A Tale of Two Cities:
The relationship of density and morphology varies among populations of the maritime earwig *Anisolabis maritima*

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Abstract

For organisms that live in groups, the spatial distribution of individuals according to size and sex can provide insight into social interactions, including aggression (intrasexual selection for armaments) and mating preferences (intersexual selection for ornaments). To gain insight into how group dynamics may influence the mating system, we investigated the relationship of density and morphology in the maritime earwig, *Anisolabis maritima*, an insect found in high densities beneath pieces of driftwood above the high-tide line in coastal ecosystems throughout the world. There are fundamental differences in the behavior and morphology between the sexes. Males and females differ fundamentally in their aggression during agonistic encounters with conspecifics; males more readily cohabitate with conspecifics and resolve their disputes non-lethally whereas females often kill conspecifics in close proximity as they vigorously guard their offspring. Males also differ markedly from females in both body size (males are more variable in size, and sometimes substantially larger, than females) and weaponry (males possess asymmetrical, curved forceps whereas females have straight forceps). Given previously observed variation in both body size and forceps asymmetry, we investigated the possible correlation between population density and morphology of individuals in two populations on San Juan Island, WA to determine whether these parameters affect group dynamics and social interactions. Specifically, we lifted 10-15 logs at two sites (False Bay and Cattle Point) at two different times during the breeding season (June and July) and determined the overall density, average body size and average forceps asymmetry for individuals under each log. Comparing the area occupied to the body size and forceps asymmetry of individuals, we found that the relationship between body size and population density varied both by site and by the period in the breeding cycle. Additionally, we found a greater, more morphologically diverse population of males at False Bay, a site with lower tidal action and more predictable habitat availability. We posit, therefore, that the breeding cycle varies from site to site based on the stability of the environment, and that a more turbulent environment can disrupt the population and delay the breeding cycle, leading to a less diverse, more unstable population. Our results also suggest that larger individuals are more likely to live in higher densities before the breeding cycle, possibly due to their increased fighting ability and willingness to compete with others for mates, and at lower densities early in the breeding cycle due to their increased conspecific aggression during courtship and nesting. This research lays the foundation for future studies regarding the social dynamics of this species where we can monitor individual interactions and group distributions in a more controlled laboratory setting.

Introduction

The morphology and spatial distribution of social organisms provide insight into the nature of conspecific interactions, particularly aggression and competition between individuals in a mating context (Emlen & Oring 1977, Arnqvist & Rowe 2005). While weaponry is often used for predation and defense, it is also a common element in both intrasexual selection, where armaments are used for competition over access to mate, and intersexual selection, where such traits may provide potential mates with information about quality. Elucidating the relative contributions of these selective forces is a critical step in understanding mating systems, particularly given the potential combinations and complexities that arise when both sexes possess weaponry.

The maritime earwig (*Anisolabis maritima*, Order Dermaptera) is an insect widely distributed throughout the world and is commonly found in high densities under driftwood and seaweed at or above the high tide line (Bennett 1904). They are, however, relatively inconspicuous on most beaches because they spend most of their time under beach debris to avoid desiccation and escape predators, emerging only at night to forage on small arthropods (Langston & Powell 1975). Beneath these shelters, females construct nests and lay eggs that they defend from predators, including cannibalistic conspecifics (Miller et al. 2011). Sex, body size and forceps have been shown to play important roles in both aggression and courtship among earwigs (Munoz & Zink 2012, Nolan-Tamariz & Iyengar 2016), and *A. maritima* males and females differ fundamentally in their aggression during agonistic encounters with conspecifics. Males typically resolve their disputes non-lethally by squeezing each other's abdomen, perhaps a means to assess size, strength and fighting ability (Munoz & Zink 2012). Females, on the other hand, often kill conspecifics while vigorously guarding their nests, and larger females defend their eggs or juveniles against conspecific cannibalism more effectively due to their increased size and resulting dominance in intraspecific competition (Miller et al. 2011).

Males differ from females in both body size (males are more variable in size, and sometimes substantially larger, than females) and weaponry (males possess asymmetrical, curved forceps whereas females have straight forceps), which have ramifications for intrasexual contests in the maritime earwig. Previous studies of sexual selection in *A. maritima* have shown that body size rather than the degree of forceps asymmetry has been the object of interest in females regarding mate choice (Tomkins & Simmons 1998, Nolan-Tamariz & Iyengar 2016, Kendall-Bar & Iyengar 2017). The curvature and varying asymmetry in male forceps appear to allow assessment of other males without lethal strikes, and the degree of forceps asymmetry in males has been shown to be beneficial in competition for food among small males (Munoz & Zink 2012). All these results, however, do not explain the wide variation in both body size and (male) forceps asymmetry we have observed in natural populations.

Due to the limited availability of shelters in their natural habitat, maritime earwigs are often found cohabitating in large numbers under a single shelter. The higher population densities increase the frequency of conspecific interactions; these interactions may be the key to understanding the evolution and maintenance of morphological variation in body size and forceps asymmetry. Previous work analyzing social interactions in groups of *A. maritima* showed that females distribute themselves uniformly to occupy a given space while males tend to gather in clumps (Dodgen & Iyengar 2015), suggesting that females are generally more aggressive than males. That study, however, only monitored the positions of individuals over the course of 24 hours in a laboratory setting. In this study, we examined the correlation between natural population densities and morphometrics at two different sites to gain insight into the social interactions occurring within the fluid aggregations of the maritime earwig, *Anisolabis maritima*.

Methods

The suitability of driftwood as a shelter depends largely on its proximity to the tideline, the dimensions of the wood itself, and the moisture and texture of surrounding substrate (Bennett 1904). Because pieces of driftwood vary enormously in suitability and are so sporadically distributed along the tideline, transect surveys would only prove beneficial if conducted on a much larger scale, which was a task too large to take on in a single summer of research. Instead, we focused on the density and distribution of individuals beneath individual driftwood shelters. On San Juan Island, WA (Figure 1), we sampled earwig populations at two sites at two different points (False Bay on June 25th and July 20th; Cattle Point on June 30th and July 21st) in the breeding season. At each site, we lifted 10-15 logs (each with a meter stick in the frame for scale) and used an iPhone 6s camera to photograph the distribution of individuals beneath, collecting as many individuals as possible in the process. The photos were analyzed using the program ImageJ to identify the sex of the individuals and determine the area of the space occupied by the earwigs. After photographing the area, we collected all adult individuals present and brought them back to Friday Harbor Laboratories. After being frozen, the individuals were viewed through a Nikon SMZ800 dissecting scope and photographed using the program QCapture. These images were analyzed using ImageJ to determine the sex and body size of all collected individuals and forceps asymmetry in males. Body size was determined using pronotum width (mm), and the degree of forceps asymmetry was determined using a ratio of left and right forcep curvature (Munoz & Zink 2012). Statistical analyses were completed using JMP wherein we used an ANCOVA to determine the interaction effects of population density, body size, and date of collection for female and male earwigs at False Bay and Cattle Point. We used a Welch's t-test to compare the body size of males at both sites, and we used a Levene test to compare the variance in male body size at each site. We also used regression and ANCOVA analyses to determine the relationship between male forceps asymmetry and body size at the two different sites.

Results

For both females and males at False Bay, there was a negative correlation between body size and density in June but no such relationship in July (Figures 2 & 3). There were no significant correlations between male forceps asymmetry and population density in June ($F_{1,12}$=2.37; p=0.149; R^2=0.165) or July ($F_{1,10}$=4.80; p=0.053; R^2=0.324).

For females at Cattle Point, there was a positive correlation between body size and density in June and a negative correlation in July (Figure 4). For males, there was no relationship between body size and density in June but a negative correlation, similar to females, in July (Figure 5). There were no significant correlations between male forceps asymmetry and population density in June ($F_{1,8}$=2.14; p=0.181; R^2=0.211) or July ($F_{1,12}$=3.75; p=0.077; R^2=0.238).

Males at False Bay were, on average, about 6% larger than males at Cattle Point (Figure 6). Male size was also more variable at False Bay than at Cattle Point (Levene test: $F_{1,48}$=6.40; p=0.015). We also found a positive correlation between male body size and forceps at both sites (Figure 7).

Discussion

Overall, we found that the relationship between body size and population density varies depending on both the time and site of collection. In June at False Bay, larger females were found in lower densities while smaller females were found in higher densities. In July, however, there was no correlation between body size and population density. We attribute this to the timing of the breeding cycle, as the maritime earwig breeding season typically occurs in the summer (Bennett 1904). We posit that June is the time in which breeding is at its height for this population, which means that many females are likely to be aggressively protecting their young from predators as well as cannibalistic conspecifics (Miller et al. 2011, Hack & Iyengar 2013). In this respect, larger females are more proficient at protecting their nests – likely due to increased aggression and fighting ability (Miller et al. 2011) – which would lead to greater spacing (and lower densities) among large females. A similar trend occurred in males at this site in June, although the reasons may differ given that there is no record of male parental care. While males are generally more willing to cohabitate and interact with one another (Hack & Iyengar 2013, Dodgen & Iyengar 2015), there are larger male morphs that are markedly more aggressive scattered throughout maritime earwig populations (Dodgen & Iyengar 2015). We believe that lower densities among large males is either due to larger males aggressively chasing away other individuals, other individuals avoiding interaction with these intimidating large males, or a combination of both (Dodgen & Iyengar 2015, Kendall-Bar & Iyengar 2017). The lack of a relationship between size and density for both males and females in July is likely due to the fact that this population was sampled at a later point in the breeding season. At this point, the majority of mating and nesting had likely taken place, resulting in reduced aggression and increased tolerance for cohabitation among and between both sexes given the lower reproductive stakes.

At Cattle Point, the relationship between female body size and population density was entirely different. In June, female body size increased significantly with increasing density while their relationship in July at Cattle Point is more similar to the correlation in June from False Bay. In June, larger females were found in higher population densities than smaller females while in July larger females were found in lower densities than smaller females. We believe that this pattern is also associated with the timing of the breeding cycle. Because of the similarities between the data from Cattle Point in July and False Bay in June, we posit that there was some sort of delay in the breeding cycle (reasons for this will be discussed shortly). If this is the case, the data from Cattle Point in June represents a period of time either before the breeding season or during its earliest stages. Although the female size-density relationship could imply that there was decreased aggression leading to an increase in cohabitation, meaning there would be little to no reproductive stakes, it is possible that the females there had more recently matured and were, therefore, still somewhat near their nest site as juveniles, reflected in the higher population densities. The relationship shown, however, could also be a result of larger females being more willing to compete for high-quality shelters (in preparation for the breeding season) than smaller females (Miller et al. 2011, Dodgen & Iyengar 2015, Kendall-Bar & Iyengar 2017). The males at Cattle Point in June, however, had a non-significant relationship between body size and population density. This further supports the notion that male and female earwigs may have different emergence times (from juvenile to sexually mature adult). This trend is characteristic of males having more time after maturation to disperse from their juvenile nest. Additionally, while non-significant, the trend was slightly negative and could be represent a transition in male population densities between pre-breeding and early breeding stages of the breeding cycle.

We believe the trends shown in these data demonstrate a time lag in the breeding cycle of maritime earwig populations at Cattle Point compared to that of populations at False Bay. This time lag can be explained by the distinct differences in the habitat fostered by these two sites. False Bay is a mudflat on the south-east side of San Juan Island. This area is well protected from the tides and experiences little wave action. As a result, there is a substantial amount of driftwood at the high tide line that is not subject to frequent movement. As a result, there is a large source of predictable, more stable habitat for maritime earwigs which cohabitate, breed, and nest under driftwood at False Bay. Conversely, Cattle Point is a strip of beach at the southern-most tip of the Island that is exposed to large tidal exchanges, causing large amounts of driftwood to become water-logged and shift along its shores. Due to the constant exposure to high wave action, the driftwood shifts around the beach very frequently. This makes the habitat very unstable and susceptible to frequent change that is not ideal for breeding and nesting purposes. Due to the increased stability and availability of habitat at False Bay, the earwig populations are likely able to breed sooner than those at Cattle Point that have limited habitat availability and stability.

We also found other notable differences between our two field sites. False Bay has slightly larger males on average and greater variation in male body size than Cattle Point. This pattern may be a reflection of the habitat and food availability at each site. False Bay not only has more suitable habitat that can support a larger, more variable population, but has more stability and a constant food availability to promote larger individuals. At Cattle

Point, however, the habitat is limited and unstable, which leads to increased competition (less variability) combined with fewer resources (smaller size). More studies should be done to determine whether habitat variability influences size-density relationships across other populations.

One of our main goals was to investigate the evolution of male forceps asymmetry by determining whether male forceps asymmetry is affected by density (or vice versa). Previous work in the European earwig was able to demonstrate that density drives forceps morphology, as higher densities lead to selection for large-forcep males (Tomkins & Brown 2004). Our current study in the maritime earwig did not allow us to distinguish between whether density influenced size or whether size influenced density (although we suspect the latter in our case). Furthermore, we found that the patterns regarding male forceps asymmetry were similar to those regarding body size – however, since larger individuals were more asymmetrical, we were unable to disentangle these two characteristics in our analyses. Given the large amount of variation among males, we suggest that more research is done to examine the genetic and environmental factors that affect the forceps and how that asymmetry may affect both inter- and intraspecific interactions.

Conclusions

We found that the relationship between density and body size of maritime earwigs change throughout the breeding cycle. During the height of the breeding season, larger individuals, who are often more aggressive, tend to be the driving force in the variation of population densities. Furthermore, the breeding cycles varies from site to site based on habitat availability and stability. The patterns in the data for False Bay in June and very similar to those observed for Cattle Point in July, suggesting there is a time lag in the breeding cycle for Cattle Point. This is likely due to the limited habitat stability caused by increased wave action, whereas False Bay is far more protected and experiences greater habitat stability, fostering more ideal breeding conditions. Additionally, habitat stability affects the diversity and durability of a population. By sampling populations at two different sites, we found that the site with a more stable, predictable habitat fosters a larger and more morphologically diverse population while a site with unstable conditions is characterized by higher selective pressures and, therefore, has a smaller, less diverse population.

This study was the first natural density sampling conducted on the maritime earwig, and there is much more to explore concerning the social dynamics, functional morphology, and relative contributions of varying selective pressures acting on this species.

Acknowledgments

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Figures

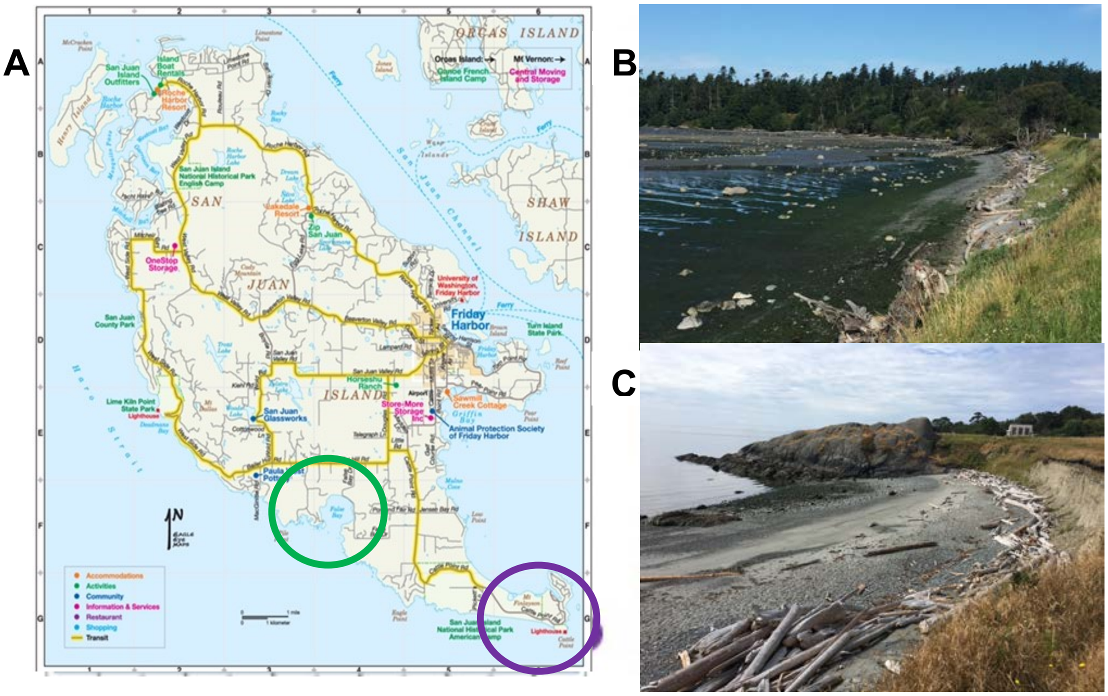

Figure 1. (A) Map of San Juan Island, WA (www.sanjuanisland.org.maps.htm), with the two field sites circled in green (False Bay) and purple (Cattle Point). False Bay (B) is a mudflat that is more protected from wave action than Cattle Point (C).

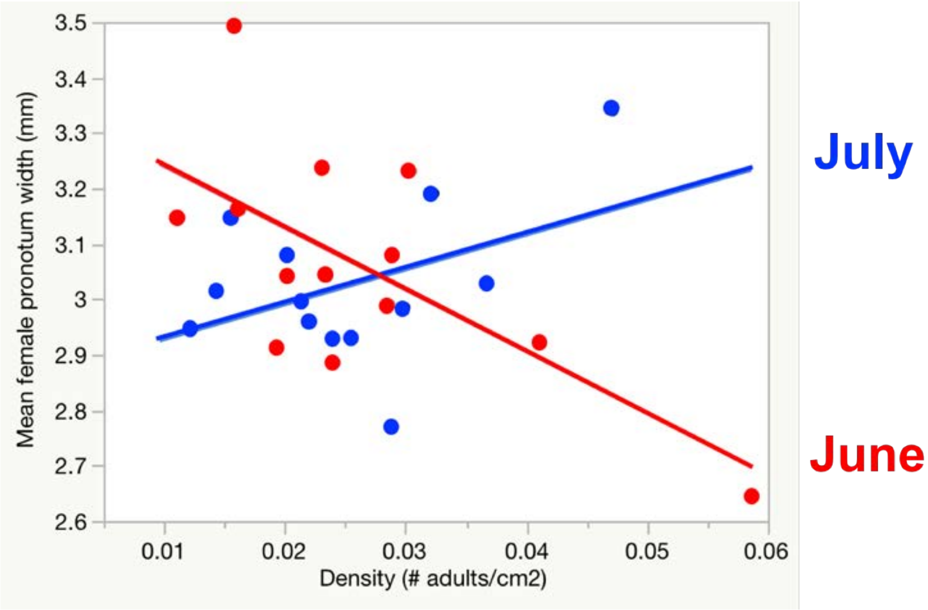

Figure 2. The relationship between female pronotum width (mm) and density (adults/cm^2) at False Bay. There was a negative relationship between size and density in June (red: $F_{1,11}=8.97$; $p=0.012$; $R^2=0.449$) but not in July (blue: $F_{1,11}=2.50$; $p=0.142$; $R^2=0.185$). There were differences in this relationship between the two time periods (ANCOVA: $F_{1,22}=9.83$; $p=0.0048$).

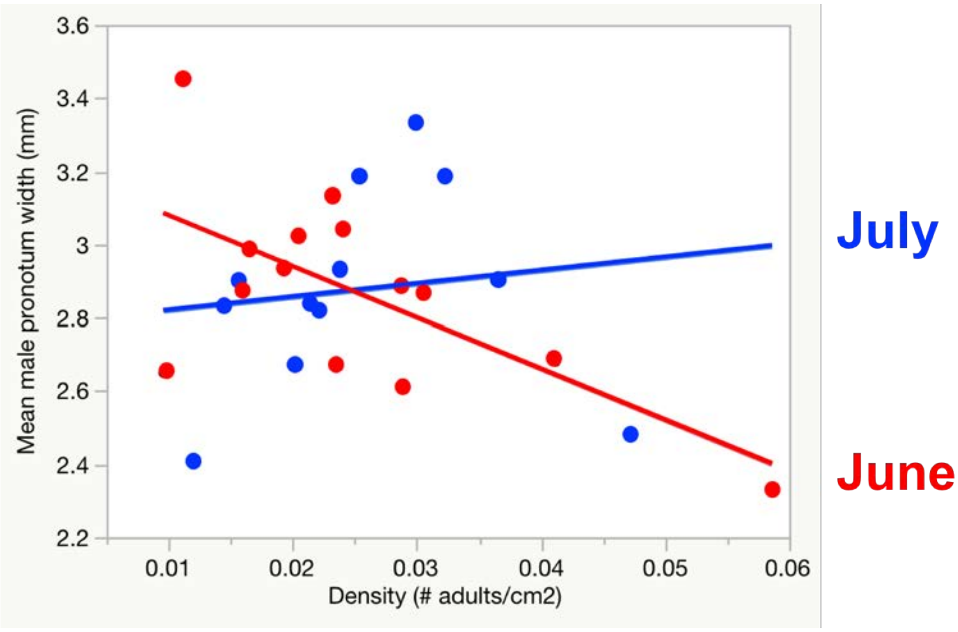

Figure 3. The relationship between male pronotum width (mm) and density (adults/cm^2) at False Bay. There was a negative relationship between size and density in June (red: $F_{1,12}=8.95$; $p=0.011$; $R^2=0.427$) but not in July (blue: $F_{1,10}=0.18$; $p=0.679$; $R^2=0.018$). There were no differences in this relationship between the two time periods (ANCOVA: $F_{1,22}=3.67$; $p=0.069$).

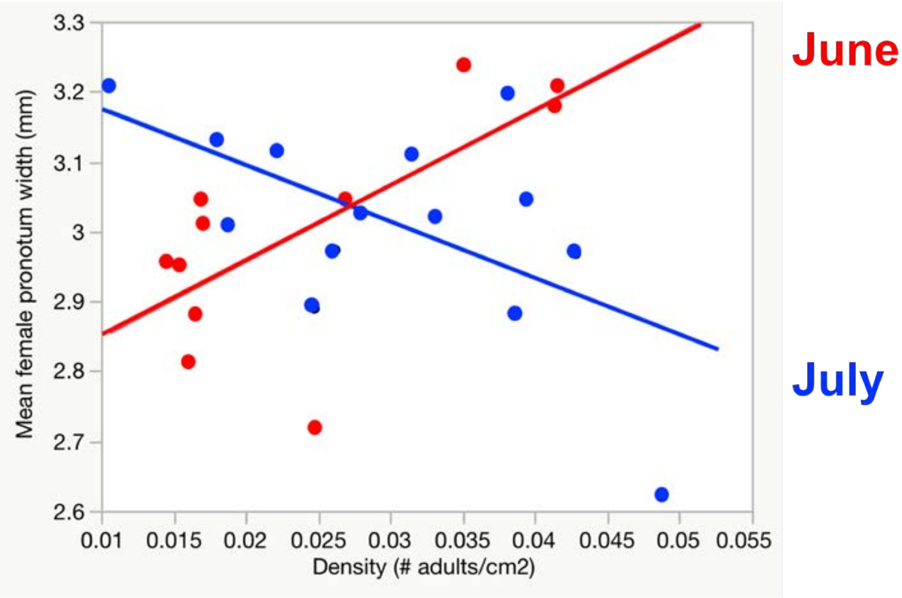

Figure 4. The relationship between female pronotum width (mm) and density (adults/cm^2) at Cattle Point. There was a positive relationship between size and density in June (red: $F_{1,9}$=8.69; p=0.016; R^2=0.491) and a negative relationship in July (blue: $F_{1,9}$=6.06; p=0.030; R^2=0.336). There were differences in this relationship between the two time periods (ANCOVA: $F_{1,21}$=14.56; p=0.001).

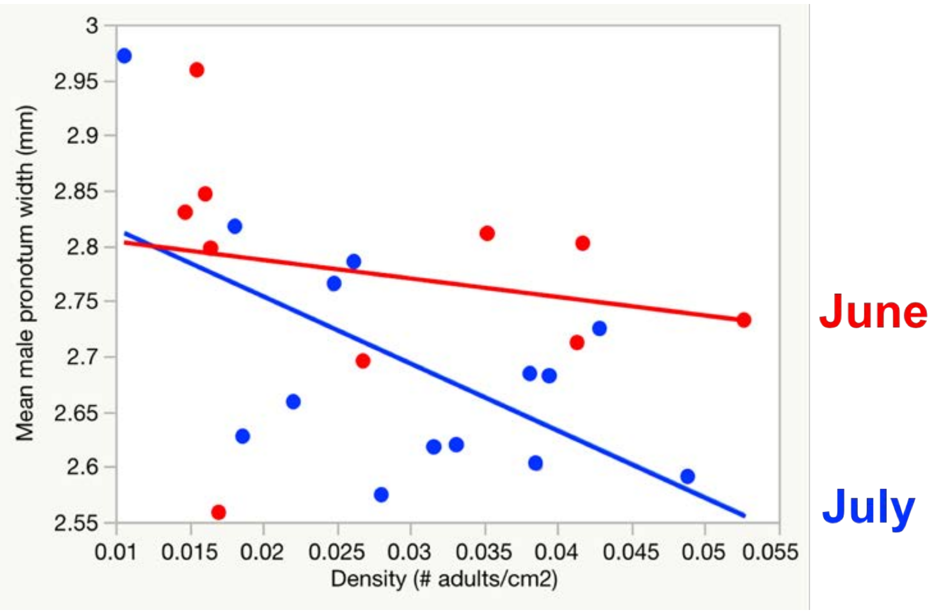

Figure 5. The relationship between male pronotum width (mm) and density (adults/cm^2) at Cattle Point. There was no relationship between size and density in June (red: $F_{1,8}$=0.40; p=0.543; R^2=0.048) but a negative relationship in July (blue: $F_{1,12}$=6.64; p=0.002; R^2=0.356). There were no differences in this relationship between the two time periods (ANCOVA: $F_{1,20}$=1.56; p=0.226).

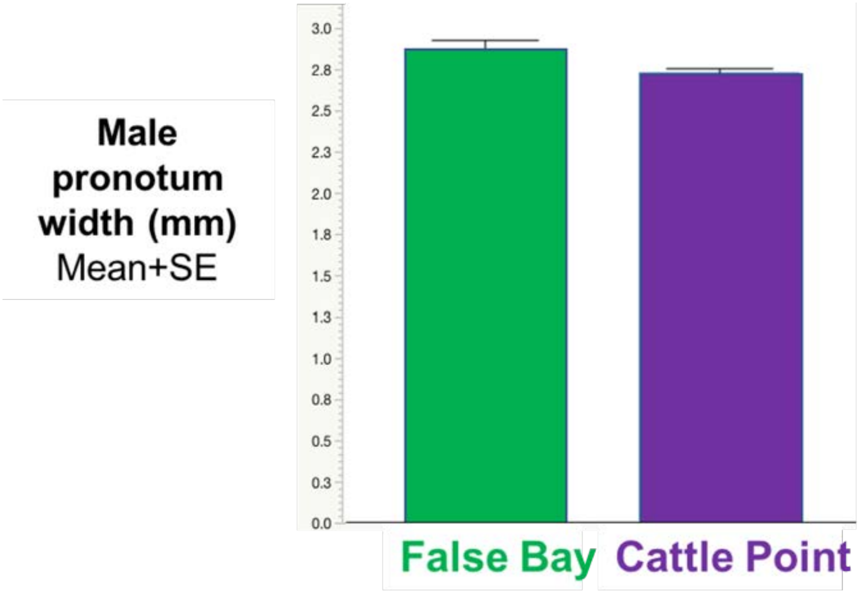

Figure 6. Mean male pronotum width (mm) at False Bay and Cattle Point. Males at False Bay were significantly larger than those at Cattle Point (t=2.58; df=48; p=0.014).

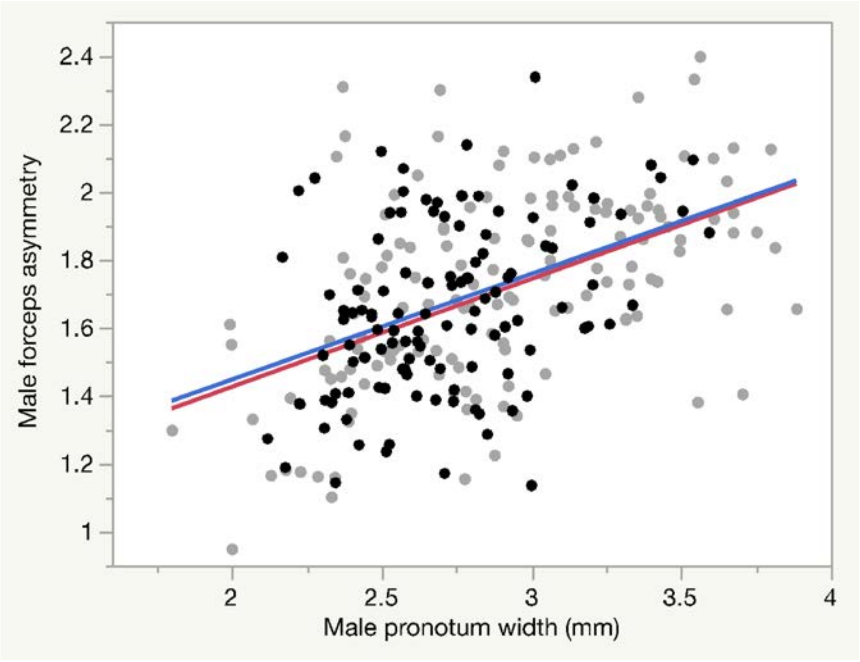

Figure 7. The positive relationship between male pronotum width (mm) and forceps asymmetry. The blue line and grey points represent data from False Bay ($F_{1,141}$= 45.43; p<0.0001; R^2=0.244), and the red line and black points represent data from Cattle Point ($F_{1,115}$= 23.15; p<0.0001; R^2=0.168). There were no difference between the sites (ANCOVA: $F_{1,256}$=0.005; p=0.944).

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