in Gascoigne et al., 2009). Moreover, male-biased sex ratios can negatively affect population growth via relatively few female gametes, reduced female survival possibly due to male harassment of females (empirical: Le Galliard et al., 2005) or by increasing inbreeding (empirical: Aspbury et al., 2017; Rönn et al., 2006; modelling: Rankin & Kokko, 2007). Skewed propagule sex ratios may also reduce the efficacy of mate searching, which can slow or prevent establishment after introduction, although this effect may be small in polygynandrous species (modelling: Shaw et al., 2018). Importantly, the effects of male- or female-biased propagules could vary over time depending on the persistence of skews in the adult population sex ratio. Thus, biased propagule sex ratios could result in several different outcomes for introduced populations, which makes population-wide effects difficult to predict.

The dynamics of populations introduced to novel environments have been of broad interest to ecologists, evolutionary biologists

and conservation biologists, and thus have been given considerable theoretical and empirical research attention (Lockwood et al., 2013). While the concepts described above are relatively well studied, we often do not have empirical data during early, transient stages of invasion because of the difficulty in identifying colonisation events (Lockwood et al., 2013; Marsico et al., 2010). Consequently, many studies take place after invasive organisms are already established. Moreover, many introduced populations likely go extinct before being monitored, making it difficult to assess the role of propagule size or composition in the early stages of invasion (Dlugosch & Parker, 2008). In this study, we overcome some of these problems by using an experimental approach that manipulates founding populations of lizards on several small islands, which can provide realistic assessments of the role of propagule size and composition during the early stages of population establishment.

We aimed to identify factors that influence population growth during invasion by using spatially replicated experimental introductions of the brown anole *Anolis sagrei*. This lizard species is native to Cuba and the Bahamas but invasive in the southeastern United States and elsewhere (Kolbe et al., 2004, 2007). Brown anoles produce a single egg approximately every 4–10 days from April to October (Mitchell et al., 2018; Pearson & Warner, 2018), but overall fecundity varies among females. For example, females can produce between 9 and 38 eggs (mean = 25.7) over the reproductive season in the laboratory (Hall et al., 2020). This species has a polygynandrous mating system, and mating occurs continuously throughout the reproductive season. Additionally, females can store viable sperm from previous matings for at least 2 months (Calsbeek et al., 2007). Females are unlikely sperm limited, but sperm limitation is plausible if adult sex ratios become heavily female biased. Mate competition among males can be strong (Tokarz, 1998) and there is indirect evidence of male avoidance by females, possibly due to costly mating interactions (Moon & Kamath, 2019). Individuals can reach sexual maturity within about 5 months of age, and the majority of adults typically die before reaching a second breeding season (Calsbeek, 2009; Cox & Calsbeek, 2010a). This species also has genotypic sex determination, suggesting balanced primary sex ratios (Cox et al., 2011; Urbach et al., 2013), yet adult population sex ratios can vary considerably (Schoener & Schoener, 1980). These aspects of reproductive biology may have facilitated the invasion success of *A. sagrei*, and they make this species well-suited for addressing the effects of propagule size and sex ratio on population growth and establishment.

We manipulated propagule size and sex ratio on small islands, using founders from the nearby mainland. We then monitored population growth, survival of founders and their descendants, and population sex ratio over three generations. Our approach enabled us to describe the effects of propagule size and sex ratio on population demographics during establishment while controlling for propagule number and population density. We tested

two predictions. First, we predicted decreased fecundity and population growth rate for the smallest propagules. Second, we predicted that patterns of female fecundity, survival and population growth would differ between populations with male- versus female-biased propagules. Specifically, in the first generation, we predicted high offspring production and population growth rate in populations with a female-biased propagule (due to greater numbers of females). While reduced per-female fecundity is also plausible in female-biased populations due to sperm limitation, this is unlikely due to mating system of *A. sagrei*. For populations with male-biased propagules, we predicted low fecundity and reduced population growth accompanied by reduced female survival (possibly due to sexual harassment). Because we expected a balanced sex ratio to be restored in our populations within a generation or two, we predicted the effects of our sex ratio manipulation to remain relatively transient. To address these predictions, we also assess temporal variation in adult sex ratios and individual survival rates to provide additional insight into variation in offspring production and population growth.

2 | MATERIALS AND METHODS

2.1 | Study site

Fieldwork took place on three islands at Tomoka State Park (TSP; Ormond Beach, FL, USA) and six islands ~30 km north at the Guana Tolomato Matanzas National Estuarine Research Reserve (GTM-NERR; Palm Coast, FL, USA; Table 1, Figure 1). These islands were created between 1928 and 1970 from dredging the Intracoastal Waterway on the east coast of Florida (Baker, 2014). The islands vary in shape, size and the distribution of suitable habitats for *A. sagrei* (grass, shrubs, palm and cedar trees). We observed high densities of lizards during informal surveys on the islands at TSP from 27 to 30 April 2009, suggesting that these islands can support large populations of *A. sagrei* (Warner, pers. obs.). However, no lizards were found on these islands 2 weeks prior to release; this was likely due to a flood during winter 2009. Informal surveys at the GTM-NERR indicated that lizards were present on some islands, but in low numbers; no lizards were observed when founders were released.

2.2 | Release and recapture

In early spring 2011, adult lizards (431 males, 392 females) were collected from the mainland near our field sites (St. Augustine, Palm Coast and Ormond Beach, Florida). All lizards were uniquely marked by toe clipping, measured (snout-vent length, SVL), weighed and their sex was identified. Lizards were then randomly assigned and released on one of the nine islands (Table 1). Lizards we released will be referred to as 'founders' and we assume other lizards to be the descendants of these founders.

TABLE 1 Description of the islands and founding populations at Tomoka State Park (TSP) and the Guana Tolomato Matanzas National Estuarine Research Reserve (GTM-NERR). Founders were captured between 29 March and 13 April 2011. Numbers of individuals of each sex released are in brackets [number of males: Number of females]. The F and M for the island names refer to female biased and male biased respectively

Island	Location	Area (m ²)	Date of release	Propagule size	Sex-ratio bias	Density (individuals/m ²)
F1	TSP	450	14 April 2011	37 [11:26]	Female	0.082
F2	GTM-NERR	1,200	13 April 2011	73 [25:48]	Female	0.061
F3	GTM-NERR	1,700	13 April 2011	111 [36:75]	Female	0.065
F4	GTM-NERR	1,920	13 April 2011	121 [40:81]	Female	0.063
M1	TSP	711	14 April 2011	45 [30:15]	Male	0.063
M2	TSP	840	14 April 2011	51 [33:18]	Male	0.061
M3	GTM-NERR	1,720	13 April 2011	106 [70:36]	Male	0.062
M4	GTM-NERR	1,970	13 April 2011	120 [82:38]	Male	0.061
M5	GTM-NERR	2,680	13 April 2011	159 [104:55]	Male	0.059

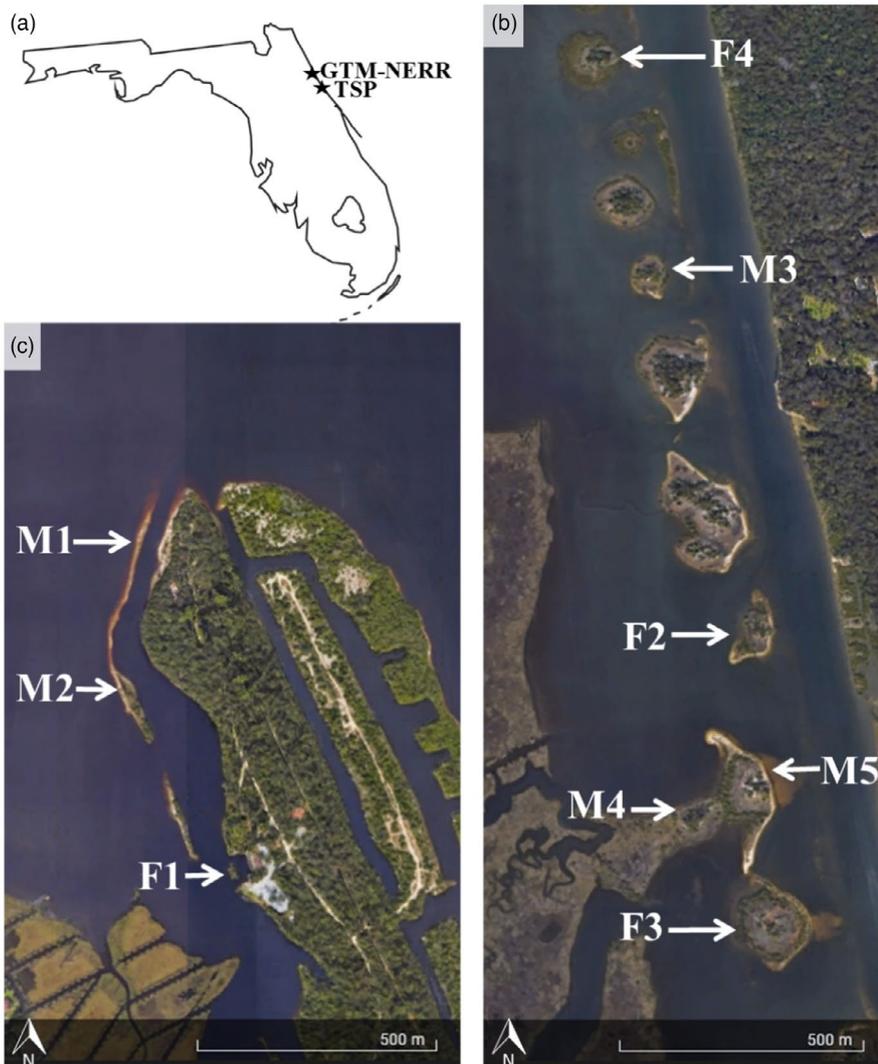


FIGURE 1 (a) Location of the sites in Florida. (b) The six islands in the Guana Tolomato Matanzas National Estuarine Research Reserve (GTM-NERR, 29°6'N, 81°2'W). (c) The three islands in Tomoka State Park (TSP, 29°3'N, 81°1'W). The F and M for the island names refers to female biased and male biased, respectively. All islands are isolated from the mainland, but islands M5 and M4 at the GTM-NERR, and M1 and M2 at TSP are occasionally connected at low tide (we never detected evidence of lizards moving between islands). Copyright Google Earth 2021

2.2.1 | Propagule size and sex ratio manipulations

We manipulated propagule size by adjusting the number of founders released to each island, keeping initial population density between

0.06 and 0.08 lizards/m². This density is near the low end of the range recorded for other *A. sagrei* populations (Calsbeek & Smith, 2007; Schoener & Schoener, 1980). Consequently, propagule size ranged from 37 to 159 individuals (a 4.3-fold difference) among islands.

We manipulated the founding adult sex ratio to obtain four propagules (each released on one of four islands) of different size with a female-biased sex ratio (0.33 male) and five propagules (each released on one of five islands) of different size with a male-biased sex ratio (0.67 male) (Table 1). These sex ratios are within the range reported for natural populations (Schoener & Schoener, 1980), and our manipulations ensured that sex ratio was not confounded with propagule size.

Importantly, propagule treatments were not truly replicated in that each island population had a different number of founders; this is an inevitable consequence of using islands that differ in size and would be difficult, if not impossible, to overcome in any natural field experiment. Nevertheless, this approach provided a continuous range of propagule sizes that allowed us to examine relationships between propagule size with offspring production and population growth after introduction while keeping propagule density constant.

2.2.2 | Resampling

Each island was resampled in August 2011, and then at the beginning (March/April) and end (October) of each subsequent reproductive season from October 2012 to April 2014 (Figure 2; Table S1 for specific dates), resulting in seven capture–mark–recapture (CMR) events (including when islands were seeded with founders). We captured

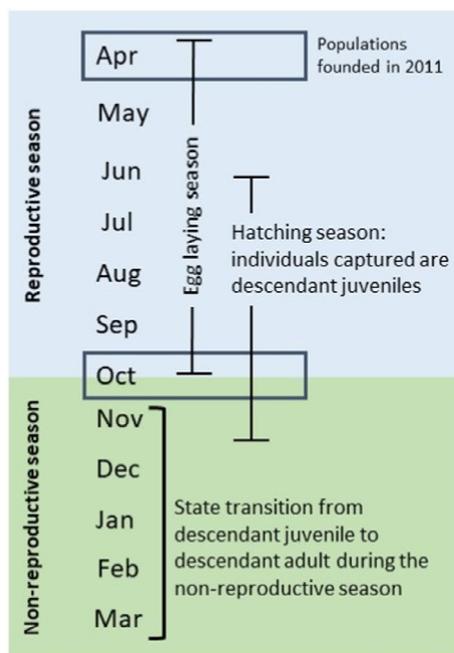


FIGURE 2 Seasonal timeline illustrating the reproductive season (light blue shading), non-reproductive season (light green) and state transitions. All populations were founded in April 2011. Populations were censused in August 2011, and then in April and October thereafter (denoted by the rectangular boxes). All non-adult lizards captured were classified as descendant juveniles that hatched sometime during the hatching season in that same year; those that were recaptured the following spring transitioned to the descendant adult state

lizards by hand or with hand-held snare poles, individually placed them in a bag and recorded the nearest tree to each capture location (trees were labelled with forestry tags). We identified lizards by their toe clip and gave unmarked lizards (descendants) a unique toe clip. A total of 5,276 unique descendants (excluding founders) were obtained over the study on the nine islands with 6,407 captures or recaptures. We measured SVL for all individuals and classified females <34 mm and males <39 mm SVL as juveniles, and those larger as adults (Lee et al., 1989). We released all lizards within 24–48 hr at the tree nearest to their capture location. In October 2013 and April 2014, we permanently removed lizards from the islands at TSP and deposited them in the Auburn University Museum of Natural History. While the study continued at the GTM-NERR, we terminated our population surveys on some islands at different times over the following 3 years. This research was approved by the University of Alabama at Birmingham Institutional Animal Care and Use Committee (protocol: 130709913), the Florida Department of Environmental Protection (permit# 12111213) and the Guana Tolomato Matanzas National Estuarine Research Reserve.

2.3 | Statistical analyses

To test our two predictions, we needed to quantify temporal and among-island variation in population growth rate, fecundity and individual survival rate. To do this, we first estimated population size and survival rate using parameterised multistate statistical models based on a conditional Arnason-Schwarz model (Schwarz et al., 1993). We defined four states: (a) individuals introduced on islands (Founder), (b) individuals that were descendants of the founders and their age defined as juvenile (Descendant Juvenile), (c) individuals that were descendants of the founders and their age defined as adult (Descendant Adult) or (d) individuals that were dead. The Arnason-Schwarz model estimates survival-transition probabilities (probability of being alive in the adult state at time $t + 1$ if alive in the juvenile state at time t) along with detection probabilities (probability of capturing an individual at time t). Survival-transition probabilities are decomposed into s , the probability that an individual present and alive at time t will be alive at time $t + 1$, and Φ , the probability that an individual is in the adult state at time $t + 1$ if alive in the juvenile state at time t (conditional of surviving between t and $t + 1$; Choquet, 2008; Schwarz et al., 1993). Our survival-transition probabilities refer to the probability of a descendant juvenile to survive and become a descendant adult (Figure 2; Table S2), and this transition was only possible between October and March/April (i.e. winter). We sometimes recaptured individuals as juveniles in March/April (spring), but they were never re-encountered at following capture events. Because hatchlings produced early in the season (after our spring survey) could transition to adulthood before our fall survey, young adults could not be distinguished from older individuals that we did not encounter in previous capture events. However, since relatively few individuals would transition to adulthood over the summer, we did not consider those individuals as potential juveniles.

2.3.1 | Estimation of detection probability and survival rate

We estimated state–state transition probabilities with the E-SURGE program (Choquet et al., 2009), using relaxed parameters for survival and detection probabilities. We did this for two reasons: (a) transition and survival probabilities are difficult to distinguish from each other using capture/recapture events, and (b) estimating survival, transition and detection probabilities within the same models can give poor estimates (Schwarz et al., 1993) and/or models may fail to converge. Based on convergent results from our preliminary models with relaxed parameters, we defined a fixed probability of 0.15 for descendant juveniles to remain descendant juveniles and a probability of 0.85 for descendant juveniles to become descendant adults. Transition parameters were entered into the E-SURGE program (Choquet et al., 2009), and we then ran models to estimate detection probability and survival rate. The models included time, population (i.e. island) and sex as covariates. These parameters were applied across populations and time periods.

We set estimated frequencies of each state to 1 for founders and 0 for descendants (juvenile and adult) for the introduction event (i.e. no descendants were present when founders were released). To account for variation in survival rate, we ran different models using time, state, sex and population as covariates, allowing two-way interactions among these variables. For detection probability, we tested time, sex and population as covariates, assuming equal detection probability among founders and descendants (juvenile or adult) (Rodda et al., 2015). To optimise parameter estimation, we used a model selection approach using Akaike information criteria (Anderson & Burnham, 2002). Additional details are in Supporting Information (Tables S2 and S3).

2.3.2 | Estimation of offspring production, population growth and sex ratio

We estimated the number of individuals at each capture event by dividing the number of individuals captured by the detection probability for that event (Table S1). To calculate offspring production, we divided the estimated number of juveniles (both sexes) at the end of the reproductive season (j_t) by the estimated number of adult females (founders and descendants) at the beginning of the reproductive season (f_t) (i.e. number of offspring produced over a breeding season and alive at the end of that season; offspring production = j_t/f_t). This value estimates the average number of offspring per female within each population based on all hatchlings that survived and were captured as juveniles. We used the estimated number of adults (founders and descendants of both sexes) at the beginning of each reproductive season (defined as n_t) to estimate annual population growth; annual population growth = $(n_{t+1} - n_t)/n_t$. Finally, we used the estimated number of adult males (founders and descendants) at the beginning of each reproductive season (m_t) and the estimated number of adult individuals (n_t) to estimate annual sex ratio; annual sex ratio = m_t/n_t . Because we permanently removed all

lizards captured in October 2013 at TSP, we did not use data from the following capture event (April 2014) in any analysis except for estimating number of individuals. Likewise, we only estimated survival rate for descendant juveniles during the winter season.

2.3.3 | Testing predictions

We used two linear mixed models (package LME4 in R; Bates et al., 2015; R Core Team, 2020) to test our predictions of decreased fecundity and population growth rate in populations with a small propagule size. These models included propagule size, year and their interaction as independent variables and offspring production or annual population growth as dependent variables; propagule size was standardised by subtracting the mean and dividing by the standard deviation, and population was a random effect. We complemented this analysis with an additional test that only included the number of females released as the value for propagule size, since females can limit population growth. To test our predictions that the direction of sex-ratio bias will affect population growth and offspring production, we used Student's *t*-tests to quantify differences between initially male- and female-biased populations in offspring production and population growth only for the first year of study. We limited this analysis to the first year of the study because initial biases in adult sex ratio did not persist over time and tended to be similar for initially male-biased and initially female-biased populations in 2012 and 2013 (see Section 3). To further investigate our hypothesis that propagule sex ratio can drive Allee effects, we also quantified the effect of propagule sex ratio on survival rate with a linear mixed model. This model was fitted with a binomial distribution including estimated survival rate for each sex and state from the two first time lapses (April to August 2011 and August 2011 to March 2012) as the dependent variable, and state, sex, propagule sex ratio, and two-way interactions (state x propagule sex ratio and sex x propagule sex ratio) as independent variables; population was a random effect.

Lastly, to integrate spatiotemporal variation in survival rate, we used model selection with Arnason-Schwarz models that included time, state, sex and population as covariates. Additionally, we used a linear mixed model fitted with a binomial distribution (package LME4) to quantify differences in survival rate among sexes and states; this model also included a two-way interaction between sex and state with population as a random effect.

3 | RESULTS

3.1 | Effect of propagule size on offspring production and population growth

Offspring production was low during the first and second reproductive seasons (except for one population), and then increased during the third reproductive season (Figure 3a; Table S5). Offspring production was positively associated with propagule size (Wald $\chi^2_1 = 6.36$,

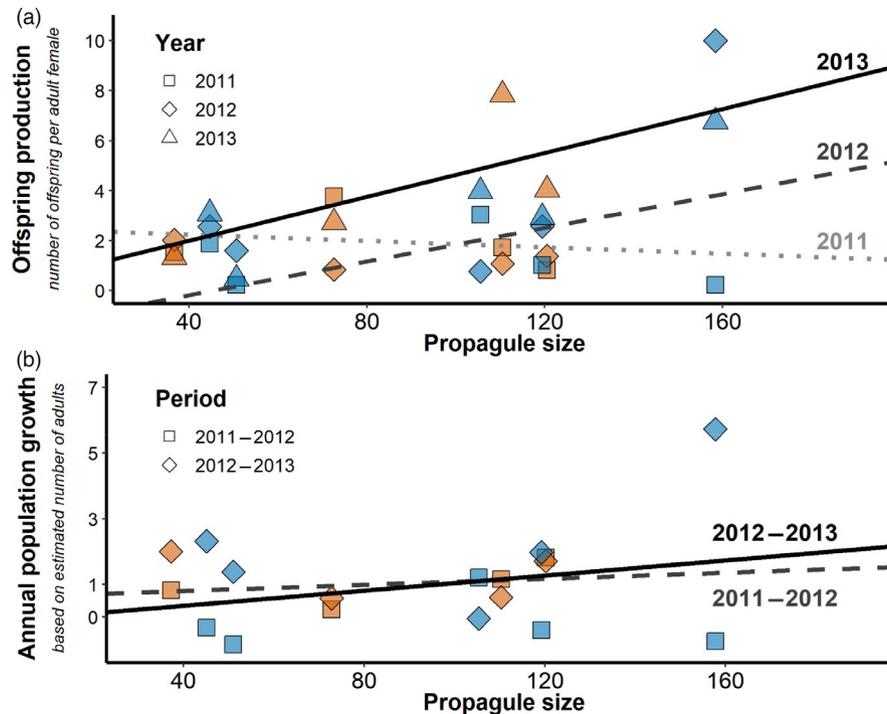


FIGURE 3 Influence of propagule size on offspring production and annual growth across years for each population. (a) Relationships between propagule size and offspring production for each year (the 2013 relationship was statistically supported). A value of two juveniles produced per female would double the population size when every individual survived. (b) Relationships between propagule size and population growth for each period (relationships were not statistically supported). An annual growth rate of one represents doubling of the estimated number of individuals. In all graphs, propagule size is a standardised continuous variable, while the x-axis is back-transformed to illustrate real propagule sizes. Populations with male- and female-biased propagules are denoted by blue and orange points, respectively

$p = 0.012$), but this relationship varied slightly among years (Wald $\chi^2_2 = 5.52$, $p = 0.063$); this relationship was positive in 2012 and 2013 and slightly negative in 2011 (Figure 3a). Annual population growth increased over time (Wald $\chi^2_1 = 5.28$, $p = 0.022$), but was not associated with propagule size (Wald $\chi^2_1 = 1.26$, $p = 0.262$) or the interaction between propagule size and year (Wald $\chi^2_1 = 0.688$, $p = 0.407$) (Figure 3b). Results from analyses that used the number of females (rather than total number of females and males) as propagule size showed similar patterns but with weaker statistical support. See supplemental information for values for offspring production and population growth (Table S4) and output from all statistical models (Tables S5–S8).

3.2 | Effect of propagule sex ratio on offspring production, population growth and survival rate

Offspring production in the first year did not differ between populations with male-biased propagules (mean = 1.27 offspring/female) and those with female-biased propagules (mean = 1.96 offspring/female) (Student $t = 0.829$, -1.315 to 2.691 95% CI, $p = 0.44$; Figure 4a). Annual population growth from 2011 to 2012 was lower in populations with male-biased propagules (mean growth rate = -0.220) than those with female-biased propagules (mean growth rate = 1.003 ; Student $t = 2.463$, 0.048 – 2.397 95% CI, $p = 0.043$; Figure 4b). Four of the five populations with a male-biased propagule had negative

growth in the first year after founders were released whereas all populations with female-biased propagules had positive annual growth during the first year, with two of them more than doubling. In the second year, all populations had positive growth rates regardless of propagule sex ratio (Figure 4b). Survival rates of males and females over the first year (i.e. from April 2011 to March 2012) were not affected by propagule sex ratio (sex \times sex ratio: Wald $\chi^2_1 = 0.558$, $p = 0.455$, Table S9). All but one population shifted towards a balanced or female-biased sex ratio in the second year (Figure 4c).

3.3 | Variation in survival rate

Survival rate varied considerably across time and populations, and differed among states (founder, adult, juvenile) and sexes (Figure S2; Table S10). Survival rates of founders was lower than that of descendant adults (Wald $\chi^2_2 = 9.395$, $p = 0.009$; Figure 5), and females had a higher survival rate than males (Wald $\chi^2_1 = 6.807$, $p = 0.009$; Figure 5, Table S11).

4 | DISCUSSION

Our study aimed to understand how propagule size and sex ratio influence survival, offspring production and population growth during early stages of biological invasion. Consistent with our first

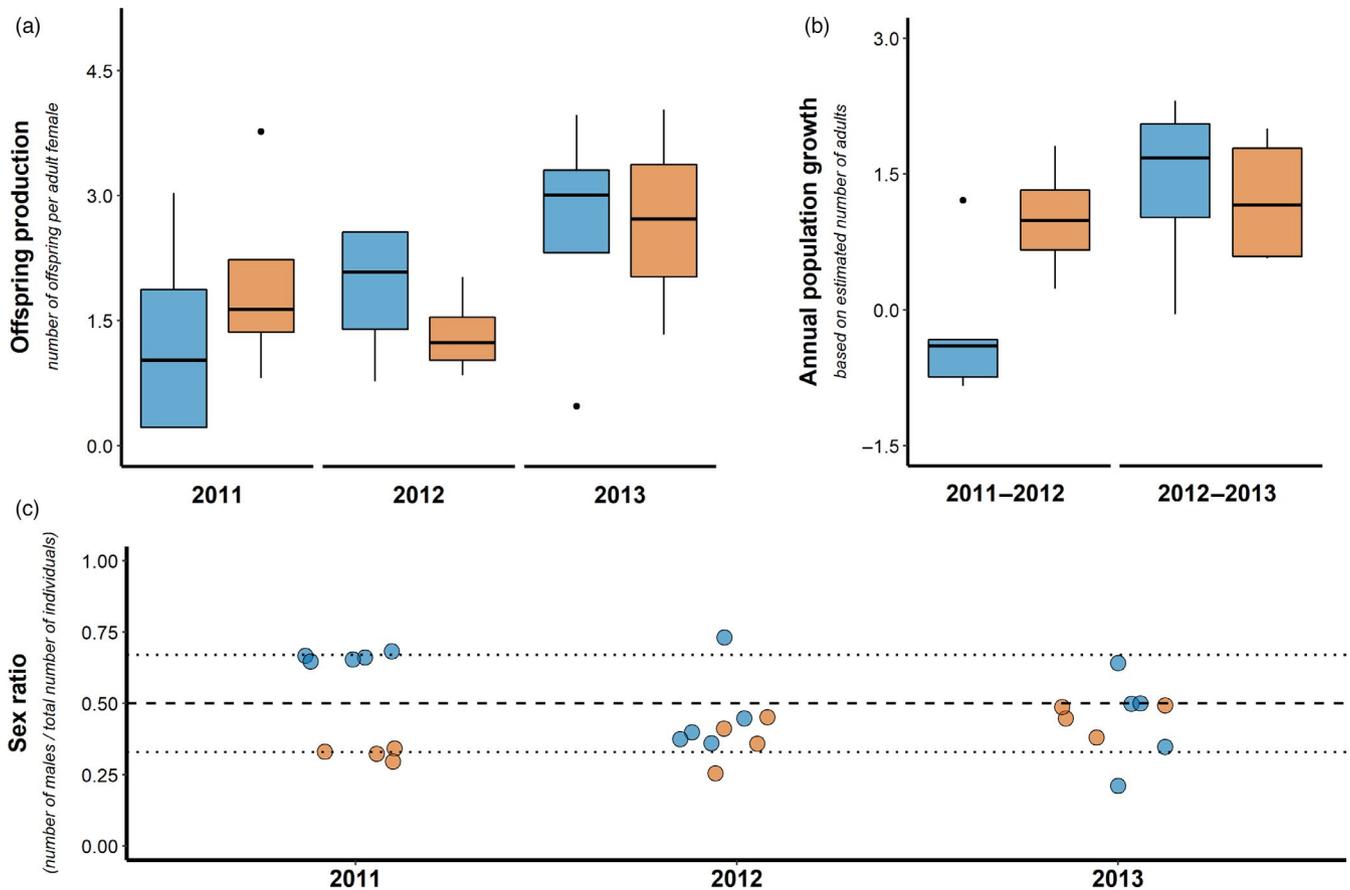


FIGURE 4 Box plots of (a) offspring production across years for populations with male-biased (blue) and female-biased (orange) propagules; (b) annual growth for populations with male- and female-biased propagules. (c) Shifts in population sex ratio among years on each island. The bold dashed line delimits a balanced sex ratio (1:1). The dotted lines delimit a 2:1 male-biased sex ratio ($y = 0.67$) and a 1:2 female-biased sex ratio ($y = 0.33$). Estimated values are available in Table S5

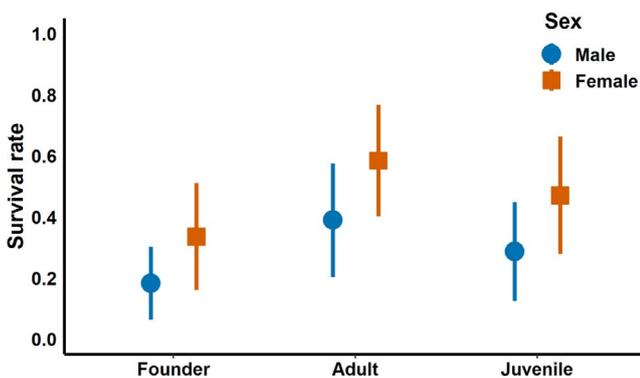


FIGURE 5 Mean survival parameter estimates for founders, adults and juveniles of each sex. Error bars represent the standard deviation. Values are in Table S11

prediction, we found that offspring production remained low over three generations for the smallest propagules, while it increased in larger propagules. However, this effect of propagule size on offspring production was not accompanied by annual population growth. Consistent with our second prediction, we found reduced population growth in initially male-biased populations. However, we also predicted reduced female survival and offspring production

in male-biased populations; these predictions were not supported. Although populations with female-biased propagules had increased annual growth in the first year after introduction compared to those with male-biased propagules, this difference disappeared in the following year, likely due to temporal shifts in adult sex ratio. Lastly, survival rates varied across populations, time and state, which can have important effects on population establishment in novel environments. Overall, these results show that different components of population fitness have different responses to propagule size and sex ratio in ways that likely affect the early stages of biological invasion.

4.1 | Propagule size

The Allee effect refers to a positive relationship between population growth rate and either density or population size, which puts small populations at higher risk of collapse than larger populations (Stephens et al., 1999). The low offspring production we observed on islands with a small founding propagule fits with this prediction. Notably, a population with one of the smallest propagules was on the verge of collapse (M2 Island) by the end of the study, whereas

the other populations persisted (Table S1; Figure S1). Interestingly, increased offspring production on islands with large founding propagules was generally not evident until the third generation. Although time-lags in population growth are expected after introduction (e.g. Crooks & Soulé, 1999; Kelly et al., 2021; Rilov et al., 2004), we do not have a compelling explanation for why a marked increase in offspring production was delayed until the third generation on islands with large propagules, whereas it remained low on islands with small propagules. This time-lag may result from an unstable stage structure after introduction (indicative of the temporal variation we observed in survival; Figure S2), and increased offspring production from larger propagules may enable populations to reach a stable stage structure sooner than those founded by smaller propagules (Iles et al., 2016). Consequently, the size of the propagule may affect the length of the time-lag in offspring production (and possibly population growth), and potentially influence population expansion after establishment. These observations warrant further investigation, but regardless of the cause of this delayed effect, the positive increase in offspring production in populations with large propagules is consistent with a weak Allee effect.

Although anole populations with large founding propagules had increased offspring production, they did not exhibit increased population growth. This discrepancy could be generated by decreased recruitment to the adult stage (via juvenile survival or growth) in populations with large propagules. Additionally, survival and abundance varied considerably among populations, among states and over time, which could reduce the likelihood of detecting a clear relationship between offspring production and population growth. Alternatively, this discrepancy may be the result of quantifying only one component of individual fitness (e.g. offspring production in our case) rather than the sum of all possible fitness components (Stephens et al., 1999), such that the effect on offspring production did not translate into a measurable demographic effect. Additionally, Allee effects on a component of fitness might be compensated by demographic factors (e.g. number of breeding females, high fecundity rate: Bessa-Gomes et al., 2004), which could lead to a weak demographic Allee effect on population growth, and thus a lower probability for population extinction (Stephens et al., 1999).

Our results are consistent with past studies showing that populations founded from large propagules have increased offspring production (Bessa-Gomes et al., 2004; Blackburn et al., 2011; Lockwood et al., 2013), but here we provide evidence of this pattern at a *per female* scale. While this result provides insight into the drivers of population growth after introduction, we do not know the mechanism responsible for the effect on reproduction. Nevertheless, we offer some possible explanations that warrant investigation. First, female fecundity might exhibit plasticity in response to population size (Karjalainen et al., 2016; Părvulescu et al., 2015) or correlates of population size. High frequency of encounters with conspecifics may indicate that conditions are favourable for supporting large populations and females may increase their reproductive output accordingly. This reproductive plasticity might be exacerbated if food

resources are abundant (Hall et al., 2018), and food abundance may positively correlate with population size. Such reproductive plasticity might facilitate a positive feedback loop and cause rapid population growth in newly introduced populations. Reduced offspring production per female on islands with small propagules may also be a signature of inbreeding depression (Frankham et al., 2002), but a pronounced effect after one generation may be unlikely in our study system. Alternatively, this pattern may reflect influences of factors that we could not control in our study, such as among-island variation in location, size and habitat, or even the lack of replication of propagule size across islands.

The high fecundity of *A. sagrei* over a long reproductive season (Lee et al., 1989) and their 'fast' life-history strategy may explain the successful establishment of populations (Allen et al., 2017; Fetters & McGlothlin, 2017). Indeed, populations derived from small propagules may experience an early lag in growth, but their probability of collapse might be reduced by high fecundity. This is supported by previous experimental introductions of *A. sagrei* to islands using considerably smaller propagule sizes than those used in our study. For example, populations persisted on 18 small islands (of 24) in the Bahamas with only 5–10 founders (Losos et al., 1997; Schoener & Schoener, 1983). Other introductions of brown anoles involved 18 and 19 founding individuals on two small islands (~0.09 lizards/m²); both populations quickly established (Campbell & Echternacht, 2003) and remained present for two decades (Stuart et al., 2014). In addition, releases of male/female pairs on small islands in the Bahamas resulted in positive increases in population size over 2 years followed by considerable among-island variation in population fluctuation (Kolbe et al., 2012). Thus, populations with small propagules can persist over long periods, but they are more vulnerable to founder (Kolbe et al., 2012) and Allee effects (Bessa-Gomes et al., 2004) and may do poorly over longer periods. Indeed, most populations in the Kolbe et al. (2012) study exhibited little to negative growth after the second year, and some had <10 individuals 4 years after release. Such patterns may have been driven by decreased offspring production due to small founding propagules as observed on some islands in our study. Nevertheless, our results provide additional empirical support that organisms with 'fast' life-history traits can overcome the negative consequences of small propagule size and successfully establish in novel environments (Allen et al., 2017).

4.2 | Propagule sex ratio

Our prediction of high offspring production in the first reproductive season on islands with female-biased propagules (i.e. more females, resulting in more offspring production) was not supported. This lack of an effect of propagule sex ratio on offspring production in the first reproductive season could have been due to sperm storage from matings prior to introduction and high male copulation rate (Calsbeek et al., 2007; Kahrl & Cox, 2015). As expected, population sex ratio rapidly shifted towards 0.5 (or slight female bias) after the first year (Figure 4c), confirming that the sex ratio manipulation was

ephemeral and that long-term effects of sex ratio were unlikely. The rapid shift in adult sex ratio after introduction was likely related to high fecundity and short life span in our study species. Additionally, these life-history characteristics of anoles, coupled with their genotypic sex determining mechanism (Rovatsos et al., 2014) and their limited capacity to adjust offspring sex ratios (Urbach et al., 2013; Warner, unpubl. data; but see Cox & Calsbeek, 2010b), could cause rapid shifts towards balanced population sex ratios. The polygynandrous mating system of *A. sagrei* may also facilitate population persistence even when propagule sex ratio is heavily skewed (Shaw et al., 2018). Overall, several reproductive and demographic factors can rapidly drive population sex ratios towards 0.5 even if the propagule is heavily sex biased, which may contribute to the establishment of this invasive species.

Islands with female-biased propagules exhibited greater annual growth in the first year than those with male-biased propagules (Figure 4b). Indeed, population growth on islands with male-biased propagules was mostly negative over the first year. Male-biased sex ratios can negatively affect hatchling/juvenile survival (Delaney & Warner, 2017), which could reduce annual population growth, but differences in juvenile survival rate between initially male- and female-biased populations were not evident in our data (Table S9). Sexual conflict could also be higher in male-biased populations, and may reduce female fertility and survival rate resulting in decreased population growth. Yet, the lack of difference in offspring production between initially female- and male-biased populations does not support sexual conflict as a potential explanation for the difference in annual growth. Likewise, our prediction of low female survival in male-biased populations (due to sexual harassment: Le Galliard et al., 2005; cannibalism: Reedy et al., 2013) was not supported. Instead, females consistently had higher survival than males regardless of propagule sex ratio and state (founders, descendant juveniles and adults) (Tables S9–S11). Other studies have also shown females to have similar or higher survival than males (Cox et al., 2010; Delaney & Warner, 2016; Schoener & Schoener, 1982). A 0.67 propagule sex ratio was enough to detect a difference in annual population growth, but a greater bias may be necessary to affect offspring production or female survival rate (Bessa-Gomes et al., 2004). Notably, annual population growth was positive during the second year after introduction regardless of propagule sex ratio (Figure 4b), which may have been due to the rapid shift in adult sex ratio enabling initially male-biased populations to rebound from the initial negative annual growth. Consequently, initially male-biased populations may have slower colonisation dynamics but equal chance of colonising success.

4.3 | Variation in survival rate

We show substantial variation in survival rate across islands, time and states (Figure S2), which may be explained by biological and logistical factors. For example, habitat structure, predation and prey availability vary across islands and over time, which could impact

how individuals use habitat (Calsbeek & Irschick, 2007; Delaney & Warner, 2016). Additionally, variation in survival may reflect demographic stochasticity of an unstable population structure during early, transient periods of establishment (Iles et al., 2016; Stott et al., 2011). Indeed, estimated population sizes also showed considerable temporal fluctuations across islands (Figure S1). As previously noted, populations were not truly replicated because each population had a different combination of propagule size and sex-ratio treatment, which could contribute to the variation observed. Moreover, detectability was relatively low on some islands and in some cases had large confidence intervals (Figure S3), which could give rise to high spatial and temporal variation in survival and population estimates. Nevertheless, effects of our propagule treatments on other demographic parameters were still detectable despite the high variation in estimates of survival and population size. Consequently, we are confident that our study provides biological insight into the role of propagule size on population establishment in wild populations.

The variation that we observed among states (i.e. founders, descendant juveniles and adults) has important implications for establishment success. For instance, founders (by definition) relocate outside their home ranges, and thus must acclimate to new habitat and compete for new territories. Consequently, reduced founder survival immediately after introduction is expected (Calsbeek & Irschick, 2007), and we show that founders had lower survival than the juvenile and adult descendants that were produced on the islands (Figure 5). Similar patterns have been observed in relocation and restoration studies (Hardman & Moro, 2006; Jenni et al., 2015) and may be associated with stress induced by being in unfamiliar areas (Armstrong & Seddon, 2008; Dickens et al., 2010). Importantly, one caveat for experimental studies like ours is that founders are randomly drawn from a source population and forced to disperse, but there may be non-random subsets of individuals dispersing into novel areas during natural or accidental invasions. Although *A. sagrei* populations seem resilient to reduced founder survival, this could have large negative impacts on population establishment in other species (particularly those with slow life-history strategies or longer reproductive life spans; Capellini et al., 2015; Sol et al., 2012), and is important for managers to consider in restoration and reintroduction efforts.

5 | CONCLUSIONS

Our results support the prediction that populations founded by a small propagule experience lower offspring production than those founded by a large propagule, but this effect did not contribute to annual population growth. We observed an effect of propagule sex ratio on population growth during the first year (but not on offspring production), with a negative annual growth for populations founded by male-biased propagules. However, the rapid shifts towards balanced sex ratios lead to similar annual growth between initially male- and female-biased populations in the second year after introduction. Intriguingly, the effects of propagule size on offspring production and population growth were

opposite to the effects of propagule sex ratio. Despite the effects of propagule size and sex ratio, the life-history traits of *A. sagrei* (e.g., short life span, high fecundity) likely enabled populations to overcome Allee effects and enabled all populations to persist over the duration of this study. These results have broad implications for understanding the early stages of biological invasion. Indeed, different demographic factors of founding populations can have varied impacts on offspring production and population growth, and the consequences manifest at different times after introduction. Our rare experimental test of propagule pressure can also inform predictions of colonisation dynamics in response to different compositions of founding populations, which is critical in the context of species colonisation and invasion dynamics.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

D.A.W. and A.M.R. designed the research; A.M.R., A.F.K., T.S.M., A.M.D., D.M.D., P.R.P., R.M.C. and D.A.W. collected data; A.F. performed statistical analyses and wrote the first version of the manuscript, and all authors contributed substantially to revisions of the manuscript.

DATA AVAILABILITY STATEMENT

Data are available from Auburn University Data Repository (AUra) at: <https://doi.org/10.35099/aurora-91> (Fargevielle et al., 2022).

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