A change in competitive context reverses sexual selection on male size

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Abstract

In studies of sexual selection, larger size is often argued to increase male fitness, and relatively smaller males are explained by genetic and/or environmental variation. We demonstrate that a size–development life-history trade-off could underlie the maintenance of a broad, unimodal distribution of size in male redback spiders (*Latrodectus hasselti*). Larger males are superior in direct competition, but redback males mature rapidly at small size in the presence of females. In field enclosures, we simulated two competitive contexts favouring development of divergent male sizes. Relatively smaller males lost when competing directly, but had 10 times higher fitness than relatively larger males when given the temporal advantage of rapid development. Linear selection gradients confirmed the reversal of selection on size, showing that it is critical to consider life-history decisions underlying the development of traits related to fitness.

Introduction

In studies of sexual selection across taxa with unimodal phenotypic distributions, the traits most often considered to maximize fitness under competition are large size and weaponry (Andersson, 1994; Blanckenhorn, 2005). Understanding processes maintaining small males in populations where there is a combat advantage for large males (Andersson, 1994; Blanckenhorn, 2005) is essential to help refine concepts of male quality and predict the evolution of male phenotypes. One potential explanation for the maintenance of relatively small males is that adult phenotypes are a result of genetic variation in resource acquisition in a variable environment (Rowe & Houle, 1996; Hunt *et al.*, 2004). Such a hypothesis predicts that all males attempt to develop an optimal, large phenotype, but relatively smaller males are of inherently lower quality and have decreased fitness relative to larger males. Although there are a number of studies that

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demonstrate dominance of larger males (Andersson, 1994; Blanckenhorn, 2005), the majority of these studies examine male success in a single competitive context without taking into consideration life-history trade-offs inherent in the development of size. The few studies that have considered both the mating system and specific life-history traits of the species under study demonstrate a benefit to relatively smaller males. For example, small male midges (*Chironomus plumosus*) have an acrobatic advantage over larger males within three-dimensional leks (Crompton *et al.*, 2003). Small male yellow dung flies (*Scatophaga stercoraria*) also have an advantage over larger males as they replenish their reserves more quickly while foraging, allowing them to resume searching for females more quickly than larger males (Blanckenhorn & Viele, 1999). Finally, smaller male seed beetles (*Stator limbatus*) have a searching advantage in cooler temperatures as they can heat up more rapidly, allowing them to begin searching more quickly (Moya-Laraño *et al.*, 2007). Together, these studies demonstrate that relatively small males are not necessarily of poorer quality; rather, they may have a selective advantage under specific competitive contexts. These studies also highlight the necessity of understanding the biology of the organism under study and the nature of competitive challenges

males face to truly understand phenotype–fitness associations and quantify male quality.

Another explanation for the maintenance of phenotypic distributions is that Gaussian distributions exist as a result of developmental plasticity in response to a competitively variable environment. Phenotypic selection is known to vary temporally and spatially within a season (Jann *et al.*, 2000; Caruso *et al.*, 2003; Kasumovic *et al.*, 2008; Punzalan *et al.*, 2008) and there is evidence from laboratory studies (Gage, 1995; Stockley & Seal, 2001; Tan *et al.*, 2004; Kasumovic & Andrade, 2006; Walling *et al.*, 2007) that phenotypes may vary in response to variation in local selection pressures triggered by variable conspecific density. As competitive environments can fluctuate within a season, there may be no single optimal phenotype, and to maximize fitness, individuals must match their phenotype to the specific competitive challenges they are likely to encounter at maturity. This hypothesis predicts that relatively smaller males would have an advantage over large males if tested in the environment that led to the development of the phenotype.

Males that mature with a particular phenotype at an inappropriate time may suffer a decrease in fitness as the phenotype may not match the environmental challenges at the time of maturity. It may therefore be critical that effects of development time are considered, as the ontogenetic pathway required to attain a particular phenotype under a given set of conditions may also affect male performance relative to rivals. Moreover, under variable selection for male size, possible trade-offs between adult size and timing of maturity (Roff, 1992; Stearns, 1992) may yield a continuous distribution of male size at the level of the population. Our primary goal in this paper was to examine whether this trade-off between size and development time can help explain the maintenance of phenotypic variation in a species with a unimodal distribution of male size, but demonstrated advantage to relatively large males in direct competition (Stoltz *et al.*, 2008). Here, we use the Australian redback spider (*Latrodectus hasselti*), to examine whether the size–development time trade-off maximizes male fitness in different competitive contexts.

Male redback spiders have a broad unimodal distribution of body size and weight in nature (Andrade, 2003), and some of this variation could arise from adaptive developmental plasticity (Kasumovic & Andrade, 2006). Redback males alter their development time in response to pheromones that provide cues of the local density of virgin females and rival males. These cues indicate the type of competitive challenges males are likely to face upon maturity (Kasumovic & Andrade, 2006), and thus whether a more rapid development or larger body size are likely to be favoured by selection. For example, males can encounter up to six rivals on a female's web (Andrade, 1996) and larger spiders are competitively superior when males compete directly

(Stoltz *et al.*, 2008). By contrast, if virgin females are nearby and few rival males are present, rapid development may be favoured to ensure mating priority given the high first-male sperm precedence in this species (Snow & Andrade, 2004, 2005; Snow *et al.*, 2006). Consistent with this scenario, redback males mature more rapidly (on average 2 days earlier) at a smaller body size and lower body condition at high female densities compared with at low female densities (Kasumovic & Andrade, 2006).

Redback females overwinter at several developmental stages, develop much more slowly than males and produce new egg sacs throughout the summer (Forster & Kingsford, 1983). Spiderlings develop from these egg sacs throughout the season and so males mature at different times (Andrade & Banta, 2002; Andrade, 2003). Development time varies as a result of resource availability, female availability and male density (Kasumovic & Andrade, 2006). The local density of available mates changes throughout the season as individuals mature and mate (Kasumovic *et al.*, 2008; M. C. B. Andrade, unpublished data). Virgin females are preferred by mate-searching males (Andrade & Kasumovic, 2005) and newly mated females no longer produce attractive pheromones (Stoltz *et al.*, 2007). However, males do sometimes settle with previously mated females, which recommence pheromone production only after producing a number of egg sacs (Perampaladas *et al.*, 2008). Males are able to detect rapid changes in the local availability of receptive females and rival males as airborne pheromones, which are apparently used as indicators of the competitive environment, trigger developmental shifts (Kasumovic & Andrade, 2006). As a result, each maturing cohort of males in a given area exists within a different array of potential mating opportunities and risks of direct competition, probably resulting in within-season temporal and spatial fluctuations in the strength of selection on size (Kasumovic *et al.*, 2008).

There are currently no data on the relative success of smaller redback males as a function of their faster development and thus earlier mate searching. Our secondary goal was thus to examine whether the developmental plasticity male Australian redback spiders (*L. hasselti*) demonstrate in response to demographic variation (Kasumovic & Andrade, 2006) is adaptive by testing whether phenotype–fitness associations change depending on the context of the competition males face. We predicted that earlier maturity would allow smaller (rapidly developing) males to reach virgin females and mate first, increasing their fitness relative to larger (slower developing) males (Kasumovic & Andrade, 2006). When the sex ratio is male biased and direct competition is likely to be common, male redbacks develop more slowly but are larger and better provisioned (i.e. have increased body condition) as adults (Kasumovic & Andrade, 2006). As in other systems, we

predicted that larger size would increase male success in direct inter-male competition (Andersson, 1994; Stoltz *et al.*, 2008). Thus, if the developmental plasticity shown by male redbacks (Kasumovic & Andrade, 2006) is adaptive, we predict a switch in the competitive context (direct competition over females vs. a protandry advantage) should lead to a switch in the phenotype that maximizes fitness and, therefore, a reversal in the direction of selection on body size.

To test whether the different phenotypes result in higher fitness in the environment where they would be induced, we performed a reciprocal experiment (*sensu* Gotthard & Nylin, 1995) where we examined mate searching and copulatory success of large and small males released in field enclosures. First, we examined the outcome of direct competition over mates when we released small and large males simultaneously in enclosures; second, we examined the outcome of protandric competition in a staggered release treatment where smaller males were allowed to initiate mate search sooner. If phenotypes are context specific, we expect a shift in the direction of selection in the two treatments. To examine this prediction, we calculated linear selection gradients on size and body condition in the different treatments based on known relationships between paternity and the pattern and frequency of mating (Snow & Andrade, 2005).

Materials and methods

Collecting and housing spiders

Redback spiders were collected from the campus of Macquarie University in Sydney, NSW, Australia. Males were collected as adults or in the penultimate instar (Forster & Kingsford, 1983) and reared to maturity in the laboratory in $2 \times 2 \times 3 \ cm^3$ clear plastic cages. We ensured that all males collected as adults had intact copulatory organs and thus were virgins (copulatory organ morphology changes with mating, see Snow *et al.*, 2006; Snow & Andrade, 2005). We did not use males until 5 days after capture or final eclosion to ensure they had induced sperm into their palps (Foelix, 1982). We collected females as juveniles or adults. To distinguish between mated and virgin adult females, we housed females in the laboratory for a month prior to the experiment, fed them *ad libitum* and checked them daily for egg sac production (females survive up to 2 years in the laboratory, Andrade & Banta, 2002). Mated females usually produce an egg sac within 2 weeks under such a feeding regime (M. M. Kasumovic, personal observation). All spiders were held in individual plastic cages and fed *Drosophila melanogaster* (male spiders) or appropriate sized *Acheta domesticus* (female spiders). We weighed all spiders before experiments began, and measured size as the average length of the patella–tibia of the two front legs. We estimated condition as the residuals of the log-
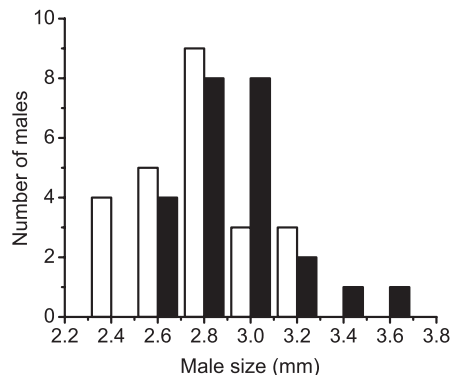

Fig. 1 The distribution of male sizes in each size class. White bars represent the small male class and black bars represent the large male class.

cubed root of weight on log size after estimating the allometric coefficient (=3) using another population of spiders (Schulte-Hostedde *et al.*, 2005 for greater details, see Jakob *et al.*, 1996; Kasumovic & Andrade, 2006).

For all experimental trials, females were housed in aluminium cylinders 15 cm in length and 10 cm in diameter (with open ends covered in plastic wrap) for a minimum of 1 week to allow the construction of large webs. Males were separated into two relative size classes to mimic early and late developing males. As redback males show a large distribution of continuous variation in weight and size (Andrade, 2003), we ensured that small males (mean 2.67 mm, SD 0.24) were a minimum of 1 SD smaller in size than large males (mean 3.03 mm, SD 0.25) in each trial. However, across all replicates, we ensured that the distribution of male size classes overlapped (Fig. 1). This ensured that we were examining the effect of being relatively larger or smaller than competitors, rather than the effect of sizes only at the extremes of the natural range of variation. Males from each size class were randomly assigned to one of two treatments (see below). There was no difference in the proportion of field-collected compared with laboratory-reared adult males placed in either size class (Fisher's exact two-tailed test, $P = 0.77$) or treatment group (Fisher's exact two-tailed test, $P = 0.77$).

We painted adult males with individual colour markings using nontoxic fluorescent paint (Luminous paint; BioQuip Products, Rancho Dominguez, CA, USA) on the tibia of each front leg, and on the abdomen to allow individual identification during the experiment. Males were marked the day before a trial by placing them between two pieces of fibreglass screening under a dissecting microscope to minimize movement.

Experimental procedure

All trials were completed in $3 \times 3 \times 2 \ m^3$ screened outdoor enclosures in the Fauna Park at Macquarie

University. This field enclosure size is reasonable given typical web distributions in the field (nearest neighbour distances between conspecifics is 2.40–3.40 m, Andrade, 2003) and average male mate-search distances in the field (∼3 m, Andrade, 2003; Fig. 3). Each trial consisted of a simultaneous release enclosure where all males competed simultaneously with one another (simultaneous release treatment) to simulate an environment where a relatively large male phenotype would be developed, and a treatment where we delayed the release of larger males by 1 day (staggered release treatment) to simulate an environment where a relatively small male phenotype would be developed (i.e. reciprocal experiment, Gotthard & Nylin, 1995). As smaller males develop on average 2 days earlier than larger males (Kasumovic & Andrade, 2006), releasing smaller males only 1 day earlier in the staggered release treatment provided a conservative examination of the effect of the temporal advantage relatively smaller males would gain due to their faster development. As the experiments were completed outdoors, the two different treatments were run simultaneously in individual enclosures separated by 20 m to ensure that treatments experienced the same environmental effects. There were six adult females (four virgin and two mated), six juvenile females and six males (three large and three small) in each treatment. Juvenile and mated females were included to simulate distributions found in nature (Andrade, 2003). We completed four replicates of each treatment.

To simulate these natural distributions, the cylinders of adult and juvenile females were randomly (but equally) distributed through four columns and three rows set up in one half of the enclosure (Fig. 2). The openings to the cylinders were parallel to the wind direction to allow effective transmission of pheromones. As the two treatments were run simultaneously, each treatment was subject to the same wind conditions. Males were placed in the centre of the opposite end of the enclosure, downwind of females. Both males and females were placed in their individual containers within the enclosure a day before the trial began to allow individuals to acclimate to environmental conditions. Each spider was used only once, except for juvenile females, which were used again as virgin adults once they matured (total females, $n = 74$).

On the first day of the trial, we removed the plastic wrap from each female's cylinder 1 hour before dusk (redbacks are nocturnal). We released males from their cages once all females became active, typically with web construction/repair. In the staggered treatment, we released only the small males on the first day. After releasing the small males, we checked all female's webs in the first hour then every half hour after release using a black light to illuminate males' markings. We noted male arrival, number of matings and mating order. When males and females became inactive at dawn, we covered
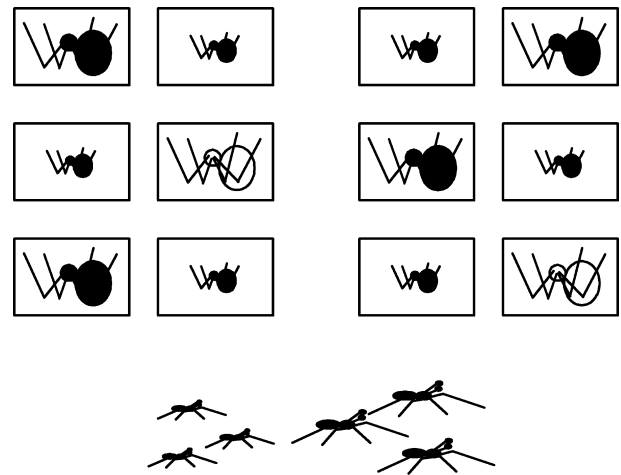

Fig. 2 A sample distribution of females in a field enclosure and the relative location of male release. Each female is inside an open cylinder in which they have built a web. Larger females are adults (black = virgins, $n = 4$ and white = mated, $n = 2$), whereas smaller females are juveniles. Female location was assigned randomly with respect to age and mating status during replicated trials.

all the cylinders, enclosing all individuals within to ensure any predators present in the enclosure could not kill our study animals. On the second day, we once again removed the plastic wrap from the ends of the cylinders 1 hour before dusk. We then released the three larger males simultaneously after females became active and again observed male arrival, the number of matings and mating order until dawn.

We followed the same procedure in the simultaneous release treatment except that both relatively small and large males were released simultaneously, and no additional males were released on the second day. All males began searching for females immediately after release; we never observed inter-male interactions during searching. Mated females were monitored after the experiment to ensure they produced viable eggs.

As copulation duration in redback spiders ranges from 6 to 31 min (Andrade, 1996), copulations may have occurred between our scans. However, males typically do not abandon female's webs once they arrive (Andrade, 2003; Kasumovic & Andrade, 2004; Andrade & Kasumovic, 2005), and they are usually injured or killed during copulation (Andrade, 1996, 1998); so, we would have found dead males wrapped in or under females' webs even if we missed a copulation. Moreover, courtship lasts a median of 4.6 h (Andrade, 1996) when single males are courting, and a minimum of 50 min when males are competing (Stoltz et al., 2008), which reduces the likelihood we missed any copulations. Finally, the number of copulations achieved by males (0, 1 or 2) was later confirmed by examining male copulatory organs under a dissecting microscope. Males lose the terminal sclerite from their intromittent organ at copulation; this sclerite

acts as a sperm plug inside the female's genitalia (Snow *et al.*, 2006). Males have paired copulatory organs that are functionally sterile after they have copulated once with each organ (Andrade & Banta, 2002); so, examining sclerite loss provides a good estimate of male copulatory success. We assessed male reproductive success with a single female as male redbacks are limited to mating with only one female in nature (Andrade & Banta, 2002; Andrade, 2003).

Estimating paternity and calculation of selection gradients

Redback spiders have complex sperm-use patterns because of their pair of independent sperm storage organs (spermathecae) and the deposition of sperm plugs (Snow & Andrade, 2005; Snow *et al.*, 2006); so, fitness cannot be accurately estimated from mating success alone. We estimated fitness by predicting each male's paternity based on the number and order (determined by observation) of copulations with a given female and known sperm-use patterns in redbacks (Snow & Andrade, 2005; Snow *et al.*, 2006). Each of the female's two spermathecae is inseminated by one of the male's two pedipalps. Sperm are apparently released equally from the two spermathecae and mix at fertilization (Snow & Andrade, 2005; Snow *et al.*, 2006), and the first male to inseminate both spermathecae deposits a sperm plug which ensures 89% of the fertilizations if a rival male mates second (Snow & Andrade, 2005; Snow *et al.*, 2006). We used these empirical results to estimate paternity in the following way. First-mating males were assigned 89% paternity if they copulated with both organs and a rival also mated with both organs. If the rival mated with only one spermatheca, the first male's paternity was 94.5% [1/2 × (100% from one organ + 89% from the second organ)]. If the first male mated with only one spermatheca, paternity would be shared equally (50%) with a later-mating rival that mated once (second-mating males always copulate with the empty spermatheca, Snow & Andrade, 2005). If the first male copulated once but the second male copulated twice, paternity of the first male would be 45% (89% × 50%). We assigned 0% paternity to males that were the third to copulate with a given female, or that did not copulate. We assigned 100% paternity if a female mated with only one male. For each scenario above, the paternity of the second male would be 100% − (paternity of the first male).

We calculated standardized linear ($\beta \pm$ SE) selection gradients on male size and body condition using a multiple linear regression of relative fitness on size and body condition (Lande & Arnold, 1983; Brodie *et al.*, 1995). We used estimated paternity as our measure of relative reproductive success and used mean-standardized values for both male size and body condition.

Results

Male success

A total of 68.8% (33/48) of males successfully located females across all trials. All males that located females during the 2-day experiment did so within the first hour following their release. There was no difference in body condition (residual mass, see Materials and methods) between large and small males ($t = 0.25$, d.f. = 46, $P = 0.81$), males used in either treatment ($t = 0.38$, d.f. = 46, $P = 0.71$) or males that did and did not successfully find females ($t = -1.11$, d.f. = 46, $P = 0.27$). Males had a significant preference for settling on the webs of virgin females ($\chi^2 = 36.88$, $P < 0.0001$).

All analyses of male performance are at the level of the trial to avoid pseudoreplication. In these analyses, we compared the average performance of small and large males, providing two data points for each trial. To examine whether there was a significant difference in various levels of male performance between large and small males in the two release treatments, we performed a two-way ANOVA with: (1) male size and (2) release treatment as the categorical independent variables, and the average number of males that: (a) successfully found a female, (b) successfully mated, (c) mated first and the (d) average estimated paternity as the dependent variables.

The average number of males that successfully found female's webs was higher in the simultaneous release treatment than in the staggered release treatment due to substantially reduced searching success of relatively larger males in the staggered release treatment (Table 1, Fig. 3a). There was also a treatment × size interaction as relatively small males performed better in the staggered release treatment (Table 1, Fig. 3a). There was no overall difference in the average number of relatively

Table 1 Results from a two-way ANOVA examining the performance of large vs. small males in the simultaneous vs. staggered release treatment.

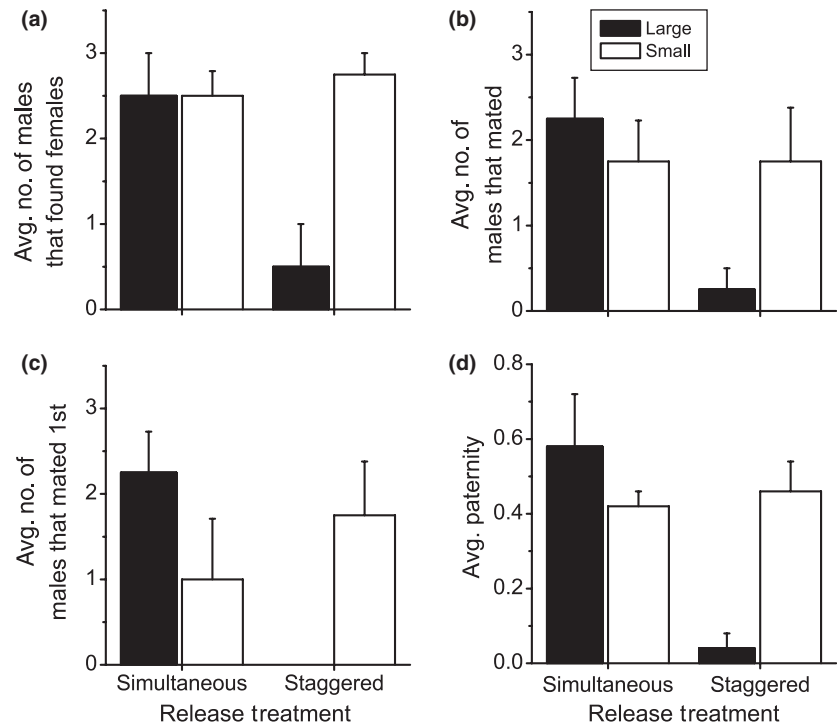| Source	d.f.	F	P
Males that found females			
Treatment	1,12	4.74	0.05
Size	1,12	7.84	0.016
Treatment × size	1,12	7.84	0.016
Males that mated			
Treatment	1,12	4.36	0.059
Size	1,12	1.09	0.32
Treatment × size	1,12	4.36	0.059
Males that mated first			
Treatment	1,12	2.00	0.18
Size	1,12	0.22	0.65
Treatment × size	1,12	8.00	0.015
Average paternity			
Treatment	1,12	3.74	0.077
Size	1,12	1.00	0.34
Treatment × size	1,12	4.94	0.046

Fig. 3 The average number of small (black bars) and large (white bars) males that (a) successfully located a female, (b) mated at least once and (c) mated first under direct competition (simultaneous release treatment) or when smaller males were given the temporal advantage associated with their more rapid development (staggered release treatment, larger males' release delayed by 1 day) in a field enclosure. (d) The mean predicted paternity of small and large males in the simultaneous and staggered release treatments. Error bars are standard error.

large and small males that successfully copulated at least once (Table 1, Fig. 3b), although relatively larger males tended to outcompete relatively smaller males in the simultaneous release treatment (Table 1, Fig. 3b). However, relatively larger males were significantly more likely to mate first in the simultaneous release treatment, whereas relatively smaller males were significantly more likely to mate first in the staggered release treatment (Table 1, Fig. 3c).

There was a significant interaction between effects of treatment and size on estimated paternity, which incorporates mating order and mating number. Relatively larger males were more successful in the simultaneous release treatment; however, relatively small males were more successful in the staggered release treatment (Table 1, Fig. 3d), due to the lower average paternity of relatively large males in the staggered release treatment (Fig. 3d).

Selection gradients

We calculated selection gradients on male size and body condition separately in each treatment. The selection gradient on male size was positive in the simultaneous release treatment ($\beta = 0.14 \pm 0.096$) but not significant ($F_{1,21} = 2.18$, $P = 0.15$). By contrast, the selection gradient was significantly negative in the staggered release treatment ($\beta = -0.17 \pm 0.069$; $F_{1,21} = 3.74$, $P = 0.021$). Although selection gradients were positive for body condition in both treatments (simultaneous: $\beta = 0.05 \pm 0.096$, staggered: $\beta = 0.01 \pm 0.069$), neither was

significant ($F_{1,21} = 0.29$, $P = 0.59$; $F_{1,21} = 0.02$, $P = 0.88$ respectively).

We tested for differences between standardized linear selection gradients between release treatments by using an analysis of covariance (ANCOVA) to examine whether slopes were equal (Conner, 1989; as in Caruso et al., 2003). We entered fitness as the dependent variable, and both size and body condition as the independent variables, along with treatment as the categorical variable. A significant treatment × trait interaction indicates that the strength of selection varies significantly in each treatment. There was an overall effect of treatment on reproductive success with males in the simultaneous release treatment having a higher overall fitness (Table 2). There was a significant difference in the selection gradients on size between treatments (size × treatment, Table 2). There was no difference in the selection gradients on body condition between treatments (body condition × treatment, Table 2).

Table 2 Results from an ANCOVA used to examine variation in selection.

Source	d.f.	F	P
Size	1, 42	0.0624	0.8040
Body condition	1, 42	0.2789	0.6002
Treatment	1, 42	4.7316	0.0353
Treatment × size	1, 42	7.0370	0.0112
Treatment × body condition	1, 42	0.1244	0.7261

The treatment by trait interactions test for differences in slope between selection gradients.

Discussion

In our study, we assessed the effects of male size and body condition on mating success when we varied the relative timing of male entry into the competitive arena. We demonstrated a reversal in the relationship between male size and reproductive success as a function of the context and form of inter-male competition. When relatively large and small males were released simultaneously, there was no significant difference in mate searching success, replicating the field results of Andrade (2003). However, upon arrival at females' webs, relatively larger males outcompeted smaller males resulting in higher predicted paternity. When relatively smaller males were released 1 day earlier in the staggered release treatment, relatively smaller males mated first and removed females from the population of potential mates (e.g. Stoltz et al., 2007), resulting in 10 times higher predicted paternity than relatively larger males (Fig. 3d). Along with other studies examining male fitness in different contexts (e.g. Blanckenhorn et al., 1995; Blanckenhorn & Viele, 1999; Crompton et al., 2003; Moya-Laraño et al., 2007), our study demonstrates that relatively smaller male phenotypes are adaptive in certain competitive contexts when compared with relatively larger male phenotypes.

An ontogenetic strategy that allows a trade-off between size and development time as a function of variable competitive contexts is likely to maximize fitness for male redbacks. Variation in the type of intrasexual competition (e.g. direct vs. scramble competition) males encounter at maturity is not uncommon in redbacks. First, males mature at different times because egg sacs are produced and hatch continuously throughout the season (Andrade & Banta, 2002; Andrade, 2003), and there is variance in development time as a result of resource availability, female availability and male density (Kasumovic & Andrade, 2006). Second, males may encounter lone females or females with multiple suitors (Andrade, 1996), and will thus encounter either selection for rapid location and mating with virgin females before other males arrive or intense multi-male competition for access to females. Here, we examined these two extremes in the type of intrasexual competition redback males are likely to face in nature. However, the relative importance of rapid development compared with large size is likely to lie on a continuum due to variation in social challenges. If competitive contexts have a Gaussian distribution with intense direct competition on one tail and no competition on the other tail (e.g. in nature, median number of males/web = 2, min–max = 0–6; Andrade, 1996), then plastic responses to this variation could underlie the Gaussian distribution of male body size. Our results thus suggest that plasticity-mediated variation may influence the shape of phenotypic distributions.

Consistent with the hypothesis of adaptive plasticity, in the staggered release treatment, we demonstrated that rapidly developing males, despite the potential competitive handicap of their relatively smaller size, would reach females first, copulate first and more frequently, and could thus insert a plug that ensures sperm priority (Snow & Andrade, 2005; Snow et al., 2006). Earlier arrival of small, rapidly developing males also allows males to decrease post-copulatory competition in two ways. First, copulation probably results in a change in the composition or production of airborne pheromones by females (Trabalon et al., 1997; Prouvost et al., 1999), so that mated females are less attractive to other males (Gaskett et al., 2004; Andrade & Kasumovic, 2005). Second, males can decrease the release of attractive pheromones emitted from the web by damaging and packaging the female's web (web reduction, Watson, 1986; Schulz & Toft, 1993), and thus reduce the chance that a female will attract a second mate. This is important, as pheromones can remain on the web and continue to attract males for several days after the female ceases production of these chemicals (Andrade & Kasumovic, 2005). Our results suggest that the drop in attractiveness of mated females occurs rapidly after undisturbed matings (less than 9 h), and this may explain the failure of larger males to find potential mates in the staggered release treatment. In our trials, males were never attracted to previously mated females on the first day and, on the second day, only one of the newly mated females in the staggered release treatment attracted a male. This one exception was also the only case in which the female remained unmated until the second day of the experiment (the first-arriving male did not copulate immediately).

Although relatively small males outperformed large males in our staggered release treatment, there are contexts in which early development is not advantageous because, in redbacks, it is coupled with smaller body size (Kasumovic & Andrade, 2006). The larger male phenotype is thus maintained in redbacks because it offers a benefit when the probability of rival males clustering on females' webs is high. In our simultaneous release treatment, larger males tended to exclude smaller males from mating and reduced their success at mating first, despite the smaller males' equal success at finding females. So, as in other systems, increased size is favoured when the likelihood of direct competition increases (Kingsolver & Pfennig, 2004; for a review see Andersson, 1994). This is likely in situations when the sex ratio is male biased. However, even if the population-wide sex ratio is equal, local fluctuations in the density of receptive mates can lead to males clustering with available females (Gwynne et al., 1998; Foellmer & Fairbairn, 2005; Kasumovic et al., 2007) and thus spatial variation in the strength and direction of selection (Kasumovic et al., 2008). Thus, local variation in sex ratio and density will probably cause spatial and temporal variations in the benefit of large size. Larger males might also have higher survivorship during mate

searching over the long distances expected when females are sparsely distributed, although there is currently limited empirical support for this idea (Vollrath, 1980; Andrade, 2003; Foellmer & Fairbairn, 2005; Kasumovic et al., 2007).

Our estimates of linear selection gradients also varied depending on the competitive context. Although our sample size was relatively small, resulting in limited statistical power to detect selection of 'typical' strength (see Kingsolver et al., 2001), the direction and magnitude of selection on the focal traits differed as predicted. The timing of male release yielded significant variation in the direction of selection – with relatively strong negative selection on male size under staggered release. This suggests that microspatial variation in competitive challenges can significantly alter the sign and magnitude of selection on size, in which case single-context, whole-season or population-wide estimates of the strength of selection may yield a misleading impression of how sexual selection is affecting phenotypic evolution (Kasumovic et al., 2008). For example, biases in the sex ratio on a very local scale, similar to the scale of our field enclosure (roughly 3 m^2) may be sufficient to switch selection, as this area is comparable with the distance searched by the average successful redback male (approximately 2.5–3.5 m, Andrade, 2003). Just as it is important to understand how different types of selection (e.g. natural vs. sexual selection) can interact to shape total selection on a particular trait (e.g. Hunt et al., 2008), it is critical to understand how various competitive challenges can alter a single type of selection on a particular trait. Without taking into consideration the strength of selection in multiple competitive environments, it can lead to an over- or underestimation of the strength of selection.

In many species, variation in selection in response to multiple competitive challenges has led to the evolution of different morphs (i.e. polyphenisms) that allow individuals to specialize in the different strategies suited to each context (reviewed by Moran, 1992). In redback spiders, however, rather than discrete morphs, males show adaptive plasticity in time to maturity, which yields significant, continuous variation in male size and body condition (mirroring variation seen in nature Kasumovic & Andrade, 2006). The rapid response of males to short-term variation in competitive context is most likely because males are limited to mating with a single female (Forster, 1992; Andrade, 1996, 2003), so optimize their phenotype to match the single context they are likely to encounter at maturity. Thus, despite size-mediated competitive interactions (simultaneous release results), no single size optimum exists for redback males. This study provides further evidence that sexual selection can favour context-specific changes in development rather than specialization in environments where spatio-temporal variation in competitive challenges within a breeding season are predictable (Via & Lande, 1985;

Van Tienderen, 1991). This result is predicted when life-history traits and developmental plasticity are both taken into consideration, as this is expected to yield phenotypes that are optimum for a particular set of adult challenges (Via & Lande, 1985; Scheiner, 1993; Gotthard & Nylin, 1995; Pigliucci, 2001; West-Eberhard, 2003; Doughty & Reznick, 2004).

Larger size may signal male quality to females in some systems (Andersson, 1994; Blanckenhorn, 2005); however, females have been found to mate with smaller (less dominant) males in a range of species (Qvarnstrom & Forsgren, 1998). In redbacks, by mating with the first male to arrive (irrespective of size), females may frequently select the males most capable of tactically respond to the inherent heterogeneity of the environment. Definitions of male quality should therefore include life-history decisions associated with the development of the traits under assessment. Competitive contexts are likely to vary throughout a breeding season as a consequence of variation in the availability of mature females and the number of potential competitors (Blanckenhorn et al., 1999; Kokko & Monaghan, 2001; Kokko & Rankin, 2006; Kasumovic et al., 2008; Punzalan et al., 2008). To assess the effects of selection on male traits then requires knowledge of the range of competitive challenges that males may face, the developmental paths that yield phenotypes that will maximize fitness in each situation, and how quickly and over what spatial scale competitive contexts are likely to fluctuate (Benton et al., 2006; Metcalf & Pavard, 2006; Kokko & López-Sepulcre, 2007).

Acknowledgments

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