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Reproductive consequences of male body mass and aggressiveness depend on females' behavioral types

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Abstract Relatively few investigations explicitly test for concordant versus conflicting selection pressures from intrasexual versus intersexual selection. Here, we examine the effects of male body mass and behavioral type (BT) on reproductive success in the spider *Anelosimus studiosus*, with emphasis placed on the potential interaction between intrasexual and intersexual selection influences. Female *A. studiosus* exhibit either an *aggressive*-active or *docile*-passive BT, both of which co-occur in multifemale colonies. Males, in contrast, exhibit a more continuous distribution of behavioral tendencies. We investigated the male traits favored by females in five trial types: one docile female, one aggressive female, four docile females, four aggressive females, and two docile and two aggressive females. Male reproductive success was estimated by the number eggs produced by females following staged mating trials. In previous work, it was established that large aggressive males are favored in male–male contests, an intrasexual effect. However, large aggressive males were not universally favored here. We failed to detect an effect of male body mass or aggressiveness on reproductive success in trials with all docile females; however, in situations involving aggressive females, large aggressive males experienced diminished reproductive success relative to small docile males. Large, aggressive males were also more likely to be attacked and killed by aggressive females in the first 20 min of staged encounters and were more likely to be found dead after 72 h of unobserved interactions. Taken together, our data suggest that the reproductive consequences of male traits differ based on (1) the aspect of sexual selection being considered (intrasexual versus intersexual) and (2) the BT of their prospective mates: large aggressive males enjoy advantages in intrasexual selection and when courting docile females and small docile males experience reduced risk of cannibalism and increased reproductive success with aggressive females.

Keywords Behavioral syndrome · Personality · Sexual selection · Social selection · Temperament

Introduction

The availability of receptive mates is one resource that is commonly limited in sexually reproducing organisms. Though many factors can influence individuals' mating and reproductive success, the majority of these factors can be subsumed into two broad categories: intrasexual and intersexual selection (Darwin 1859, 1871; Andersson 1994; Andersson and Isawa 1996; Houde 1997; Hunt et al. 2009). Intrasexual selection occurs when individuals of the same sex (typically males) compete for reproductive access to members of the opposite sex (typically females). In contrast, intersexual selection occurs when individuals exhibit selectivity in their mating decisions and members of one sex (typically females) favor some prospective mates over others. From classic studies of sexual selection, the view has emerged that intrasexual and intersexual selection are typically positively correlated (Berglund et al. 1996; Wiley and Poston 1996; Hunt et al. 2009). However, a more

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recent body of work has begun to challenge this classic view (Qvarnström and Forsgren 1998; Moore and Moore 1999; Wong and Candolin 2005; Hunt et al. 2009). Despite this growing literature, to date, relatively few investigations explicitly test for concordant versus conflicting selection pressures from intrasexual versus intersexual selection.

As with any aspect of selection, sexual selection is thought to erode trait variation through directional selection on preferred sexual characters (Fisher 1958). However, even a cursory review of the literature on sexual selection reveals a dramatic diversity both in (1) the kinds of traits favored and (2) the mating strategies employed by individuals, even within a single species or population (Alcock 1994; Andersson 1994; Lank et al. 1995; Berglund et al. 1996; Cook et al. 1997; Parker 1998; Hebets 2003; Hanlon et al. 2005; Kokko et al. 2006). One often invoked and potentially pervasive explanation for the maintenance of trait variation, sexual or otherwise, is social selection (Moore et al. 1997; Wolf et al. 1998, 1999). Social selection posits that the fitness effects of a trait depend on the social environment in which it is expressed. That is, in social situations (e.g., mating), the fitness landscapes in which traits evolve are influenced by the social phenotypes of other interacting individuals. Under social selection, the success of various mating strategies could depend both on (1) the phenotypes of the focal individuals and (2) the behavioral phenotypes of their intended partner/s. Interestingly, social selection has the potential to generate instances of intransitivity, frequency-dependent effects, and other variation-sustaining phenomena (Moore et al. 1997; Wolf et al. 1998, 1999).

In the present study, we consider the effects of behavioral syndromes or behavioral types (BT; i.e., the animal analog of human "personality") on individual reproductive success. Behavioral syndromes are defined as correlations in behavior across time, situation, or ecological context (Sih et al. 2004; Bell 2007). Here, we ask whether the behavioral traits which aid males in intrasexual selection (i.e., male–male conflict) are also associated with reproductive success (i.e., the composite effect of intersexual and viability selection) and whether the success of a male is affected by the BT of his intended mate. Such BT by BT interactions (i.e., social selection) have the potential to eliminate single trait optima and serve as a variance-sustaining mechanism in animal mating systems (van Oers et al. 2008).

Study system

Anelosimus studiosus (Araneae, Theridiidae) is a common cobweb-weaving spider with a range extending from the Northeastern United States to Patagonian Argentina. Both males and females of this species exhibit heritable variation in social tendency and aggressiveness, where females can be assigned to one of two behavioral classes: (1) a *docile* (formerly "social") phenotype, which exhibits reduced activity levels, shorter dispersal distances, and diminished aggressiveness towards predators, prey, and mates and (2) an *aggressive* (formerly "asocial") phenotype, which exhibits heightened activity levels, greater dispersal distances, and elevated aggressiveness towards predators, prey, and mates (Jones et al. 2007; Riechert and Jones 2008; Pruitt et al. 2008, 2010; Pruitt and Riechert 2009a, b, c). Both phenotypes can be found in varying proportions both as singleton individuals (Jones et al. 2010) and in multifemale colonies (Pruitt and Riechert 2009c, 2011a). In contrast, males exhibit a more continuous distribution of social tendencies because, as in many spider species (Foelix 1996), mature male *A. studiosus* exhibit reduced overall aggressiveness (Pruitt and Riechert 2009a). Data from breeding studies suggest that aggressiveness and social tendency have a significant additive genetic component to their variation (heritability≈0.37–0.45; Pruitt and Riechert 2009a).

Male *A. studiosus* mature before females and leave their natal webs in search of immature females (Albo et al. 2007; Pruitt and Riechert 2009b). Males that encounter other males will engage in conspicuous male–male contests. The winners of these contests remain at the site containing juvenile females and defend them until they mature. Females are each courted and mated by dominant males as they mature, while males that have lost male–male interactions assume satellite positions (Albo et al. 2007) despite strong first male sperm precedence in the system (i.e., 100% of offspring experimentally sampled are sired by first males; Jones and Parker 2008). In previous work, we established that larger and more aggressive males tend to win male–male contests (Pruitt and Riechert 2009b). However, we presently lack understanding about which traits are associated with other aspects of reproductive success (i.e., intersexual and viability selection) and whether these traits are consistent with those favored during male–male contests. We believe that intersexual selection is a particularly potent selective force in *A. studiosus* because aggressive females attack and consume as many as 35% of males before copulation; in contrast, docile females exhibit precopulatory cannibalism in only 10% of staged encounters (Pruitt and Riechert 2009b).

We ask the following questions: (1) What traits are associated with male reproductive success, as inferred by the number of eggs produced by female following staged mating encounters? (2) Are the male traits favored the same for encounters with docile versus aggressive females? (3) Are the traits favored in male–male competition also associated with male reproductive success? (4) How might the presence of multiple females affect reproductive out-

comes? We argue that understanding the reproductive consequences of male BT and body mass with different combinations of females has important implications for the maintenance of the behavioral polymorphism in *A. studiosus*.

Methods

Collection and laboratory maintenance

Spiders were collected as early instar juveniles (two to three instars of seven) from a known polymorphic population in east Tennessee, USA (35°89′ N, 84°30′ W). Webs were collected along a riparian zone by placing a plastic bag over the web and trimming the supporting foliage. To reduce the probability of collecting siblings, only one web was collected every 3 m. Spiders were then transported back to the laboratory at the University of Tennessee, Knoxville. Each web was dissected by hand, and spiders were housed individually in 59-ml enclosures containing a small piece of poultry wire to facilitate web construction. Spiders were provided an ad libitum (three to six individuals) diet of termite workers (*Reticulitermes flavipes*) once weekly and misted with a water bottle to provide drinking water. Spiders were checked twice weekly for maturation. Mature spiders were run through the aggressiveness assay described below and randomly selected for use in one of our five staged reproductive scenarios: (1) one docile female, (2) four docile females, (3) one aggressive female, (4) four aggressive females, and (5) two docile and two aggressive females.

Aggressiveness assay

The trial used here to determine individuals' aggressiveness towards conspecifics (aggressive/docile) is designed after the protocol of Riechert and Jones (2008). Trials occurred between two individuals of unknown aggressiveness 24 h after a routine feeding event. Spiders were individually marked with colored fluorescent powder, released into the center of a clear plastic container (12.5×12×2.5 cm), and given 24 h to settle and construct webs. We assign female spiders to the "docile" or "aggressive" phenotype based on the distance between them. *A. studiosus* generally prefers to settle in corners of the container. Two females are labeled as "docile" if after 24 h they settle in the same corner. Females in either opposite or adjacent corners are termed "aggressive." It is possible in these trials that a docile female might score as aggressive because it has been repelled by an aggressive female. Therefore, a second trial is completed on all individuals scored as aggressive, where each individual is paired with a known docile individual. In these instances, we

use the second interindividual distance score as our measure of individual aggressiveness. Female aggressiveness scores are more polarized than those of males (Pruitt et al. 2008; Pruitt and Riechert 2009a, b) and are roughly bimodal distributed (Pruitt and Riechert 2009c). Thus, for our experiments, we assign females to either the "docile" or "aggressive" BT, while we treat male aggressiveness as a more continuous character. Data from a breeding study on *A. studiosus* determined that there is a significant additive genetic component to our interindividual distance measure (heritability≈0.37–0.45; Pruitt and Riechert 2009a).

To determine the distribution and repeatabilities of our aggressiveness scores, we retested a pool of males (N=100) and females (N=120) 2 weeks after their initial aggressiveness assays; in the field, mature nonbrooding females typically persist in the population for <4 weeks. Individuals used to obtain repeatability estimates were excluded from other assays.

Staged mating encounters

Forty-eight hours after a routine feeding, virgin test females (size-matched ±2% each others' body mass) were placed in a 490-ml enclosure containing poultry wiring. Females were given 48 h to settle and construct a web before a test male was released onto the edge of their web using an open-typed medical syringe. We observed the courtship for the next 20 min and noted the males' "latency to approach." We estimated males' latency to approach as the time from a male's first observable signaling behavior (web flexing; Albo et al. 2007) to his initial directional movement towards any test female. We also noted instances of sexual cannibalism at this time. Male mortality during the first 20 min was always the result of attacks by females. After the 20-min observational period, we left males in the test enclosure for another 72 h. To allow males an escape route, the lids to our enclosures were left 2 cm ajar.

After 72 h, we disassembled the web, isolated females in 59-ml containers, and recorded their egg case production for the next 2 months. Test females never produced more than one egg case. One week after parturition, we dissected egg cases and counted the number of eggs therein; nonviable egg cases were smaller, discolored, and flattened relative to viable egg cases and were consumed by females within 1 week of parturition (Pruitt, personal observation). In spiders, egg production and yoking occurs in two phases, and the second occurs immediately after copulation (Foelix 1996). Thus, females have the opportunity to differentially provision their egg cases (e.g., increasing egg number and/ or provisioning per egg) following cues during courtship and copulation, thereby influencing male fitness (*Schizocosa*: Rundus et al. 2011; *Pardosa*: Hoefler et al. 2009; *Scytodes*: Koh et al. 2009; *Anelosimus*: Pruitt and Riechert 2011b). By

noting the number of egg cases produced and the number of individual eggs per egg case, we account for potential effects of postcopulatory manipulation by females.

We also noted whether males were alive after 72 h. Although we lack quantitative data on the frequency of sexual cannibalism over the 72-h period, we commonly observed females feeding on males during the duration of our trials. Sexual cannibalism is common in *A. studiosus* (Pruitt and Riechert 2009b, 2011b).

Statistical analyses

To determine repeatabilities of aggressiveness scores, we used analysis of variance and partitioning of variance into within-individual versus among-individual components after Boake (1989). The distribution of male and female aggressiveness scores are presented in histograms.

First, we used a combined model to test for conflicting effects of male aggressiveness, latency of approach, and/or body mass on reproductive success between treatments. Males' relative reproductive success was our response variable in our model (i.e., number of eggs produced/ average number of eggs produced in that treatment), and we include the following predictor variables: treatment (1D, 4D, 2D2A, 1A, and 4A), male body mass, male aggressiveness score, latency to approach, and interaction terms (treatment×male body mass, treatment×male aggressiveness score, and treatment×latency of approach). Following two significant interactions terms (treatment×male aggressiveness and treatment×male body mass), we report the results of each treatment independently. In all treatment-specific analyses, males' relative reproductive success was our response variable, and we include the following predictor variables: male body mass, male aggressiveness score, and male aggressiveness score×male body mass.

We tested for associations between male survival (predictor) and reproductive success (response variable) using general linear models. We then tested which male attributes predicted survival using multiple logistic regression, and we used chi-squared statistics to test for differences in male survival among treatments over (1) our 20-min observational period and (2) the full 72-h encounter duration.

Results

The distribution of male and female aggressiveness scores are summarized in Figs. 1 and 2, respectively. In our test males, aggressiveness was weakly, positively associated with body mass ($r=0.21$, $P=0.001$, $df=214$). As suggested in previous studies, we observed more polarized behavioral responses towards conspecifics in female *A. studiosus*, whereas male scores exhibited a more continuous distribu-
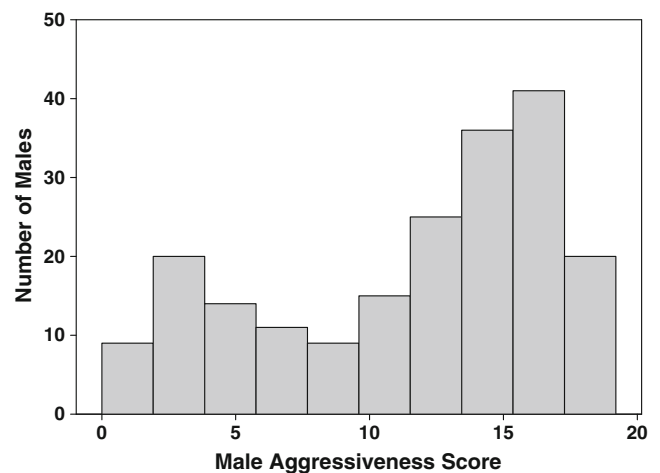

Fig. 1 Histogram depicting the distribution of male aggressiveness scores ($N=100$)

tion. Additionally, aggressiveness scores were repeatable for both males (repeatability (r)=0.55, $F_{59,119}=3.50$, $P<0.0001$) and females (repeatability (r)=0.70, $F_{99,199}=5.78$, $P<0.0001$).

We detected significant effects of male body mass and aggressiveness score on males' relative reproductive success across trials ($F_{19,215}=6.88$, $r^2=0.40$, $P<0.0001$; Table 1); however, as evidenced by significant interaction terms (treatment×male body mass: $F_{4,215}=11.70$, $P<0.0001$, Fig. 3; treatment×male aggressiveness score: $F_{4,215}=4.71$, $P=0.001$, Fig. 4), the effects of male attributes on reproductive success differed among treatments. Thus, for the remainder of our analyses, we consider each treatment independently. To determine whether differences in male fitness were the result of (1) a greater number of egg cases sired or (2) a great number of eggs per egg case, we reran our combined analysis with the number of eggs produced per egg case as our response variable. Our combined model was
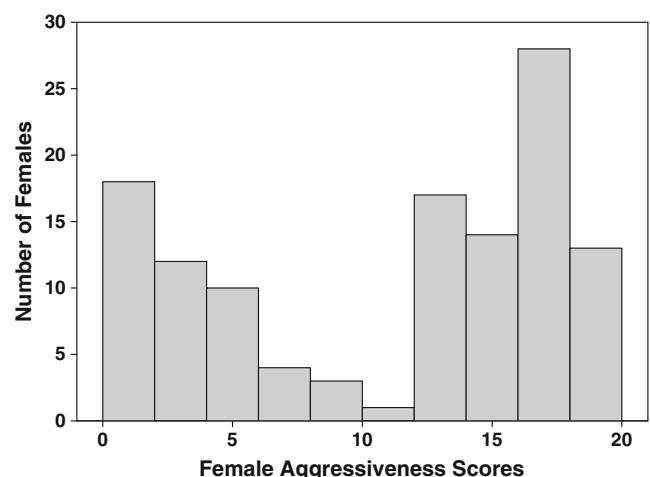

Fig. 2 Histogram depicting the distribution of female aggressiveness scores ($N=120$)

**Table 1** Summary of effect tests for our combined model ($F_{19,215}$= 7.65, r^2=0.43, P<0.0001)

Source	df	F ratio	P value
Treatment	4	0.32	0.86
Male body mass	1	19.4	<0.0001
Latency of approach	1	0.43	0.51
Male aggressiveness score	1	10.93	0.001
Treatment×male body mass	4	14.2	<0.0001
Treatment×latency if approach	4	0.21	0.94
Treatment×male aggressiveness score	4	3.82	0.005

Relative reproductive success (total number of eggs produced following a staged mating encounter/average number of eggs produced from encounters in each treatment) was the response variable in our analysis

nonsignificant, indicating fitness differences among males are the result of more egg cases sired and not more individual eggs per egg case ($F_{19,165}$=1.30, r^2= 0.14, P=0.19; Table 2).

Parameter estimates of our treatment-specific models are summarized in Table 3. Our combined model predicting males' relative reproductive success in encounters with all docile females were nonsignificant: one docile female ($F_{4,36}$=1.85, r^2=0.20, P=0.12) and four docile females ($F_{4,36}$=1.70, r^2=0.18, P=0.17). Furthermore, the majority of males survived the 72-h trial duration in encounters with all docile females (Table 4), and thus, we failed to detect an association between male survival and reproductive success in these trials: survival over 20 min (one docile female: $F_{1,36}$=1.11, r^2=0.04, P=0.29; four docile females: $F_{1,36}$= 1.65, r^2=0.04, P=0.21), survival over 72 h (one docile female: $F_{1,36}$=3.97, r^2=0.10, P=0.06; four docile females: $F_{1,36}$=0.26, r^2=0.01, P=0.61). We also failed to detect associations between male attributes and their survival over our 20-min observational period or 72-h encounter duration (Table 5).
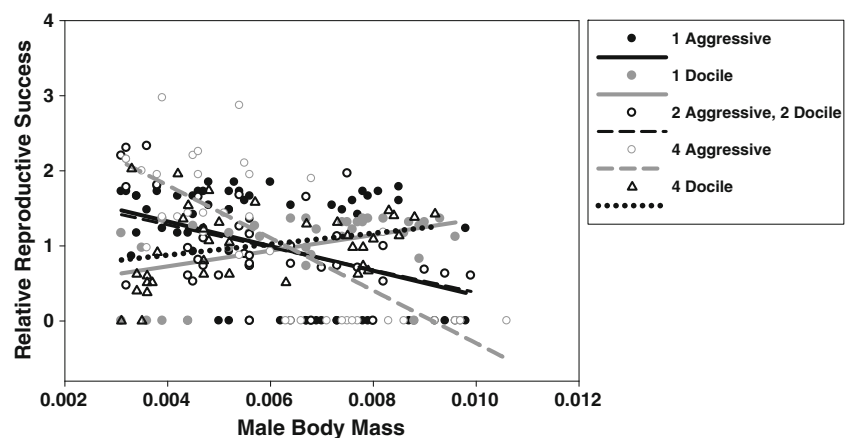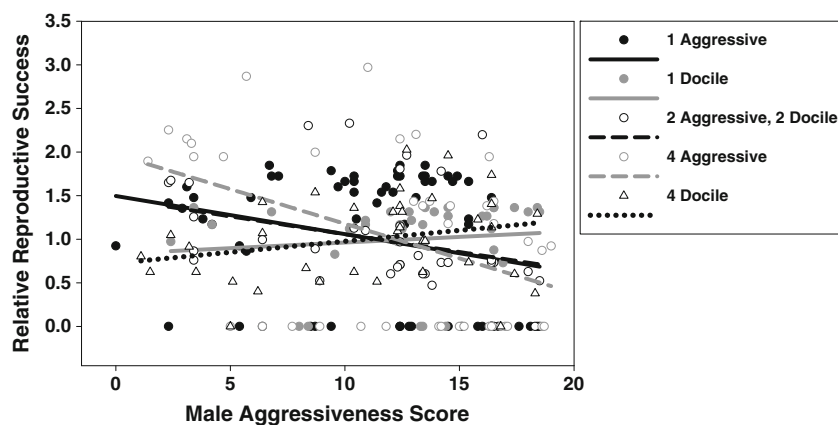
In trials involving aggressive females, all of our combined treatment-specific models predicting male reproductive success were significant: single aggressive female ($F_{4,36}$=4.51, r^2=0.23, P=0.003), four aggressive females ($F_{4,39}$=21.48, r^2=0.65, P<0.0001), and two docile and two aggressive females ($F_{4,37}$=3.56, r^2=0.30, P=0.02). In trials with a single aggressive female, we detected significant negative effects of male body mass ($F_{1,37}$=9.87, P=0.002) and aggressiveness score ($F_{1,37}$=4.41, P=0.04) on reproductive success. In other words, smaller and more docile males experienced superior reproductive success. Similarly, in trials involving four aggressive females, we detected a significant negative effect of male body mass ($F_{1,39}$=62.72, P<0.0001) and male aggressiveness score ($F_{1,39}$=7.59, P= 0.009) on males' reproductive success. In trials involving two docile and two aggressive females, again, male body mass ($F_{1,37}$=9.49, P=0.004) and aggressiveness ($F_{1,37}$= 4.52, P=0.04) were negatively associated with reproductive success. Taken together, large aggressive males experienced diminished reproductive success in all trials involving at least one aggressive female. The interaction term between male aggressiveness score and body mass was nonsignificant in all of our treatment-specific models predicting male reproductive success (P>0.15; Table 3).

In trials involving aggressive females, we detected positive relationships between male survival and reproductive success: survival over 20 min (one aggressive female: $F_{1,63}$=108.99, r^2=0.64, P<0.0001; four aggressive females: $F_{1,39}$=14.17, r^2=0.27, P=0.001; two docile and two aggressive females: $F_{1,37}$=7.20, r^2=0.17, P=0.01), survival over 72 h (one aggressive female: $F_{1,63}$=144.08, r^2=0.82, P<0.0001; four aggressive females: $F_{1,39}$=6.71, r^2=0.15, P=0.01; two docile and two aggressive females: $F_{1,37}$=7.71, r^2=0.18, P=0.009). Thus, males which survived longer also enjoyed higher reproductive success. We next tested for associations between male attributes and survival probability (summarized in Table 5). Generally, male body mass and aggressiveness were negatively associated with survival probability

Fig. 3 Regression plot depicting the relationship between male body mass (in grams) and relative reproductive success among treatments (treatment×male body mass: $F_{4,119}$=14.20, P<0.0001). Relative reproductive success was calculated as the total number of eggs produced following a staged mating encounter divided by the average number of eggs produced from encounters in each treatment

Fig. 4 Regression plot depicting the relationship between male aggressiveness score and relative reproductive success among treatments (treatment×male aggressiveness score: $F_{4,119}=$ 3.83, P=0.005). Relative reproductive success was calculated as the total number of eggs produced following a staged mating encounter divided by the average number of eggs produced from encounters in each treatment

over both our 20-min observational period and the full 72-h encounter duration. For comparison, male mortality was at least twice as high in all trials involving aggressive females (Table 4).

Discussion

Identifying the mechanisms maintaining trait variation is a central goal in ecology and evolutionary biology, and in behavioral ecology, BT by BT interactions could be one important variance-sustaining mechanism. In *A. studiosus*, male reproductive success depends on a number of factors. First, males must gain access to females by fending off rival males. Perhaps unsurprisingly, larger and more aggressive males dominate these interactions (Pruitt and Riechert 2009a). Interestingly, our data here indicate that dominance is not enough to ensure reproductive success, and depending on the female phenotype/s, large aggressive males can even be disadvantaged. In encounters with docile females, males of various body masses and BT appear to experience similar reproductive success; thus, intrasexual selection seems the more important selective force in these scenarios. However, large and aggressive

males experience reduced survivorship and reproductive success when courting aggressive females, and thus, their performance in male–male contests does not necessarily confer improved reproductive success. Instead, we found that large, aggressive males were more likely be attacked and consumed in the first 20 min of staged encounters with aggressive females, thus diminishing their reproductive potential. In these circumstances, large aggressive males are perhaps merely "winning" their way into lethal circumstances and sating females for subsequent suitors (i.e., smaller subordinate males). In contrast, despite poor performance in male–male contests, small passive males outperformed their larger rivals in all encounters involving aggressive females (Pruitt and Riechert 2009a; Fig. 3). Taken together, our data imply that male reproductive success depends on both (1) the aspect of selection being considered (i.e., intrasexual versus intersexual and viability selection) and (2) the BT of the prospective mates.

In most classic examples of sexual selection, the male traits favored in male–male contests are also preferred by females (Qvarnström and Forsgren 1998; Hunt et al. 2009): large dominant males tend to win contests, and concordantly, male size and social standing are used by females as indicators of male quality (Ryan et al. 1990; Morris et al. 1992; Clark and Moore 1995a, b, c; Howard et al. 1997; Rasmussen and Schulte 1998; Calsbeek and Sinervo 2002a, b; Hagelin 2002; Hunt et al. 2009). Though, in most of these systems, males are the larger, more ornate, and aggressive of the sexes, and it is often presumed that sexual size dimorphism is the result of sexual selection (Clutton-Brock et al. 1977, 1980; Harvey et al. 1978; Harcourt et al. 1981). In contrast, in some systems, females are the larger and more dangerous sex (e.g., many invertebrates), and under these circumstances, selection might favor traits which aid males in mating without eliciting predatory responses from females. This feat could be achieved in a number of ways: selection might favor

Table 2 Summary of effect tests for our combined model ($F_{19,165}=$ 1.30, r^2=0.14, P=0.18) predicting the number of eggs produced per egg case following staged mating encounters

Source	df	F ratio	P value
Treatment	4	0.38	0.82
Male body mass	1	0.08	0.78
Latency of approach	1	0.04	0.85
Male aggressiveness score	1	6.67	0.01
Treatment×male body mass	4	0.83	0.51
Treatment×latency if approach	4	1.20	0.31
Treatment×male aggressiveness score	4	0.96	0.43

Table 3 Parameter estimates (±SE), adjusted r^2, and P values for our combined treatment-specific models predicting males' relative reproductive success

Treatment	Body mass	Aggressiveness	Body mass×aggressiveness	r^2	P value
One aggressive female	−149.68 (±47.62)[a]	−0.04 (±0.02)[a]	−11.35 (±11.15)	0.23	0.003
One docile female	59.19 (±41.45)	0.04 (±0.05)	−2.40 (±9.20)	0.20	0.12
Four aggressive females	−335.64 (±42.37)[a]	−0.05 (±0.02)[a]	12.44 (±8.54)	0.67	<0.0001
Four docile females	53.25 (±44.01)	0.02 (±0.02)	−7.43 (±11.19)	0.18	0.17
Two docile and two aggressive females	−159.65 (±51.82)[a]	−0.04 (±0.02)[a]	12.48 (±13.59)	0.30	0.02

[a] Significant term at $\alpha=0.05$

larger males which are less likely to be killed when/if attacked (Wilder and Rypstra 2008; Wilder et al. 2009) or, alternatively, selection might favor traits which help distract dangerous females (e.g., nuptial gifts) (Svensson et al. 1990; Lang 1996) or evade detection altogether (e.g., cataleptic pheromones, sneaker males) (Gering 1949; Becker et al. 2005; Pruitt and Riechert 2009b). In *A. studiosus*, smaller and more passive males experience superior survivorship and reproductive success with aggressive females. Although the mechanism behind small males' survivorship is unresolved, we propose they employ a kind of sneaker strategy and either (1) approach females in a less threatening manner (i.e., owing to their small body mass) or (2) approach females without ever being detected. Alternatively, aggressive females might merely prefer the courtship tactics of small docile males. In any case, the expression of sexual cannibalism in *A. studiosus* appears to be more labile than previously proposed (Pruitt and Riechert 2009b), and thus, it does not appear to be an invariant element within a broader syndrome (i.e., it is not merely a "spillover"; Johnson and Sih 2005, 2007).

Variable susceptibility to sexual cannibalism appears to drive the differences in male reproductive success with aggressive females. Even though we lack observational data for the full 72-h encounter duration, we believe male

Table 4 The sample size and percent mortality for each trial type

Trial type	Number	Percent mortality	
		20 min	72 h
One aggressive female	64	26.56	34.38
One docile female	37	5.40	10.80
Four aggressive females	40	22.50	53.50
Four docile females	36	8.33	16.66
Two docile and two aggressive females	38	15.78	39.47

The distribution of male mortality deviates significantly from a null expectation of equal probability (20 min: $\chi^2_4 = 9.72$, $P=0.045$; 72 h: $\chi^2_4 = 20.1$, $P<0.001$). Significance is driven by low probability of death in trials with docile females and high incidence of mortality in trials with aggressive females. Mortality observed in the first 20 min was always the result of sexual cannibalism

mortality is most frequently the result of sexual cannibalism (i.e., because deaths are only common in trials with *aggressive* females; Table 4). Concordantly, the traits associated with male survival over our 20-min observational period (i.e., where cannibalism was *actually* observed) were also associated with male survival for the full 72-h encounter duration (Table 5). Perhaps intuitively, male survival was positively associated with greater reproductive success in all encounters with aggressive females; thus, traits which increase males' survival probability (i.e., docile BT, small body mass) also appear to increase males' reproductive success (Tables 3 and 5). Other mechanisms that might diminish the reproductive success of aggressive males with aggressive females include: (1) aggressive females might be exerting some downstream regulatory mechanism that biases male reproductive success (e.g., rejecting aggressive males' sperm); (2) the trend could be the result of genetic incompatibility with like BT; (3) aggressive males could literally be courting themselves to death. The first hypothesis is unlikely, given that molecular assessments of paternity in multiply mated females revealed that 100% of offspring sampled were sired by the first male to mate (Jones and Parker 2008). Thus, it seems unlikely that females manipulate sperm utilization in this system. The second hypothesis is weakened by results obtained from a breeding study with *A. studiosus*; in that study, experimental crosses between aggressive males and aggressive females consistently resulted in the production of viable offspring (Pruitt and Riechert 2009a). Finally, the third hypothesis is at odds with the finding that males almost universally prefer to court docile females (Pruitt and Riechert 2009b), and in the present study, relatively few males were found dead after attempting to court these preferred females.

Our data also indicate that disassortative mating might aid in maintaining the social behavior polymorphism of *A. studiosus*. In situations involving docile females, the majority of males which attempt courtship succeed in siring viable egg cases. Thus, the major selective forces in these circumstances are during intrasexual selection, and these favor large aggressive males (i.e., docile females×aggressive males). In contrast, in situations involving aggressive females, all males

Table 5 Summary of multiple logistic regressions predicting male survival over our 20-min observational period and the 72-h mating encounter

	20 min			72 h		
	r^2	χ^2	P	r^2	χ^2	P
One aggressive female						
Combined model	0.28	22.96	<0.0001*	0.36	26.92	<0.0001*
Male body mass		12.85	0.0003*		4.32	0.02*
Latency of approach		0.03	0.86		0.01	0.95
Male aggressiveness score		9.28	0.002*		10.71	0.001*
One docile female						
Combined model	0.11	2.84	0.41	0.09	1.38	0.71
Male body mass		0.20	0.65		0.05	0.82
Latency of approach		0.89	0.35		1.09	0.29
Male aggressiveness score		1.23	0.27		0.78	0.38
Four aggressive females						
Combined model	0.18	9.88	0.019*	0.54	21.87	<0.0001*
Male body mass		6.21	0.012*		9.87	0.002*
Latency of approach		0.03	0.87		0.08	0.77
Male aggressiveness score		6.88	0.01*		10.59	0.001*
Four docile females						
Combined model	0.04	1.38	0.71	0.02	0.29	0.96
Male body mass		0.01	0.99		0.11	0.74
Latency of approach		0.12	0.72		0.22	0.63
Male aggressiveness score		1.06	0.31		0.03	0.86
Two docile and two aggressive females						
Combined model	0.17	8.60	0.035*	0.21	33.15	<0.0001*
Male body mass		4.28	0.039*		17.61	<0.0001*
Latency of approach		1.07	0.30		2.77	0.09
Male aggressiveness score		2.33	0.10		25.08	<0.0001*

Mortalities during the first 20 min are known to be the result of attacks by females

*Significant term at $\alpha=0.05$

suffer higher mortality, but these scenarios favor small passive males (i.e., aggressive females with docile males). Also, in previous work, we demonstrated that aggressiveness runs in families, and there is an association between the aggressiveness of males and females (Pruitt and Riechert 2009a). Taken together, the combinations of docile females with aggressive males and aggressive females with docile males could promote the maintenance of mixed-phenotype broods. Results similar to our own were observed from a study on Great Tits (*Parus major*), where females in social pairings with males of like BT were more likely to procure extrapair copulations (van Oers et al. 2008). van Oers et al. (2008) suggest that there could be fitness advantages to mating with unlike BT (e.g., heterozygote advantage). Similarly, it could be argued that mixed-phenotype broods might serve as sort of diversifying bet-hedging strategy in *A. studiosus*.

Synthesis and future directions

Identifying the mechanisms maintaining diversity is one of the central goals of ecology and evolutionary biology, and arguably, one of the most important modern advancements towards this goal is the acknowledgement that different aspects of diversity interact and diversity of one type can promote diversity in others (Crutsinger et al. 2006; Johnson et al. 2006; Johnson and Stinchcombe 2007). Individual differences in behavioral tendencies (aka temperament, personality, behavioral syndromes, BT) have been documented in a variety of taxa and in countless aspects of behavior (sensu Sih et al. 2004; Bell 2007); and yet, only rarely have the factors maintaining this variation been identified. One viable and potentially broadly applicable hypothesis is that behavioral variation is self-promoting, and variation in one aspect of behavior could facilitate variation in others. Our data here from *A. studiosus* are consistent with this facilitative hypothesis, whereby through the interaction of social and sexual selection, variation in one trait type (i.e., female aggressiveness) appears to promote variation in others (i.e., male aggressiveness and body mass). While intuitively appealing, the general importance of such positive feedback loops among behavioral traits awaits further data from this and other animal systems.

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