Evidence for developmental plasticity in response to demographic variation in nature

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Abstract. Adaptive developmental plasticity has been demonstrated across a number of taxa in response to variables such as photoperiod, resource abundance, and predator presence. Demographics also vary temporally and spatially within populations, but few studies have examined the possibility that developmental plasticity in response to changes in these variables can alter phenotypic distributions. Plastic responses to variable population density and sex ratio may play an important role in explaining phenotypic variation in nature. In this study, we examine two species of spiders (*Nephila plumipes* and *Argiope keyserlingi*) to examine whether there is evidence that males alter their development in response to demographics in natural populations. We studied spiders in which developing males can use pheromones as a cue of the density of conspecific males and females. We used published information about the mating systems and life history of each species to make predictions about expected patterns of plasticity in development time and correlated changes in adult body size in response to demographic variation. Within each species, male size and mass were positively correlated with the density of males but negatively correlated with the density of females, and as predicted, this was true only when calculated at spatial scales relevant to selection in each species. In contrast, seasonal variation in photoperiod could not explain measured variance in male size. Our results support the idea that developmental plasticity in response to demographics has a significant effect on phenotypic distributions in natural populations. Our results suggest that a proportion of variation in male phenotypes could be explained as a plasticity-mediated evolutionary response to variation in population demographics rather than as a physiological response to resource abundance and/or photoperiod.

Key words: *Argiope keyserlingi; demographic variation; developmental plasticity;* Nephila plumipes; *phenotypic variation; spider.*

Introduction

Developmental plasticity is adaptive as it allows individuals to maximize their fitness by altering their ontogeny to develop a phenotype that best matches a particular environmental challenge (Scheiner 1993, Nylin and Gotthard 1998, Pigliucci 2001, West-Eberhard 2003). Such plasticity has evolved across a wide range of taxa in response to changes in selection pressures that result from fluctuations in a variety of biotic and abiotic variables (Adler and Harvell 1990, Harvell 1990, Nylin and Gotthard 1998, Agrawal 2001, Pigliucci 2001, West-Eberhard 2003, Bateson et al. 2004). Developmental plasticity can evolve as long as there are reliable cues of how selection will fluctuate, and therefore the competitive challenges individuals will

encounter upon maturity (Lively 1986, Harvell 1990, Van Tienderen 1991, Scheiner 1993, Getty 1996). The necessity for reliable cues has led to a focus on systems where changes in selection are seasonally predictable, so the majority of studies examining developmental plasticity in nature report links to variables such as the time remaining in the breeding season (Moran 1992). For example, manipulated photoperiods that mimic the end of the breeding season have a direct effect on developmental trajectories in invertebrates, leading to individuals altering their critical sizes at maturation (Davidowitz et al. 2003) with the result that individuals mature at a smaller size (Abrams et al. 1996, e.g., Johansson and Rowe 1999, Shama and Robinson 2006). Another common focus of these studies is presence of predators which can be detected using a number of reliable cues (e.g., chemical cues from predator or prey; Relyea 2001, LaFiandra and Babbit 2004) and can have both a direct and indirect effect on development. Directly, it can result in the development of traits that decrease the risk of predation (e.g., spines in *Daphnia*; Green 1976), while indirectly, it can alter individual foraging behavior (Sih 1988, Johansson et al. 2001) and therefore, nutrient intake and use. Cues of time of

TABLE 1.   Comparison of the mating systems of the spiders *Nephila plumipes* and *Argiope keyserlingi*, studied in Sydney, Australia.

System component	*N. plumipes*	*A. keyserlingi*	References
Number of male mating opportunities	one	two	Elgar and Fahey (1996), Schneider and Elgar (2001), Schneider et al. (2001)
Mate guarding?	yes, if males survive	yes	Schneider and Elgar (2001), Herberstein et al. (2005*a*)
Can males determine female developmental stage using airborne pheromones?	yes	no	Gaskett et al. (2004), Kasumovic et al. (2007)
Sperm mixing?	yes	yes	Elgar et al. (2000), Schneider and Elgar (2001), Elgar et al. (2003)
High web-site tenacity	yes	no	Herberstein (2000), Griffiths et al. (2003)
Selection for larger male size?	yes	yes	Elgar and Fahey (1996), Herberstein et al. (2005*a*)

season and predator presence are relatively simple to measure, manipulate, and study.

However, not all important sources of selection on plasticity vary in a seasonal manner, nor do they vary evenly across the entire population. For example, the strength and direction of selection varies according to density and sex ratio (Kokko and Monaghan 2001, Kokko and Rankin 2006); factors that are known to vary within a single breeding season (e.g., Blanckenhorn et al. 1999, Kasumovic et al. 2008). Population demographics can also vary on a more local scale, and this scale may be more critical than population-wide dynamics if individual fitness depends on local conditions (e.g., if individuals are patchily distributed; Kasumovic et al. 2008). Furthermore, if individuals survive for only a portion of the breeding season, individual fitness may be dependent on within-season variation in demography. Given that strong variance in local demographics can lead to spatial variation in selection for size, mass, and condition (Blanckenhorn et al. 1999, Kasumovic et al. 2008), it would benefit individuals to match their adult phenotype to the specific competitive challenges they are likely to encounter at maturity. In other words, individuals should demonstrate developmental plasticity in response to demographic variation at the scale most relevant to their success if such variation is reliably predictable.

There are several laboratory studies that demonstrate that juvenile males are developmentally plastic in response to various characteristics of the adult population such as density and sex ratio (Gage 1995, Stockley and Seal 2001, Tan et al. 2004, Kasumovic and Andrade 2006). However, examinations of adaptive developmental plasticity in response to variation in density and sex ratio in natural populations are necessary to determine how relevant demography is in maintaining phenotypic variation. Here, we test the hypothesis that developmental plasticity in response to demographic variation can explain a significant amount of phenotypic variation in nature. Two predictions of this hypothesis are that individual traits associated with increased fitness should

vary with demography, and correlations between phenotypes and population demographics should only occur at a scale that is relevant to the life history of the species under study. To test these predictions, we examined the size and mass of adult males and compared them to population density at two different scales (see *Materials and methods*).

We used field populations of two different spider species, the golden orb-web spider (*Nephila plumipes*) and the St. Andrew's cross spider (*Argiope keyserlingi*). We chose these species for two main reasons. First, we predicted that developmental plasticity tuned to local conditions was likely as in both species, short-lived males travel short distances within a population to relatively sedentary females (Kasumovic et al. 2008; M. E. Herserstein, *personal observation*). Local, but not population-level variation in the density of potential mates and competitors (Kasumovic et al. 2008) is thus likely to affect the fitness of these adult males (e.g., Kasumovic and Andrade 2006). Developing males may have reliable cues of future competitive challenges as males of both species use pheromones to locate and potentially select females of a particular age and mating status (Gaskett et al. 2004, Kasumovic et al. 2007). In other web-building spiders, males are also able to detect the presence of competing males using pheromones (e.g., Kasumovic and Andrade 2006). Thus, juvenile males could use pheromonal signals as a reliable cue of population density of each sex.

The second reason for choosing these two species is that differences in their mating systems (summarized in Table 1) predict different relationships between male phenotypes and population demographics under our plasticity hypothesis. In *N. plumipes*, males are monogynous due to a high frequency of fatal sexual cannibalism (~60%), a high injury rate while mating (Elgar and Fahey 1996, Schneider and Elgar 2001, Schneider et al. 2001), and a 76% mortality rate during mate searching (Kasumovic et al. 2007). As a result, we predict that males should develop a phenotype that maximizes fitness for the single mating opportunity they are likely to

obtain after they mature. Male mating success is dependent upon outcompeting up to five rival males for access to the female (Vollrath 1980, Elgar and Fahey 1996) and males attempt to mate guard if they survive their mating (Schneider and Elgar 2001). We therefore predict that male size will be positively correlated with the density of adult males (competitors). The value of a mating depends on finding and mating with virgin females as mating with a previously mated female results in a reduction of paternity due to sperm mixing (Schneider and Elgar 2001, Elgar et al. 2003). Regardless, attempting to mate with a virgin female may maximize fitness as previously mated females vary in how long they wait before accepting a mating from a second male (1–15 days; Schneider and Elgar 2001) and may lay an egg sac before remating. Thus virgin females are most valuable to males, and finding a receptive female may be difficult. Males may assess the availability of sexually mature females using airborne pheromones (Kasumovic et al. 2007). Thus, when receptive females (particularly virgins) are at high density, we predict males should reduce the critical size at maturation (e.g., Davidowitz et al. 2003) resulting in males maturing more quickly to reach and mate with females before other males arrive (selection for protandry). This would produce a negative correlation between male size and female density. Thus, in the monogynous *N. plumipes*, we predict male size and mass will be positively correlated with the density of males but negatively correlated with the density of females. Furthermore, we predict that these correlations should occur between male traits and demographic variables within web aggregations (groups of webs that share support strands, Elgar 1989), but not at a broader scale. Effects of scale are expected because the majority of males of this species mature within web aggregations that include webs of juveniles and females, and males rarely travel between aggregations (Kasumovic et al. 2008).

In contrast, *A. keyserlingi* males attempt to mate once with two different females (Herberstein et al. 2005*b*). On the first mating, males attempt to escape cannibalism by females with a 40–50% success rate (Herberstein et al. 2005*b*). If they survive, males remain on the web and guard the female from other potential suitors for up to a day (Herberstein et al. 2005*a*). After mate guarding, males resume searching for a second mate, and with this second female they passively succumb to cannibalism (Herberstein et al. 2005*b*). Even though there are no mating order effects on paternity in *A. keyserlingi* (Elgar et al. 2000), successful guarding either prevents rival males from mating or decreases the duration of copulation by rivals (Herberstein et al. 2005*a*), thereby decreasing sperm transfer of rival males (Elgar et al. 2000). Larger males are likely to be more successful at guarding (Andersson 1994) so male size should also be positively correlated with male density in this species. Since more than half of *Argiope* males attempt two matings, detecting the relative density of males is likely

to provide information relevant to the expected intensity of competition for both of the male's mating attempts.

However, although *A. keyserlingi* males also wander and use pheromones to locate females, juvenile males of this species are unlikely to have access to reliable cues about the density of receptive females that will be encountered as adults. Female *A. keyserlingi* frequently change their web locations throughout the breeding season. Almost 50% of females relocated their web over a three-week period (Herberstein 2000), compared to only 18% of *Nephila* females (Griffiths et al. 2003). In addition, whereas males can detect virgin females via pheromones, once those females mate, they are no longer available to mate-searching males (Gaskett et al. 2004). Therefore, the local density of receptive *A. keyserlingi* is likely to change between the male's juvenile stage and sexual maturity, and between the male's two mating opportunities. Moreover, male *A. keyserlingi* build solitary webs whereas male *N. plumipes* develop within clusters that frequently contain multiple females. Thus, movement or mating of a single female will have a more significant affect on the local density of receptive females for male *A. keyserlingi* than for male *N plumipes*. Cues of female density detected by developing males will not necessarily reflect the conditions under which males will attempt their first and second matings for *A. keyserlingi*.

Thus, in the polygynous *A. keyserlingi*, we predict a similar positive correlation between male density and male size, but no relationship (or a significantly weaker relationship) with the density of females. Whereas web clustering in *N. plumipes* leads us to predict effects of local (within-aggregation) demography only, this is not the case for *A. keyserlingi*. In *A. keyserlingi* web density is relatively low and males must search further for females, so we predict that the positive correlation between male density and male phenotype will only occur at a broad scale, rather than in local areas surrounding males' webs.

A number of other variables can also change over the course of a breeding season and affect male body size at maturity. We considered one of the most likely alternative cause of variation in male size, the time of season (Johansson et al. 2001, De Block and Stoks 2004, Shama and Robinson 2006). For example, males may accelerate their development prior to the end of the breeding season, with the result that they mature at smaller body size (Johansson et al. 2001, Shama and Robinson 2006). This predicts a change in mean male traits in each species as the season progresses regardless of overall changes in spider population density.

MATERIALS AND METHODS

Male collection

We surveyed field populations of *A. keyserlingi* in 2006 and *N. plumipes* in 2005, in Bicentennial Park, Pymble (Sydney, New South Wales, Australia). In Bicentennial Park, *A. keyserlingi* spiders almost exclu-

sively build webs in *Lomandra* spp. and *Pandanus* spp. bushes (Herberstein and Fleisch 2003, Rao et al. 2007). Males and females build their own webs apart from other conspecifics and rebuild their webs daily (Herberstein 2000). We surveyed the *A. keyserlingi* population eight times throughout the breeding season between the months of November and January between 10:00 and 14:00 hours. As male *A. keyserlingi* mature on their own webs, males must leave their webs to search for females who frequently change the location of their webs (M. E. Herberstein, *personal observation*). Thus males found on female's webs are not generally in the area where they matured, and likely represent only a subset of the males that matured in the population (due to mortality during mate search). To avoid these sources of error in examining links between male development and local demography, we only collected and measured adult males found on their own webs (i.e., prior to mate search). To determine whether there is an effect of scale on links between phenotype and demography in *A. keyserlingi*, we counted and aged all the males (including males on females' webs) and females within a 2 m (local scale) and 5 m (broad scale) radius for each male collected. We used these counts to calculate population density at each spatial scale.

Nephila plumipes was found mainly in habitat containing shrubs and eucalypts, which was distinct from the habitat of *A. keyserlingi*. We tested our predictions for *N. plumipes* in two separate populations separated by a mowed, grassy field (170 m wide) that served as a barrier to dispersal (Kasumovic et al. 2008). The sites differed in spider population density and measured approximately 5500 m^2 (low-density site) and 1700 m^2 (high-density site; see Kasumovic et al. 2008 for details). Males likely find mates within the aggregation in which they are developing, thus aggregations are the relevant spatial scale for predicting selection on males in this species (Kasumovic et al. 2008). Although the overall density differed between the two sites, the size of the aggregation was similar between sites (Kasumovic et al. 2008) allowing us to combine data between the two sites. Each site was surveyed every two weeks between 10:00 and 14:00 hours throughout the breeding season for a total of three surveys (early, mid, late season). For each survey, we located all *N. plumipes* webs at each site. Webs can either occur solitarily or as part of aggregations that can house multiple males and females of different ages (Elgar 1989, Herberstein and Elgar 1994, Kasumovic et al. 2007). We found female's webs in the same location each day as females are stationary, continually adding to their web (Higgins 1990, Herberstein and Elgar 1994). Web elevation varied from low to the ground in shrubs and saplings, to the upper canopy of trees (Herberstein and Elgar 1994). We surveyed all webs that were below 2 m in elevation; only two aggregations above 2 m were observed. We collected all adult males found during these surveys and aged, sexed and counted any other individuals found on the web or

within the aggregation (local scale). We added to this the number of adult and penultimate instar females found within 5 m of the aggregation from which males were collected to calculate broad scale demographics (adult males were rarely found outside aggregations).

Adult males of both species were identified by the development of mating appendages on the anterior of the cephalothorax (pedipalps) which become sclerotized when males reach sexual maturity (Foelix 1982). We determined female age using the coloration and shape of the epigyne. Adult females of both species have a protruding epigyne that has two clear openings, penultimate females have the same protrusion, but the openings are covered, and juvenile females lack a protrusion (Levi 1983, Higgins 1992, Kasumovic et al. 2007). All collected males were brought into the laboratory where they were immediately weighed and measured using the average length of the patella-tibia of the two front legs as a measure of male size. None of the males collected were released back into the field populations.

Statistical analyses

We examined whether male size and mass varied through the breeding season. We included both size and mass in our analyses because previous work on plasticity in spiders (Kasumovic and Andrade 2006) suggested that males with accelerated development may differentially allocate resources to size or mass depending on other variables (not controlled in this study) such as diet. For *N. plumipes* we used a two-way ANOVA using mass and size as the dependent variables, and sampling time and site as the independent variables. Since there were more sampling periods throughout the breeding season for the *A. keyserlingi* population, we were able to perform a multiple regression using male size and mass as the dependent variables, and time as the independent variable.

To examine which male and female density variables were related to male size and mass, we used a stepwise regression model and chose the model that minimized the Akaike information criterion (AIC). To reach this model, we performed separate forward and backward stepwise regression models and individually added/removed parameters that minimized the AIC with each step. In each case, the models determined from forward and backward regression were identical. To better understand the relationship between the significant phenotypic traits and demography, we then performed weighted linear regressions for all the variables that remained in the model and examined whether there were any interactions if more than one parameter was included. All variables were normally distributed.

RESULTS

We collected a total of 58 *A. keyserlingi* males, and a total of 327 *N. plumipes* males: 192 males from the low-density site (early = 32, mid = 80, late = 80), and 135 males from the high-density site (early = 44, mid = 53,
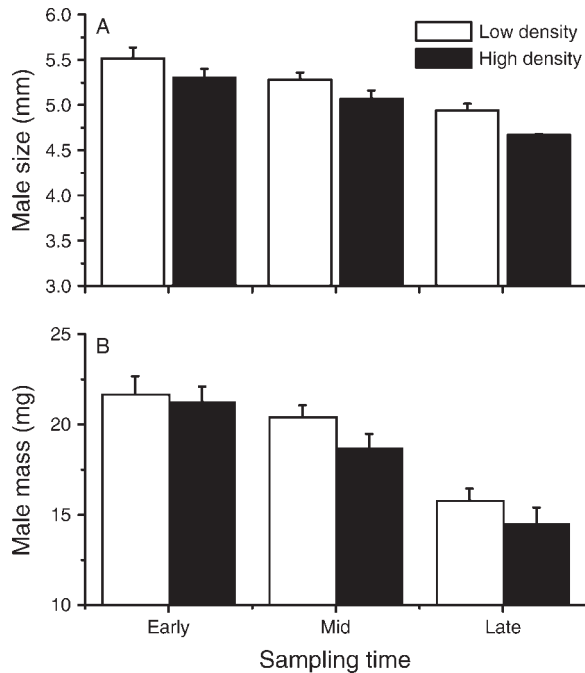
FIG. 1. Average male (A) size and (B) mass in high-density (black bars) and low-density (white bars) populations of the spider *Nephila plumipes* throughout the breeding season in Sydney, Australia. Values are means + SE.

late = 38). There were a total of 245 aggregations in both sites for *N. plumipes*.

Male size in *N. plumipes* decreased through the season ($F_{2, 320} = 18.37$, $P < 0.0001$), however, males were significantly larger in the low-density site ($F_{1, 320} = 8.82$, $P = 0.003$; Fig. 1A). There was no time × site interaction for male size ($F_{2, 320} = 0.05$, $P = 0.95$). Male mass also decreased through the season ($F_{2, 320} = 32.27$, $P < 0.0001$), and there was a trend toward heavier males in the low-density site (two-way ANOVA, $F_{1, 320} = 3.22$, $P = 0.074$; Fig. 1B). There was no time × site interaction for male mass (two-way ANOVA, $F_{2, 320} = 0.33$, $P = 0.72$). In *A. keyserlingii*, there was no difference in male size as the season progressed ($F_{1,52} = 1.51$, $P = 0.22$; Fig. 2A), although there was a trend toward males losing body mass as the season progressed ($F_{1,52} = 2.88$, $P = 0.096$; Fig. 2B).

In the stepwise regression for *N. plumipes*, the parameters used were the density of juvenile females, penultimate instar males and females, and adult males and females within the aggregation (local scale), and the total number of adult and penultimate instar females at the broad scale. For the examination of male size, only the number of adult females and adult males at the local scale predicted adult male size in the model that minimized the AIC ($R^2 = 0.077$, AIC = 1121; see Appendix: Table A1). In contrast, juvenile, penultimate instar, and adult female density significantly predicted male mass in the model that minimized the AIC ($R^2 = 0.04$, AIC = −1675; Appendix: Table A1). In the linear

regression models, adult male size was positively correlated with local density of adult males ($F_{1, 314} = 6.82$, $P = 0.009$; Fig. 3A) and negatively correlated with the local density of adult females ($F_{1, 314} = 4.14$, $P = 0.043$; Fig. 3B). The interaction between the density of adult males and adult females was not significant ($F_{1, 314} = 0.009$, $P = 0.92$). Adult male mass was positively correlated with the number of juvenile ($F_{1, 312} = 4.53$, $P = 0.034$; Fig. 4A) and penultimate instar females ($F_{1, 313} = 6.44$, $P = 0.011$; Fig. 4B) and negatively correlated with the number of adult females at the local scale ($F_{1, 312} = 9.39$, $P = 0.002$; Fig. 4C). None of the interactions terms were significant (all $P > 0.27$).

In stepwise regression for *A. keyserlingi*, the parameters used were the number of juvenile females, the number of penultimate instar males and females, and the number of adult males and females at both the local and broad scales (Appendix: Table A2). Only the number of adult males at the broad scale significantly predicted
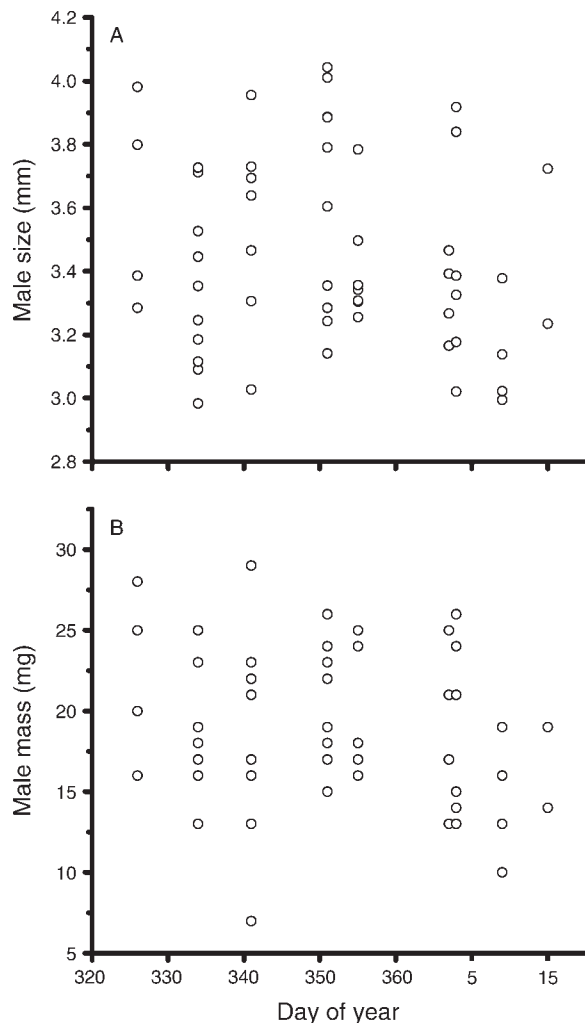

FIG. 2. Relationship between male (A) size and (B) mass and collection date in the spider *Argiope keyserlingi* in Sydney, Australia.
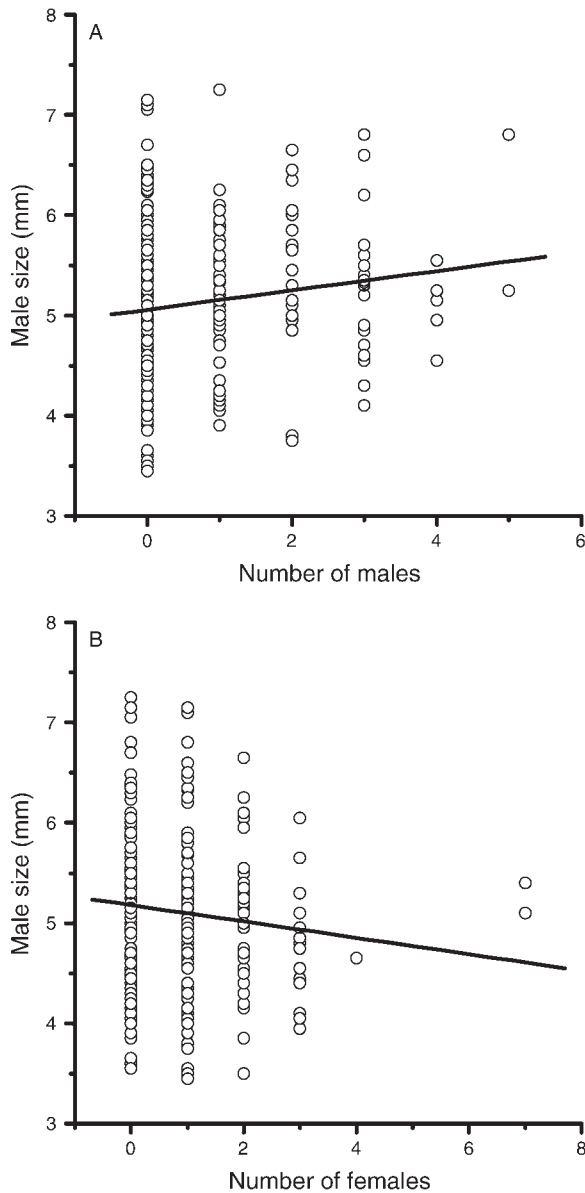
FIG. 3. Relationship between male size and the number of (A) males and (B) females within an aggregation in *Nephila plumipes*.

male size and mass in the models that minimized the AIC for each model (size, $R^2 = 0.10$, AIC $= -189$; mass, $R^2 = 0.11$, AIC $= -623$; Appendix: Table A2). In the linear regressions, both male size ($F_{1,52} = 10.89$, $P = 0.002$; Fig. 5A) and mass ($F_{1,56} = 7.11$, $P = 0.01$; Fig. 5B) were positively correlated with the number of males at the broad scale.

DISCUSSION

We have shown that variation in male size and mass is correlated with the density of conspecifics in ways that provide support for the hypothesis that male traits are shaped by adaptive plasticity in the field. Male size
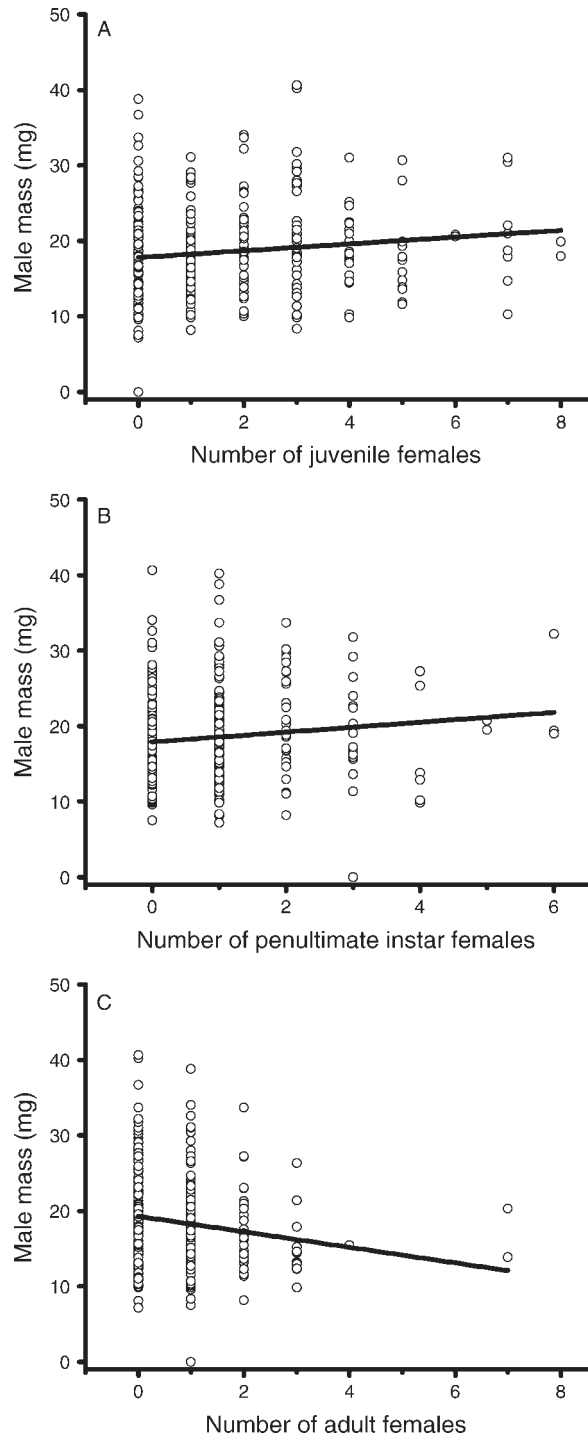

FIG. 4. Relationship between male mass and the number of (A) juvenile females, (B) penultimate instar females, and (C) adult females within an aggregation in *N. plumipes*.

and/or mass in two species of spiders were related to the density of conspecifics, but only when density was assessed at spatial scales known to be important to sexual selection on males from each species. This is expected if sexual selection drives the evolution of
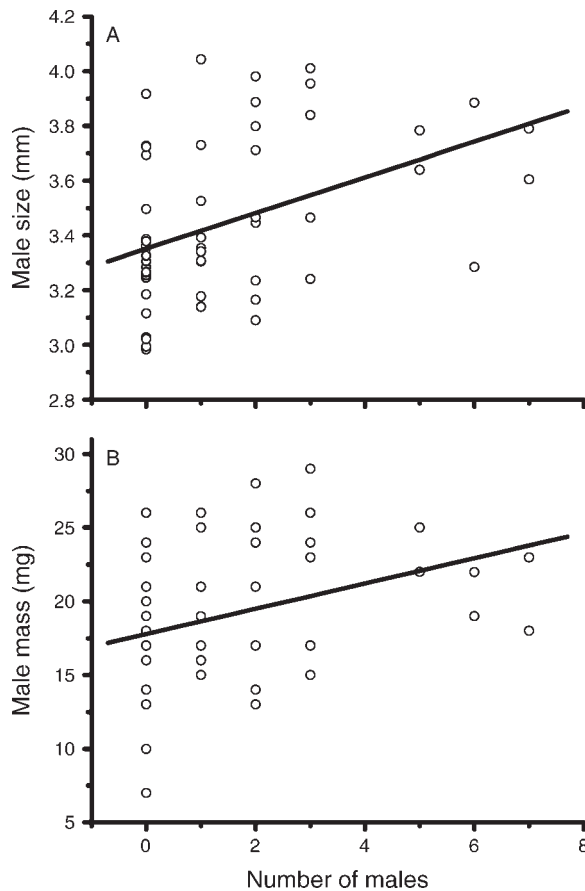
FIG. 5.   Relationship between male (A) size and (B) mass with the number of males within 5 m (broad scale) of the collected male in *A. keyserlingi.*

plasticity in development time and adult size. Critically, the polarity of these correlations differed for density of males and females in a monogynous species (*N. plumipes*) in which increasing numbers of competing males would lead to selection for larger body size, but increasing numbers of potential mates (females) would decrease selection for larger body size. The polygynous mating system of the second species (*A. keyserlingi*) predicted no relationship between male size and female density, but a positive relationship with male density. Our data show a significant positive correlation with the density of adult males. The data also suggest there is either no relationship with female density, or that such an effect is very much weaker than the relationship with male density, which is also as predicted by our hypothesis. Our results are best explained by plasticity linked to sexual selection for variable male traits, where shifting demography yields variation in sexual selection. There was little evidence of strong effects of seasonal variation in male size and mass. Male size and mass showed seasonal decreases in only one of the two species (*N. plumipes*, Fig. 1), but even in this species, male size also depended on overall population density at the two

sites, in a way that would be predicted by our plasticity hypothesis (Fig. 1A).

Males of both species are limited in the maximum number of matings they can achieve and are relatively short lived, which is why we predicted both should show developmental plasticity linked to local competitive conditions (e.g., Kasumovic and Andrade 2005). However *N. plumipes* males mate only once after maturing, and risk decreased paternity if they copulate with a previously mated female (Elgar et al. 2003), so they are likely to experience stronger selection for developmental plasticity in response to the local density of males and females. Male *N. plumipes* must successfully locate and mate with a virgin female, and may have to fight with potential rivals when they guard their mate. As significant shifts in population density and sex ratio can occur within weeks in this species (Kasumovic et al. 2008), the competitive environment encountered by adult males will also shift. Accurate phenotype–environment matching requires that juvenile males detect reliable cues of both male and female density. The correlations between density and phenotypes of males suggest juvenile *N. plumipes* males are able to detect density cues, as they can in another web-building spider (Kasumovic and Andrade 2006). Furthermore, as predicted, these correlations between conspecific density and male phenotypes in *N. plumipes* were only seen when examined within aggregations, the scale within which males mate-search and compete (Kasumovic et al. 2008), rather than at a broader scale (within 5 m).

In contrast, male *A. keyserlingi* attempt to mate with two different females, and female density may change between attempts. Thus the female density detected by juvenile males would be an unreliable cue of the competitive challenges *A. keyserlingi* males are likely to encounter throughout their lifetime. However, as males that successfully guard females against rivals increase their fitness (Herberstein et al. 2005a), there is likely strong selection for recognizing the number of potential rivals males are likely to encounter while searching for females. Selection for larger size appears strong as it compensates for female sperm selection of relatively smaller males (Elgar et al. 2000). We found evidence for links between male density and male size as expected. Furthermore, these correlations were only seen at the broad scale (within 5 m) rather than the local scale (within 2 m), which matches the mating system of this species as males search widely to locate sparsely distributed females.

An interesting result is the dependence of correlations between male mass and female density on female age in *N. plumipes*. Male mass was negatively correlated with adult female density in the population (Fig. 4C) as predicted. However, male mass was positively correlated with the density of both juvenile and penultimate instar (one instar prior to adulthood) females (Fig. 4A, B). In situations where immature females outnumber adult females within an aggregation, it may benefit males to

delay maturity until more females mature, or at least to ensure they are sufficiently well provisioned to survive until females mature. This coincides with previous studies that demonstrate males with higher mass or body condition prefer to settle with immature females (Elgar et al. 2003, Kasumovic et al. 2007). These results suggest that the strength and direction of selection imposed on male development by females may fluctuate within a breeding season (e.g., Kasumovic et al. 2008), and that *N. plumipes* males may adopt discrete developmental strategies depending on the density of adult and juvenile females within an aggregation.

A number of studies of invertebrates show that variance in male phenotypes can be linked to time of season (photoperiod; Johansson and Rowe 1999, Shama and Robinson 2006). Although seasonal constraints are likely to contribute to phenotypic variation, it appears that relatively little of the variation in male traits can be explained by this factor in these species. In *A. keyserlingi*, male phenotypes were not correlated to the time of collection (Fig. 2), so it is unlikely that seasonal changes in photoperiod contributed to phenotypic variation. On the other hand, in *N. plumipes*, male size and mass decreased as the season progressed, suggesting a seasonal effect. However, the high- and low-density sites significantly differed in mean phenotypes (Fig. 1), implying that local demographics still play a role in determining male phenotypes in *N. plumipes*. Rather than suggesting an effect of photoperiod, the correlation between male phenotypes and photoperiod in *N. plumipes* could instead be a spurious correlation that results from a link between photoperiod and conspecific density, since the density of preferred females increases as the season progresses (Kasumovic et al. 2008). Thus, the relative contributions of developmental plasticity in response to photoperiod and developmental plasticity in response to conspecific density to systematic phenotypic variation are unclear.

We provide evidence that developmental plasticity can help explain the maintenance of phenotypic variation in populations, but our models only explain 4–11% of the variation, suggesting that other variables are also important. Although seasonal effects could not explain phenotypic variation in our study, we did not examine spatial or temporal variation in resource abundance. Previous studies have shown that variation in resource abundance can underlie phenotypic variation (Ernande et al. 2004, Dmitriew and Rowe 2005) and this is also likely the case for the sit-and-wait predators that we studied here (Wise 1993). Along the same lines, variation in male ability to acquire resources in a variable environment (i.e., genetic variation in quality; Hunt et al. 2004) could also explain some of the variation seen in male phenotypes. However, while other studies have demonstrated the importance of resource availability and acquisition, few have suggested a significant effect of developmental plasticity in the field, as we have here. This study therefore highlights the importance of examining multiple factors when attempting to explain the maintenance of phenotypic variation in nature.

Populations are often not homogeneous in sex ratio and density (e.g., Kasumovic et al. 2008), so temporal and spatial variation in these demographics can lead to variation in local selection pressures within a breeding season (Blanckenhorn et al. 1999, Kasumovic et al. 2008, Punzalan et al. 2008). Developmental plasticity in response to demographics should evolve when demographics are predictable. Several laboratory studies demonstrate that males can alter their development in response to cues of density (Gage 1995, Stockley and Seal 2001, Tan et al. 2004, Kasumovic and Andrade 2006), sex ratio (Kasumovic and Andrade 2006), and the phenotypes of potential rivals (Walling et al. 2007). Although the mechanisms by which males determine future competitive challenges is unknown in most of these studies, the majority of examples involving density are likely in response to tactile cues experienced by males interacting with conspecifics during the larval stage (Gage 1995, Stockley and Seal 2001, Tan et al. 2004). In other examples, plasticity is triggered by detection of airborne pheromones during the juvenile stage (Kasumovic and Andrade 2006), and visual cues available while males interact with conspecifics (Walling et al. 2007). These studies demonstrate that reliable cues may be available in multiple modalities during development. Therefore, if a given species has life history characteristics that predict developmental plasticity (Roff 1992, Stearns 1992) a lack of understanding of the mechanisms by which individuals could detect demographic variables should not rule out studies of the potential importance of links between population density, sex ratio, and adult phenotypes.

Our work suggests variation in local demographics may be an important factor in maintaining phenotypic variation in species with spatial or temporal stratification of demographics that can in turn alter the strength and direction of selection. The scale at which demographic variation should be examined will depend on the biology of the species under study (e.g., Table 1). However, there are several general scenarios in which developmental plasticity in response to population demographics will likely play an important role in explaining phenotypic variation. (1) In species where males have limited number of mating opportunities (e.g., semelparous or cannibalistic species), males should alter their development to best match their phenotype with the future competitive environment they are likely to encounter. This would allow males to maximize their fitness in the limited matings they can achieve. (2) In species where individuals have a relatively short lifespan compared to the breeding season, individuals will mature and die throughout the breeding season, and demographics may vary widely for different individuals. Rapid demographic fluctuations will make only a portion of the breeding season relevant to each

individual. (3) In situations where there are multiple reproductive periods (as seen in many invertebrates) rather than one synchronized breeding event, population demographics can change rapidly as the limiting sex matures and becomes mated. Selection and therefore, phenotype–fitness associations should thus vary temporally. (4) In the same manner, if individuals only sample or visit a small proportion of the larger population when choosing a mate, local spatial variation may be relevant as individuals may not be uniformly distributed throughout habitat. Individuals should thus develop according to the local demographics likely to be relevant during their lifetime.

Interactions between numerous biotic and abiotic variables are likely to make understanding phenotypic variation complex (e.g., Johansson et al. 2001, Nakamura 2002). Furthermore, the relative importance of the various biotic and abiotic variables will depend on the life-history of the species under study. Evidence for developmental plasticity in nature was found in this study because of our focus on the relevant scale of study for each species. We therefore highlight the importance of understanding the life history and the reproductive biology of the species under study as this is critical for uncovering the variables most likely to contribute to the evolution of developmental plasticity, and the maintenance of phenotypic variation. Evidence for plasticity in response to demographics may be more widespread in nature than is currently appreciated and so it is increasingly important that future studies consider demographic variation along with other factors that trigger plastic development, when trying to explain natural phenotypic variation.

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APPENDIX

Tables reporting the results of the stepwise regression analyses (*Ecological Archives* E090-159-A1).