# Sex ratio and female allocation to harems in a polygynous bark beetle

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Abstract Varying forms of polygyny are observed across many animal groups. In some species, groups of females may remain with a single male for an extended length of time. This is often referred to as harem polygyny. A femalebiased sex ratio has been associated with harem polygynous species. In such species, formation of harems may be an inevitable consequence of the relative lack of available males, rather than multiple females actively choosing to mate with a subset of specific males. The five-spined bark beetle, *Ips grandicollis*, is a secondary pest of pine plantations (*Pinus* spp.). Harem-like groups are formed when males bore into the bark creating a small nuptial chamber from where they release pheromones, attracting multiple females that build individual galleries associated with the males' chamber. We estimated the sex ratio of *I. grandicollis* in the flying population compared with those in the logs, and investigated whether females are actively choosing to join the harem of particular males, or if they simply randomly allocate themselves to harems. We also investigated how this female behaviour changes over time since the start of colonisation. The sex ratio in the flying population of *I. grandicollis* was slightly male biased while the population in pine billets was female biased. Early colonising females (within 2 to 8 days of log infestation) joined males non-randomly - being more evenly distributed than expected by chance. However, the pattern of allocation differs between these days, with females allocating themselves more randomly later in the colonisation process. In a separate experiment, data collected from logs colonised after 14 days suggest completely random allocation of females to males. These results suggest that when there is a higher proportion of males to females (during early colonisation), females allocate themselves evenly among males, reducing potential betweenfemale competition. However, as males become rarer, females must join larger harems, but do not appear to exhibit any specific choice behaviour in which harems they join.

Key words bark beetle, *Ips grandicollis*, mating behaviour, polygyny, sex ratio.

# INTRODUCTION

Polygyny is a common animal mating system. The acquisition of multiple female mates can occur in many different ways from scramble competition (Herberstein et al. 2017) and sequential polygyny (Wysocki 2004) to male defence of females or resources important to females (Emlen & Oring 1977). If males are able to maintain associations with multiple females, they increase the opportunity for greater reproductive success through higher numbers of matings (Orians 1969; Sousa et al. 2013). If groups of females aggregate, males that defend and mate with multiple females will gain advantages (Emlen & Oring 1977). Where one male defends and mates with a group of females, this mating system is often referred to as female-defence or harem polygyny (Orians 1969; Emlen & Oring 1977; but see Griffin et al. 2019 and Rowell 1987 for problems associated with defining this mating system as harem polygyny). However, for these aggregations to occur, females must either receive direct benefits from mating in a harem (e.g. protection from predators or harassment, good genes benefits and access to good quality resources), or else other drivers from the environment or population must constrain females into aggregating with a single male for mating (e.g. lack of available resources for nesting or oviposition, or intra-male aggression where males drive off rivals). In these cases, there may be no direct benefit to female aggregation.

Female-biased population sex ratios are one factor associated with harem formation in mammals. In perhaps the best-known harem polygynous species, the elephant seal *Mirounga leonina* in Patagonia, the operational sex ratio becomes strongly female biased in the peak of the breeding season when there is the greatest number of seals on land (Campagna *et al.* 1993). Similarly, harem polygynous pipistrelle bats (*Pipistrellus pipistrellus*) have consistently female-biased sex ratios (Gerell & Lundberg 1985). In red deer (*Cervus elaphus*), increasing proportions of males in populations is associated with decreases in harem size (Bonenfant *et al.* 2004), suggesting that female red deer divide themselves more evenly among males in such circumstances.

The occurrence of harem-like mating aggregations has also been described in some insects. Probably the most well-studied group of harem polygynous insects are the bark beetles (Coleoptera: Curculionidae: Scolytinae). In many of the species in the tribe Ipini, harems are initiated by adult males when they attack recently felled or stressed coniferous trees creating nuptial chambers in the phloem layer (Kirkendall *et al.* 2015). Males release aggregation pheromones to attract females into their nuptial chamber for mating (Kirkendall 1983). Once mated, several adult females build galleries radiating from each male's nuptial chamber where they lay their eggs in niches along the gallery (Kirkendall 1983, 1989; Kirkendall *et al.* 2015).

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Most species across the genus *Ips* are harem polygynous, albeit with variation in the number of females associated with a single male (Schlyter & Zhang 1996). In a few cases where it has been investigated, the sex ratio also varies between species and at different life stages. Approximately even numbers of male and female adult emerge from pine logs in *Ips grandicollis* and *Ips calligraphus* (Garraway 1986). However, the sex ratio of *I. calligraphus* actually attacking trees is female biased (3:1), while an even sex ratio has been found at all life stages for *Ips avulsus* (a monogamous species) (Cook *et al.* 1983). Kirkendall (1983) suggested that the driver for females to join the harem of an already mated male should be when there is a female-biased sex ratio in the population. In this case, females may miss out on mating altogether if they do not join an existing harem.

In this study, we investigated how the sex ratio of the fivespined bark beetle *I. grandicollis* (Eichhoff, 1868) affects the way females allocate themselves among males. *I. grandicollis* is a secondary pest of pine plantations (*Pinus* spp.), mostly in North America (Wood 1982), though with introduced populations in the Caribbean (Garraway & Freeman 1990) and on mainland Australia where it was introduced in the 1940s (Neumann 1987; Bashford 2008). Like other closely related *Ips* species, it forms chambers and galleries under the bark of pine trees, where up to seven females are associated with a single male (Latty *et al.* 2009).

We analysed the sex ratio of both the flying population of I. grandicollis and the populations of adult beetles in logs to better understand whether sex ratio influences the formation of harems in this species. We observed colonisation of the pine logs at different time intervals to determine how females distribute themselves among the available males. Previous work suggested that females distribute themselves randomly among males (Latty et al. 2009), but did not consider the possibility that the population sex ratio may affect how females are dividing themselves among available males. It is known that fewer females are attracted to the males that first arrive at logs (Symonds et al. 2012), but it is unknown whether sex ratio (or the perception of other females) influences female behaviour. We measured all the beetles to determine if females choose to join males based on their body size. We then tested the prediction that in the early infestation of logs, when the density of beetles is lower, the sex ratio will be close to even. We predicted that, as the number of beetles attacking the log increases, the relative number of males will decline as the resource becomes limited - increasing harem size. By examining the relative distribution of females among available males at both early and later colonisation stages, we sought to detect any changes in how females are allocating themselves among males.

## MATERIALS AND METHODS

#### Sex ratio

-37.80, longitude 143.45). We used Lindgren funnel traps suspended between trees to trap beetles and were baited with ipsenol 40 mg pheromone lures (West Green Global Technologies). Trapping took place between October and November 2016. To estimate the sex ratio of the flying population, we sexed beetles collected from the traps using an Olympus SZx7 dissecting microscope looking for the presence of the enlarged medial tubercle located above the epistomal margin, on the head of males (Lyon 1955; Hopping 1965; Lanier & Cameron 1969). The tubercle in females is either absent or much reduced (Lanier & Cameron 1969). When we could not see the tubercle (if the head was aligned underneath the pronotum), we instead counted the number of protibial spines. Females have four to six protibial spines while males possess only three spines (Lanier & Cameron 1969).

We also estimated the sex ratio in the adult population found in logs. To do this, five pine trees within the Bradvale plantation were felled, trimmed of branches and cut into shorter billets. The billets ranged in length from 34 to 63 cm and from 9 to 22 cm in diameter. We laid these billets in piles of 10, approximately 40 metres apart among standing pine trees and then left them for 2 weeks in an area where large numbers of bark beetles had been detected earlier in the season during the analysis of sex ratio using pheromone traps. We ensured that the billets in each of the piles comprised a random mixture of logs from different trees and with different diameters. To improve the likelihood that beetles infested the logs, a pheromone lure was attached to one of the logs in each pile. After 2 weeks, we brought the billets back to the lab. We carefully removed the bark with a chisel beginning at each entry hole (detectable by the presence of frass on the outside of the log), until all gallery arms radiating from the central nuptial chamber were exposed to locate all the beetles within the harem. Females were found at the end of gallery arms, and males were distinguished as those beetles that were found in the nuptial chambers (or elsewhere in the gallery, not at the end). When we were uncertain about a beetle's sex based on their position in the galleries, we took all the beetles associated with a single nuptial chamber and sexed them under a dissecting microscope using the above method. We also noted the number of females associated with each male (this was subsequently used as a measure of infestation patterns at Day 14).

For each beetle found in an aggregation, we measured the body length (from front of the head to tip of abdomen) and width of the pronotum. Measurements were made (in mm) using digital callipers accurate to two decimal places, and to estimate body size, we calculated beetle volume using the formula for the volume of a cylinder (Symonds *et al.* 2012). All measurements were conducted on dead beetles by the same researcher (MJG) and had high repeatability (r = 0.767, P < 0.001, comparison of four individuals measured 15 times). We used a Spearman's rank correlation test to analyse this association between male size and number of females in the harem.

#### Differences in female allocation to harems over time

In November of 2017, 100 pine billets from six different source trees, measuring between 37 and 40 cm long and 9 to 22 cm in

diameter, were cut from mature trees at Bradvale. We randomly assigned the billets to two piles of 50 logs in areas of the plantation known to have *I. grandicollis* activity. Ipsenol pheromone lures were attached to each pile to improve beetle attraction to the logs. We assessed the pattern of beetle colonisation (i.e. harem composition) at 2 and 8 days after the placement of logs (50 logs on each day). To record the number of females with each aggregation, we removed the bark from the entire log and checked both the wood and the underside of the bark for the presence of nuptial chambers and galleries. We counted each nuptial chamber on the log (representing the number of males in the log) and also the number of female galleries radiating outwards from each chamber. The assumption was that each gallery represented a single female in the harem (Latty *et al.* 2009).

To investigate how females were distributing themselves among males on different days, we used a generalised linear model with a Poisson distribution, where the response variable was the frequency (i.e. the count) of a particular harem size, and the predictors were the harem size and the assessment day (Day 2 vs. Day 8). We included an interaction term (day × harem size), to determine whether there was a difference in the way females were allocating themselves among males (i.e. the pattern of harem sizes) on different days. The GLM was carried out using R version 3.5.1 (R Core Team 2018).

We also used chi-squared tests to assess whether females were allocating themselves in a manner different from that expected by random chance. For these tests, we used data from Days 2 and 8 collected in 2017 and from the Day 14 data collected in the previous year. Here, the analysis compared the observed distribution of harem sizes with a null expectation and is therefore not a strict comparison between days. To generate the null expected values, for each day of sampling, we took the total number of females observed across all harems and the total number of males (entry holes) then used the Microsoft Excel macro function, 'randbetween' (limits set between 1 and the total number of males), to allocate each female randomly to an entry hole. This generated the expected random frequency distribution of harem sizes.

## RESULTS

#### Sex ratio

The sex ratio of *I. grandicollis* differed significantly between the flying population and that found in the logs 14 days after colonisation (Fig. 1). The sex ratio in the flying population was slightly (but significantly) male biased (1.15:1 males : females, binomial test: P < 0.001, n = 4976), while the sex ratio in the population removed from the pine billets was strongly female biased (1:3.38 males : females, binomial test: P < 0.001, n = 342). Within the logs used for the 2017 experiment, the sex ratio also changed over time from a male-biased population at Day 2 (1.45:1 males : females, binomial test: P < 0.001, n = 561) to a female-biased population by Day 8 (1:1.55 males : females, binomial test: P < 0.001, n = 927).

Males collected from these logs were significantly larger than females, both in length (mean male length = 3.93 mm, mean



*Fig. 1.* Proportion of *Ips grandicollis* populations that are males, across all samples collected, as found in the flying population and in the population of beetles under the bark.

female length 3.86 mm, independent samples *t*-test:  $t_{118} = 2.264$ , P = 0.025) and in the width of their pronotum (mean male pronotum width = 1.37 mm, mean female pronotum width 1.31 mm,  $t_{128} = 4.214$ , P < 0.001). The mean harem size of the beetles collected from the logs at 14 days was 1.8 females per male (s.d. = 1.31) with harem size ranging for zero to six females per male. There was no correlation between the size (volume) of males and the number of females associated with that male ( $r_s = 0.07$ , N = 74, P = 0.552).

#### Change in female allocation to harems over time

The distribution of females among males depended on the amount of time available for infestation. At Day 2, the mean harem size was 0.69 females per male (s.d. = 1.03). At Day 8, this had increased to a mean number of 1.55 females per male (s.d. = 1.21). There was a significant interaction between assessment day and harem size (Table 1) in predicting frequency of particular harem sizes. Females allocated themselves differently among males depending on the length of infestation. At Day 2, most males had one or no females associated with them while at Day 8, the number of males with no females was reduced and all other harem sizes had increased.

The chi-squared goodness of fit test showed that at Days 2 ( $\chi^2 = 79.57$ , P < 0.001) and 8 ( $\chi^2 = 17.74$ , P = 0.007), there was a significant difference between the observed and expected frequencies of harem sizes (Fig. 2), indicating that the number of females per male differed from the expected random distribution. Specifically, females distributed themselves more evenly among males than expected by chance earlier in the infestation of cut logs. However, the trend was significantly less pronounced at Day 8. Data taken from the previous season at 14 days

Table 1Generalised linear model with Poisson responsecomparing frequencies of different harem sizes in *Ips grandicollis*aggregations, 2 and 8 days after colonisation begins

	df	Deviance $(\chi^2)$	P value
Day	1	1.47	0.2251
Harem size	7	909.94	< 0.001
Day : Harem size	7	136.58	< 0.001

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*Fig. 2.* Frequency plots of the observed and expected number of females associated with a male at each of the assessment days and the associated chi-squared test.

after the logs were placed out suggest that this trend can be extended further. At Day 14, there was no significant difference between the observed and expected values ( $\chi^2 = 79.57$ , P = 0.430). Here, the females were distributing themselves as would be expected if they were doing so randomly (Fig. 2).

## DISCUSSION

The sex ratio of *I. grandicollis* bark beetles differs between the flying population and those found infesting logs. Additionally, the way females allocate themselves among males also changes - from appearing to allocate themselves more evenly when sex ratio is near even, during early colonisation, to allocating themselves more randomly when sex ratio becomes more female biased. The flying population caught in Lindgren funnel traps was slightly male biased. The traps would have caught newly emerged males (and females) and other males that may have mated previously and have emerged from their original entry hole to remate (as seen in other Ips species, e.g. Reid & Roitberg 1994). It is possible that pheromone traps preferentially attract males rather than females and hence may not reflect the true sex ratio of the flying population. We did not investigate sex ratio on emergence, but Garraway (1986) found that it is even in I. grandicollis in Jamaica.

By contrast, the population of beetles removed from beneath the bark was highly female biased. A female-biased sex ratio has also been observed in other species, including the closely related *I. calligraphus* (Cook *et al.* 1983), and this observed sex ratio may be a consequence of males being the pioneering sex. Males may have a higher mortality rate as they are exposed to more of the host tree defences or predation while on the outside of the bark (Cook et al. 1983; Kirkendall et al. 2015). Additionally, as the colonising sex, males must disperse to find potential breeding material, which contributes to increased male mortality (Garraway & Freeman 1990). Such differences in mortality may explain the sex ratio between beetle emergence and subsequent colonisation of a new tree for breeding (Garraway 1986). The skewed operational sex ratio may also force female bark beetles to choose already mated males because they do not encounter any unmated males during their search (Searcy & Yasukawa 1989). If females were to avoid mated males, they might not mate at all (Rhainds 2010). Female tree swallows, Tachycineta bicolor, may also lose the chance to nest altogether if they reject a male that is already mated. However, the swallows suffer reduced parental care from polygynous males through reduction in the provisioning of the nest with feathers for insulation and food, as well as reduction in defence from predators (Ferretti & Winkler 2009). Despite the costs involved, females may choose to associate with a polygynous male if the alternative is that they are not able to find a mate at all.

If females are forced to join an already mated male, it may be expected that they would choose a male that has some traits that would be advantageous for their offspring. It is a common occurrence in mammals, especially for those identified as harem polygynous, for the largest males or male with the largest secondary sexual traits in the population to acquire the most mates (Weckerly 1998). Larger male southern elephant seals (*M. leonina*) have more reserves available to remain as harem holders for longer and increase their number of copulations (Modig 1996). Similarly, when male competition was controlled in white-tailed deer, Odocoileus virginianus (males were kept separately, females only able to judge males on appearance with manipulated antler size), females choose large antlered males over males with small antlers (Morina et al. 2018). Though more commonly observed in vertebrates, this behaviour has been recorded in the Orthoptera genus Hemideina (New Zealand tree wētā). Males of the alpine tree wētā (Hemideina maori) with large heads and mandibles are able to defend rock tors from competitors and are found with more females than males with smaller heads and mandibles (Gwynne & Jamieson 1998). However, this was not the case in this population of *I. grandicollis*. Male size did not dictate the number of females that an individual was able to attract; the largest males did not attract the most females. This result is consistent with findings in other populations of I. grandicollis in Australia (Latty et al. 2009). Some evidence suggests that Ips males may have aggressive interactions, as observed in other harem polygynous species, if they encounter each other at the entrance to a nuptial chamber. Although this was a laboratory-based experiment with forced interactions between males that may not regularly occur in the natural population (Oester & Rudinsky 1975).

Other species of Ips also show little evidence that females exhibit a choice when mate searching. Schlyter and Birgersson (1989) suggest that although male bark beetles show variability in their pheromone production, females are unlikely to be able to distinguish between males in a mass aggregation. Females seem to show random search behaviour, and finding a male may be more related to chance than directional searching (Schlyter & Birgersson 1989). There was no difference in the amount of time male and female Ips typographus spent searching, after landing on a tree (Paynter et al. 1990). Females of this species may experience difficulty finding a male that will accept them, just as males experience difficulty finding a suitable site to bore into. Early in the attack of a tree, females are also more likely to leave the tree (Paynter et al. 1990). At this stage of an attack, male density is likely low and search times and costs to finding a mate would be high, so females would benefit from finding a tree with a larger density of males. Although I. typographus attacks live trees so has different ecological challenges to I. grandicollis (Raffa, 2001). There could also be costs associated with settling on a highly populated log. When breeding sites were crowded, female Ips pini laid fewer eggs and the males abandoned their nuptial chamber earlier, decreasing their paternal investment (Robertson 1998). Overcrowding in the harem can also have a negative effect on female reproduction. Females from large harems, where galleries are more likely to be densely packed, have reduced egg production (Latty et al. 2009).

As time after colonisation increased, we observed greater clumping of females. Data from the 2016 season suggest that females cease being distributed evenly, and are distributed in a manner predicted by random chance, 14 days after colonisation. Since these data were collected from a different year, we cannot rule out the possibility of other environmental (seasonal) effects determining female distribution here. However, our comparison of colonisation after Days 2 and 8 in the 2017 season does confirm significant differences in the relative frequency of harem sizes between the 2 days, with females being more evenly distributed at Day 2.

The clumping of females later in colonisation means that some males had larger than average harems while other males had attracted no females in the same time. These differences were not due to male size, so females could be using another cue to select a male or there may be external drivers associated with choosing an entry hole. Females of I. pini likely make their decision based on an assessment of the patch made before they land and their choice thresholds are able to be adjusted based on patch quality (Reid and Stamps 1997). Females were observed to only visit one or two male nuptial chambers before making a choice. Males that are first to arrive at a log and create nuptial chambers attract fewer females (Symonds et al. 2012), which suggests that females may exhibit some active choice. The presence of stridulatory organs on both sexes of many Scolytinae species may indicate that acoustic signalling has a role in mate choice (Raffa et al. 2015). Females have been observed to stridulate at the entrance of a male's nuptial chamber and continue to do so until the male allows entrance into their chamber (Wilkinson et al. 1967; Garraway 1986). Alternatively, females may seek to avoid predation by limiting the time they spend on the outside of the bark and choosing the nuptial chamber of the first male they come across. So females may be making the best of a bad situation by limiting costs where they can to ensure they are still able to breed. A disadvantage of this strategy is that they disregard the possibility of finding a better mate (Janetos 1980; Kokko et al. 2014). It is clear that further investigation is needed into whether females are actively choosing which male to join once they land on a log and how.

We cannot discount the possibility that Ips males are choosy about which females they mate with (Bonduriansky 2001). Male Ips confusus have been observed blocking the entrance to their nuptial chambers prohibiting females from entering (Borden 1967). Males of that species were more likely to refuse a female after they had already attracted three other females. This suggests that males have an optimal number of females or are selecting females that are superior in some way. Ips acuminatus males were able to distinguish between sexual females (offspring genome contained genetic material from both parents) and clonal females (female offspring that are genetically identical to their mothers) and were more likely to accept a sexual female into their nuptial chamber (Løyning & Kirkendall 1996). Hence, the patterns we observed may result not from female choices but from male behaviour, accepting or rejecting females that attempt to join the nuptial chamber, thereby regulating their harem size. The harems formed by Ips bark beetles constitute a mating system that is very uncommon in insects (Griffin et al. 2019). Although the largely female-biased sex ratio in the population may be partly driving harem formation, this does not explain why some males attract more females than others. It is possible that quality of the resource (e.g. nutrient levels), rather than aspects of the male specifically, determines female allocation among harems (Reid & Stamps 1997). More finescale observations of their search behaviours could provide useful information on female choice. Additionally, investigations into how the biotic and abiotic environment affects the behaviour of the population and their aggregations could further contribute to the understanding of this intriguing behaviour.

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