

Terminal Investment Strategies and Male Mate choice: Extreme Tests of Bateman¹

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SYNOPSIS. Bateman's principle predicts the intensity of sexual selection depends on rates of increase of fecundity with mating success for each sex (Bateman slopes). The sex with the steeper increase (usually males) is under more intense sexual selection and is expected to compete for access to the sex under less intense sexual selection (usually females). Under Bateman and modern refinements of his ideas, differences in parental investment are key to defining Bateman slopes and thus sex roles. Other theories predict sex differences in mating investment, or any expenditures that reduce male potential reproductive rate, can also control sex roles. We focus on sexual behaviour in systems where males have low paternal investment but frequently mate only once in their lifetimes, after which they are often killed by the female. Mating effort (=terminal investment) is high for these males, and many forms of investment theory might predict sex role reversal. We find no qualitative evidence for sex role reversal in a sample of spiders that show this extreme male investment pattern. We also present new data for terminally-investing redback spiders (*Latrodectus hasselti*). Bateman slopes are relatively steep for male redbacks, and, as predicted by Bateman, there is little evidence for role reversal. Instead, males are competitive and show limited choosiness despite wide variation in female reproductive value. This study supports the proposal that high male mating investment coupled with low parental investment may predispose males to choosiness but will not lead to role reversal. We support the utility of using Bateman slopes to predict sex roles, even in systems with extreme male mating investment.

INTRODUCTION

A widely-used framework for predicting sex roles has been derived from the original insights of A. J. Bateman (1948). Bateman's ideas, as refined by Trivers (1972) and others (*e.g.*, Emlen and Oring, 1977; Low, 1978; Gwynne, 1984), propose that differences in parental investment (time and energy invested in current offspring at the expense of future offspring) lead directly to a skew in the ratio of sexually active males to sexually active females (operational sex ratio, Emlen and Oring, 1977). This skew predicts the direction of sexual selection. The increase in fecundity with each additional mating achieved predicts the strength of sexual selection (Bateman slopes or sexual selection gradients, Arnold and Duvall, 1994; Andersson and Iwasa, 1996). Mating strategies of each sex arise from the interaction of the direction and strength of sexual selection with ecological and social factors that affect the profitability or feasibility of different pathways to increasing fitness (Emlen and Oring, 1977; Shuster and Wade, 2003). The result in most systems is conventional sex roles (Andersson, 1994) in which males (typically the low-investing sex) compete for relatively scarce females (and their gametes) whereas females (the high-investing sex) discriminate among a diversity of available males.

This Bateman/Trivers framework of relative parental investment has been a powerful paradigm when applied to the study of conventional and non-conventional sex roles. Experimental and observational stud-

ies have demonstrated that shifts in the relative value of parental investment can shift the direction of sexual selection and lead to broad reversals in sexual behaviour in taxa as diverse as insects, amphibians, birds and fishes (*e.g.*, Gwynne and Simmons, 1990; Jones *et al.*, 2000, 2001, 2002; Emlen and Wrege, 2004). In sex-role-reversed systems, sexual selection on males is relaxed so males are generally choosy but not competitive, and sexual selection on females is strong so females are competitive rather than choosy. The extent or nature of sex role changes with shifts in parental investment can be affected by ecological variables, life history traits, and sex ratios within each system (*e.g.*, Emlen and Oring, 1977; Jones *et al.*, 2000; Shuster and Wade, 2003).

Other types of investment have been proposed to control sexual selection by affecting the potential reproductive rates of each sex (*e.g.*, Low, 1978; Gwynne, 1984; Clutton-Brock and Vincent, 1991; Clutton Brock and Parker, 1992; Kokko and Monaghan, 2001). In particular, time and energy costs or risks incurred by males in securing a given mating could decrease the relative number of males available for mating and thus shift the direction of sexual competition and favour sex role reversal (Clutton-Brock and Parker, 1992; Kokko and Monaghan, 2001). This type of mating effort, called "non-promiscuous" mating effort by Gwynne (1984), combines with Bateman/Trivers parental investment to comprise the total reproductive investment of an individual. If sex differences in total reproductive investment determine sexual selection, then sex role reversal might be predicted in systems where males have high non-promiscuous mating effort, even if paternal investment is low.

While potential reproductive rates may explain var-

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iation in the degree of role reversal in species with significant paternal investment (*e.g.*, Clutton Brock and Vincent, 1991), they may not predict role reversal per se in systems where females invest more in offspring. A recent review of male mate choice in invertebrates (Bonduriansky, 2001) suggests that non-promiscuous mating effort alone is unlikely to affect sex roles, but may instead pre-dispose males to choosiness within otherwise conventional sex roles. Bonduriansky (2001) concludes that "partial role reversal" (where males are choosy about the females over which they compete) is widespread in nature, but arises from a separate evolutionary pathway from complete sex role reversal (where males are choosy but not competitive and females are competitive, but not choosy).

There are few studies of the effect of variation in non-promiscuous mating effort in determining sex roles or mate choice, as it is often difficult to disentangle this form of effort from paternal investment. Here we focus on species of web-building spiders with males that show high levels of non-promiscuous mating effort but apparently low paternal investment to determine whether the Bateman/Trivers parental investment approach or the total reproductive investment approach better predicts observed sexual behaviour. Mating effort in these species is high because most males die or are killed by females after one mating ("terminal investment," *e.g.*, Elgar and Fahey, 1996; Schneider and Elgar, 2001; Elgar *et al.*, 2003a; Uhl and Vollrath, 1998; Forster, 1992; Andrade, 1996; Sasaki and Iwahashi, 1995; Foellmer and Fairbairn, 2003; Knoflach and Benjamin, 2003). The mechanism of male monogamy in these species is indisputably the most extreme form of non-promiscuous mating effort, but extreme sexual size dimorphism makes it unlikely that nutrients from the male's body significantly affects his offspring (Fromhage *et al.*, 2003; Andrade, 1998; Schneider and Elgar, 2002). Thus the Bateman/Trivers paradigm would predict that terminally investing males would have steeper Bateman slopes than females and so males would compete for females whereas females would discriminate among males. Since males get only one mating opportunity, they should be choosy about the females for which they will compete ("partial role reversal," Bonduriansky, 2001). In contrast, a total reproductive investment approach would suggest that the high non-promiscuous mating effort of males should lead to complete sex role reversal. Models that emphasize the importance of the relative cost of mating predict that high mortality risks of mating for males may strongly favour male choosiness and decrease the likelihood of inter-male competition, even if the sex ratio is male-biased (*e.g.*, Kokko and Monaghan, 2001). This would manifest as indiscriminate mating by females and discrimination by non-competitive males.

Although some species with terminal male investment are well studied, there is little information on sexual behaviour for others. Here we summarized available evidence for levels of male mating effort,

parental investment, male competition, and male mate choice in selected terminally investing spiders (Table 1) to highlight the need for additional study and explore whether current patterns support the Bateman/Trivers or total reproductive investment approaches.

We also tested predictions of these approaches in studies focussed on the Australian redback spider (*Latrodectus hasselti*), a species where "terminally investing" males facilitate cannibalism by their mates and are often killed during copulation (Forster, 1992; Andrade, 1996, 2003). We first estimated Bateman slopes for redback males and females and used them to predict the relative strength of sexual selection on males and females and thus the most likely sex roles under the Bateman/Trivers paradigm. Critically, positive Bateman slopes for terminally investing males are only possible if some reproductively capable males fail to mate or fail to father any offspring if they do mate (Arnold and Duvall, 1994; Bateman, 1948; Jones *et al.*, 2000), which is the case for redback spiders (Andrade, 1996, 2003; Snow and Andrade, 2005). Since it was not known whether redback males choose among females, we assessed male preferences as a function of the potential reproductive value of females in laboratory trials. We then determined actual levels of choosiness shown by males in the field (where costs of choice can determine thresholds for accepting mates of a given reproductive value, Jennions and Petrie, 1997). We interpret our new data in light of observed patterns of sexual behaviour in terminally-investing species (Table 1) to draw conclusions about the effects of non-promiscuous mating effort on partial and complete role reversal.

METHODS

We tabulated information from the literature for 14 spider species in 5 genera. This was not intended to be a comprehensive survey, but concentrated on the few terminally investing species for which relevant information is available. For each, we noted the following: (1) Probability males mate only once. This determines the average level of non-promiscuous mating effort and was estimated in different ways depending on the information available for each species (see Table 1 footnotes). (2) Paternal investment (whether males provide paternal resources or care that affects offspring number or fitness). (3) Male competition. (occurrence and severity of direct aggression between males over females) (4) Occurrence and traits favoured by male mate choice.

Redback spiders: natural history

Males abandon their webs at sexual maturity to seek potential mates. Mortality rate is high during mate searching (~86%, Andrade, 2003) but sex ratios are male-biased throughout the season (median number of rival males per adult female web = 2, range 0 to 6 [Andrade, 1996]). Male redbacks are short-lived relative to females (Andrade, 2003), so although they could usually survive long enough to mate with any

TABLE 1. Overview of evidence for male competition and choice in selected spiders with high mating investment but low paternal investment.

Species	Probability male mates only once*	Paternal investment	Male competition	Male choice [preferred females]	Sources
<i>Argiope aemula</i>	0.67 – 0.98 ^a	Unlikely (male mass \ll female)	?	?	Sasaki and Iwahashi, 1995; Robinson and Robinson, 1980
<i>A. aurantia</i>	0.90 – 1.0 ^a	Unlikely (male mass \ll female)	Injurious fighting	?	Foellmer and Fairbairn, 2003, 2004, 2005; Robinson and Robinson, 1980
<i>A. bruennichi</i>	.70 – .80 ^a	none	?	?	Fromhage <i>et al.</i> , 2003
<i>A. keyserlingi</i>	~.50 ^a (virgin males) 100 ^a (non-virgin males)	none	Yes	Virgin males: Yes [virgin females, small females] Non-virgin males: No	Elgar <i>et al.</i> , 2000; Herberstein <i>et al.</i> , 2002; Gaskett <i>et al.</i> , 2004
<i>Echinotheridion gibberosum</i>	1.0 ^a	Unlikely (male mass \ll female)	?	?	Knoflach, 2002
<i>Latrodectus hasselti</i>	.86 ^a	none	Fatal fighting	Yes [virgin or penultimate females]	Andrade, 1998, 2003; Kasumovic (personal observation)
<i>L. pallidus</i>	.85 ^a	?	Fatal fighting	?	Segoli, M (personal communication)
<i>L. revivensis</i>	.96 ^b	?	Multiple cohabiting males	Unclear: Yes [virgin females] No [found with mated and virgin females]	Anava and Lubin, 1993; Segev <i>et al.</i> , 2003
<i>Nephila clavipes</i>	1.0 ^c	Unlikely (male mass \ll female)	Injurious fighting	?	Christenson and Goist, 1979; Christenson, 1989; Uhl and Vollrath, 1998; Robinson and Robinson, 1980; Vollrath, 1980
<i>N. edulis</i>	.28 – .32 ^a	?	Injurious fighting	Yes, increased copulation with virgin females	Elgar <i>et al.</i> , 2003; Uhl and Vollrath, 1998; Robinson and Robinson, 1980
<i>N. plumipes</i>	.60 ^a	Unlikely (males < 5% female mass)	Intense fighting	None (lab)	Elgar and Fahey, 1996; Schneider and Elgar, 2001; Elgar <i>et al.</i> , 2003
<i>Tidarren cuneolatum</i> , <i>T. sisypoides</i> , <i>T. argo</i>	1.0 ^a	Unlikely (male mass \ll female)	?	?	Knoflach and van Harten, 2000, 2001; Knoflach and Benjamin, 2003

^a Mortality rates during mating or mate searching.

^b Frequency with which males are found on only one web in nature.

^c Frequency of sperm depletion after mating.

* For males that mate once, this is the probability of dying during or after the first mating or during the search for additional mates.

newly-matured females that are first encountered as penultimate (7th) instars, they would not survive long enough to mate with females first encountered as earlier-stage juveniles.

Females have paired, independent sperm storage organs that are inseminated by the male's paired intromittent organs (palps) during two separate copulations, so females can be 2-sided virgins, 1-sided virgins, or 2-sided non-virgins (Andrade, 1998; Snow and Andrade, 2005). During copulation, redback males twist their abdomens above the female's fangs (Forster, 1992; Andrade, 1996). Females begin to cannibalize males during the first copulation, but males usually survive and achieve a second copulation following a second period of courtship (Andrade, 1998). During the second mating, 65% of males are killed by their mates (Andrade,

1996, 1998). Males deposit a portion of each copulatory organ (an apical sclerite) in each of the female's reproductive tracts at copulation, resulting in a median paternity of about 90% for the first male to mate (Snow and Andrade, 2005; Snow, 2003). Dissections of females collected in the field suggests about 17.9% remain unmated (5/28 with no sclerites), most females likely mate once or twice (7/28 with 1 sclerite and 19/28 with 2 sclerites found), and 14.3% copulate with at least two and possibly 3 males (4/28 with 3 sclerites found, Andrade, 1995, 1996).

Bateman slopes. Bateman slopes were calculated as least-squares regressions of offspring number on number of mates (Arnold and Duvall, 1994). Although the relationship between fecundity and mate number may

be non-linear (particularly for females), the linear regression (Bateman slope) is the best estimate of the sexual selection gradient (Lande and Arnold, 1983; Arnold and Duvall, 1994).

Laboratory-reared redback females were mated to 1, 2 or 3 virgin males ($n = 33$ each), and were allowed a single copulation with each (mating trial and rearing details in Andrade and Banta, 2002). Females were isolated after their final mating until their natural death and all egg sacs were collected. Spiderlings were euthanized and counted immediately after hatching.

Males were mated to 1 or 2 virgin females ($n = 33$ each, mating trial details in Andrade and Banta, 2002), with each female receiving a single palpal insertion. We included the "2 mates" class as a small percent of males survive and may reach the web of a second potential mate in nature (Andrade, 2000). Males were allowed only one palpal insertion with each mate as males are functionally sterile after each palp is used once, but sufficient sperm is transferred in a single copulation to fertilize all of the female's eggs (Andrade and Banta, 2002). Lifetime reproductive output of each male's mates was counted (as above for females) and summed for each male.

Bateman slopes depend on how mating affects fecundity and the relative size of each mating class in nature (Arnold and Duvall, 1994). The relative size of the "zero matings" class can have a strong affect on the estimate of the sexual selection gradient, particularly for non-linear relationships (Arnold and Duvall, 1994). It is critical that the "zero" class be included however, as the relative frequency of mating and non-mating individuals is an important reflection of variance in reproductive success and the expected strength of sexual selection (Arnold and Duvall, 1994; Shuster and Wade, 2003). Thus, although we report regressions based on our lab-based sample of 33 individuals in each mating class, we also adjusted the sample size of the zero matings group to match the proportion of individuals likely to remain unmated in nature and recalculated the regression. We estimated 14% of males mate in nature (maximum estimate of mate-searching survival from Andrade, 2003) so recalculated slopes assuming the sample of mated males ($n = 66$) was 14% of the total sample of males (*i.e.*, 405 males with zero matings, $n = 471$ males across all classes). We estimated that 82.9% of females mate in nature (Andrade, 1995), so recalculated the Bateman slope assuming mated females ($n = 99$, total) were 82.9% of the total sample (*i.e.*, 20 females with zero matings, $n = 119$ females across all classes). We also recalculated slopes after weighting each mating class by estimates of the frequency of remating for each sex in the field (data from Andrade, [2000]; analysis not shown). Slopes did not differ from the analysis weighting only the zero class, so we report only the latter for simplicity.

Determining male preferences. Theory predicts that levels of mate choice in nature depend on (1) variation in the quality of potential mates, which defines pref-

erence functions (rank-order of preference of potential mates based on their reproductive value, [Jennions and Petrie, 1997; Parker, 1983]) and (2) constraints on and costs of choice in nature, which will determine the likelihood of forgoing one potential mate in order to seek a mate of a higher rank-order (Jennions and Petrie, 1997; Parker, 1983). We measured male preferences in the laboratory, and examined how and when males are choosy in the field.

We considered female size, weight, condition and mating status as candidate traits for male preferences in redback spiders. While female size, weight or condition are correlated with reproductive output in redbacks and other spiders (*e.g.*, Uhl *et al.*, 2004; Andrade, 1995), preliminary analyses showed no effect of these variables on the attraction of male redbacks to female's webs in the field (M.M.K., unpublished data), or the likelihood of males courting the females (M.C.B.A., unpublished data). In comparison, due to first male precedence within each reproductive tract, female mating status is likely to have a strong effect on female reproductive value (Snow and Andrade, 2005).

We used a two-choice paradigm to determine whether males showed a preference for the webs of 2-sided virgins *versus* 1-sided or 2-sided non-virgin females. Our procedure did not include direct contact with females. Males of some spider species (including other *Latrodectus*) are attracted to and able to detect female developmental stage or reproductive status using airborne pheromones (Anava and Lubin, 1993; Gaskett *et al.*, 2004; Kasumovic and Andrade, 2004), or contact pheromones released from webs (Riechert and Singer, 1995; Searcy *et al.*, 1999; Papke *et al.*, 2001).

In choice trials, male were placed at the base (initial arm) of a horizontal, T-shaped wire frame supported on plastic blocks above a water bath. Stimulus webbing (or cotton fibres in controls) was wrapped from halfway up the initial arm of the T-frame onto one of the two terminal arms. Both stimulus webs were wrapped together in a spiral pattern on the initial arm and then each was wrapped separately on one terminal arm. Thus males sampled both stimuli initially, but, in moving onto one terminal arm, followed only one stimulus trail. Stimulus webs and cotton were handled with clean latex gloves and forceps and care was taken not to touch opposing stimuli except in the initial area of overlap. Between trials, all arena components, forceps, and latex gloves were washed with soap and hot water then ethanol, and air-dried.

We released virgin males on a plastic block initially separated from the T-frame. Males settled for 3 min, then we slid the block until it contacted the initial arm of the T-frame. Trials lasted for 5 min and began when the male exited the block onto the initial arm of the arena. If the male did not exit the block, he was removed and tried again on the subsequent day. After two failed trials, the male was discarded and not used in the experiment. All trials were video-taped for later analysis by an observer blind to treatment.

Each male was randomly assigned to one of the following choice situations: (1) 2-sided virgin *versus* 1-sided virgin ($n = 13$), (2) 2-sided virgin *versus* 2-sided non-virgin ($n = 14$), or (3) 2-sided virgin *versus* medical-grade cotton (control, $n = 14$). Each stimulus web was produced by a different female of appropriate mating history on a clean wooden frame over a 48 hr period prior to the choice trial. Females producing the stimulus web for each paired-web presentation were matched for age and weight (within 5%).

As indices of male preference, we recorded the terminal arm of first contact (male movement onto distal 1/3 of one terminal arm) and total time spent on each terminal arm in the 5 minutes following male movement onto the "T." We analyzed first contact data using Pearson χ^2 tests to determine whether the arm of first contact depended on the mating status of the female producing the stimulus web. Wilcoxon matched pairs tests were used to determine whether the difference in the total time spent on each terminal arm depended on the mating status of the females producing each stimulus web.

Measuring choosiness. We asked whether males express preferences (Jennions and Petrie, 1997) for females of different mating status in field trials conducted in Perth, Western Australia (see Andrade, 2003 for field site information) and Sydney, New South Wales (outdoor grounds of the Macquarie University Campus). Optimality modeling predicts that male choosiness should be expressed as differential arrival on the webs of more valuable females, but, due to high mate search costs, males should not abandon webs of adult females after arrival (M.C.B.A., unpublished data). We examined male choosiness in the field during initial mate search by measuring male attraction to experimentally-placed webs (Sydney site), and after arrival on a female's web by measuring male abandonment of webs (Perth site).

A. Choosiness during mate searching

We examined the relative attraction of males to webs produced by juvenile females (<7th instar, non-reproductive control), 2-sided virgin or non-virgin adult females in a randomized block design. Females used to build stimulus webs were collected in and around Sydney, then all were housed and fed in a laboratory at Macquarie University for one month to determine mating status. Well-fed mated females typically produce egg sacs within one month of mating (M.C.B.A., unpublished data) and juvenile females (<7th) are distinguishable from adults by genital development (Andrade, 2003).

We prepared stimulus webs by placing redback females in $6 \times 6 \times 6$ screen cages for 11 days. We removed females from cages, then placed cages at 22 locations at our field site (blocks). Each block had four cages: one web from each type of female and one empty cage as a non-web control. In each block, stimulus cages were placed 1 m from a central point at roughly 90° separation from other cages. We checked cages at

0800 hr each morning for three days, collecting any males found on the cages. After three days, cages were returned to the laboratory, females were replaced in their cages and allowed 4 days to refresh the webs. We then repeated the experiment over a second 3 day period.

B. Choosiness after reaching a female

We tested whether males leave some females' webs to seek an alternative potential mate, and whether the likelihood of this behaviour depends on female reproductive value. First in a female present experiment we assessed male tenure on naturally-made webs of females from one of four different categories: juveniles (<5th instar, non-reproductive control), penultimate instar, 2-sided virgin adult, and non-virgin adult. Males may disappear from these webs because they have left to search for other females, because they have mated and been cannibalized, or because they have been aggressively ejected by females (*e.g.*, Andrade, 1996). Thus, in the female absent experiment, we measured male tenure on a second set of webs from which we had removed females just prior to the start of trials, eliminating any potentially confounding effect of interaction with females. Both of these conditions are biologically relevant as (1) Males frequently cohabit with females prior to mating (M.C.B.A., personal observation) and (2) *Latrodectus* males are sometimes attracted to (Kasumovic and Andrade, 2004), and remain for days on recently-abandoned webs of females (M.C.B.A., personal observation). While this behaviour is likely the occasional maladaptive result of a behavioural "rule of thumb," we assume male tenure on webs reflects the likelihood of forgoing one type of female to seek others (choosiness).

We located 10–15 webs in each category for each of the two experiments at the Perth site. Virgin males (determined by palp inspection; Andrade, 1998) were captured from other sites in and around Perth, WA, marked with non-toxic paint (Andrade, 2003), and each was randomly assigned to a treatment within one of the two experiments. Males were placed on webs by allowing them to drop from a drag line onto the periphery of the web. We ensured males had settled, then examined webs twice each night (surveys starting at 2200 hr and 2400 hr) for 20 days and recorded the male's date of disappearance. In the female present experiment, males might disappear if they left the web or if they mated and were cannibalized, but male disappearance in the female absent experiment could only represent male abandonment of the female web. We used survival analysis (Steinberg *et al.*, 2002) to determine whether male tenure on webs varied as a function of female age/mating status within each experiment (Tarone-Ware log-rank test, Systat version 10.2).

RESULTS

In each of the species examined (Table 1) there is a high probability that males will mate only once ("terminal investment"). There is no evidence for paternal

investment in these species despite the potential transfer of nutrients to cannibalistic females. This is either inferred from extreme size dimorphism (*e.g.*, Fromage *et al.*, 2003) or concluded from field or laboratory studies of mate consumption (*e.g.*, Schneider and Elgar, 2002). Male competition has been reported in 8 of the 15 species and escalates to injurious or fatal fighting in 5 of these. Finally, there is evidence that males prefer virgin females in 4 of the 5 species where male mate choice has been studied.

1. Measuring Bateman slopes

Males gain significantly more offspring per mating ($2,111.0 \pm 146.5$ spiderlings) than do females (612.2 ± 94.3 spiderlings; Fig. 1; General Linear Model, interaction between #mates and sex, $F_{3,224} = 13.47, P < 0.001$). For females, this increase was driven by the difference between failing to mate (the “0” mating class) and mating once (Fig 1A), whereas for males, output increased linearly with each copulation (Fig. 1B). The difference between Bateman slopes for males and females increased when we used our best estimates of the number of individuals that do not mate in nature (Fig. 1A) rather than equal sample sizes across mating categories. Our data suggest the sexual selection gradient is approximately 5.5 times greater for males than females in redback spiders.

2. Male preferences

Analyses of male preference based on terminal arm of first contact or total time per terminal arm in our choice arena yielded similar results. Males distinguished webbing from cotton (Table 2) and discriminated against non-virgins relative to virgins. Males were given the opportunity to choose between virgins and non-virgins (1-sided or 2-sided) in 27 trials, in only 8 of these did males choose the non-virgin ($\chi^2_1 = 4.48, P = 0.034$), and males spent more time on terminal arms with webbing from virgin compared to non-virgin females (Wilcoxon $Z = -4.68, P < 0.001$). This difference was mainly due to discrimination against 2-sided non-virgin females (Table 2).

3. Male choosiness.

A. *During mate searching.* Twenty-three males were attracted to experimental cages over the two replicates (six days). No males were found on control cages, so these were removed from our analysis. Males were differentially attracted to webs of virgin females compared to webs of juveniles or non-virgin females ($\chi^2 = 13.94; df = 21, P = 0.0009$, Table 3).

B. *After reaching a web. Female present.* Males disappeared from webs of juveniles quickly, but remained on webs of adult and penultimate instar females for longer (Fig. 2A, All groups: Tarone-Ware Log-rank test: $\chi^2_3 = 54.13, P < 0.001$). Male tenure with non-virgin females was shorter than with virgin or penultimate instar females (Tarone-Ware Log-rank tests: excluding juveniles: $\chi^2_2 = 11.35, P = 0.003$; excluding juveniles and mated females: $\chi^2_1 = 1.54, P = 0.214$).

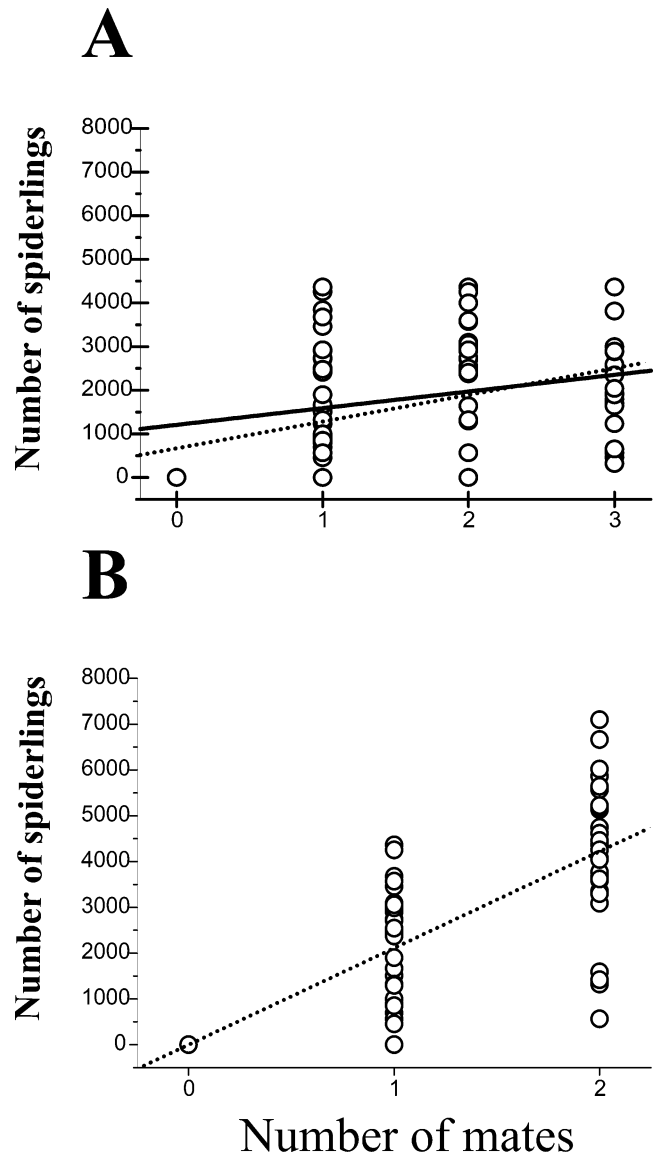


FIG. 1. Bateman slopes for female (A) and male (B) redback spiders calculated as least-squares regressions of lifetime number of spiderlings produced *versus* number of mates (=single copulations with different partners). Dotted lines are based on laboratory matings with 33 spiders in each mating treatment. For females, #spiderlings = $612.2 (\#mates) + 669.9 (P < 0.001, T = 6.49, R^2 = 0.25)$. For males, #spiderlings = $2111.0 (\#mates) + 0.005 (P < 0.001, T = 14.40, R^2 = 0.68)$. Solid line in (A) was calculated after data were adjusted to reflect estimated proportion of females that do not mate in nature ('0 mates' category). After adjustment, for females, #spiderlings = $381.6 (\#mates) + 1208.1 (P = 0.002, T = 3.15, R^2 = 0.084)$. For males, the line does not change with adjustment of '0' class.

Female absent. When no interaction with females was possible, males abandoned webs more quickly than when females were present. Males remained on webs of penultimate instar or adult females for many days (Fig. 2B), whereas webs of juveniles were rapidly abandoned (Tarone-Ware Log-rank test, $\chi^2_3 = 47.26, P < 0.001$). In contrast to when females were present, there was no difference in male tenure on the empty

TABLE 2. Two measures of male preference for webs built by virgin compared to mated females and a control in two-choice laboratory trials.

Virgin versus:	n	% choosing web of virgin ^a	χ^2 (<i>P</i>)	Median time difference ^b (range)	Wilcoxon Z (<i>P</i>)
Control	14	93	10.3 (0.001)	89.00 (202)	-3.30 (0.001)
1-sided virgin	13	62	0.69 (0.41)	21.50 (345)	-1.73 (0.084)
2-sided non-virgin	14	79	4.57 (0.03)	16.00 (257)	-2.826 (0.005)

^a % of trials where male made first contact with the terminal arm holding webbing produced by a virgin female rather than the specified alternative stimulus.

^b Total time (sec) spent on terminal arm with virgin web—time on other stimulus arm (5 min observation period).

webs of mated adult, virgin or penultimate instar females (Tarone-Ware Log-rank test, $\chi^2_2 = 0.969$, $P = 0.616$, Fig. 2B).

DISCUSSION

Despite the high frequency of terminal investment for species listed in Table 1, we found no evidence for sex role reversal. Although male mate choice occurs in some of these species, this was typically focused on female mating status, which will not impose sexual selection on females (Bonduriansky, 2001). In contrast, male competition was found in all the species in which it was examined, and escalation to injurious or fatal fighting was noted in several, suggesting intense sexual selection on males. These results are in contrast to theory that focuses on total reproductive investment by males, which predicts high levels of mating effort could shift the direction of sexual selection directly (*e.g.*, Kokko and Monaghan, 2001), or by constraining male reproductive rates (*e.g.*, Clutton-Brock and Parker, 1992). However, data from terminally investing species is in qualitative agreement with predictions from the Bateman/Trivers relative parental investment model (Bateman, 1948; Trivers, 1972), since it appears that paternal investment is low or nonexistent in all these species (*e.g.*, Fromhage *et al.*, 2003; Table 1), so complete role reversal is not expected. This analysis is necessarily qualitative since there is relatively little data available for many of these species (Table 1).

A more detailed analysis in redback spiders provides additional support for this conclusion. Terminal investment in redbacks effectively reduces male potential reproductive rate to one mating in the male's lifetime (Forster, 1992; Andrade, 1996; 2003). Despite this extreme non-promiscuous mating effort, there is evidence for female choice among rival males (Andrade, 1996; 1998; Snow and Andrade, 2005). Moreover, males engage in lethal fighting on arrival at female

webs (Table 1, M.M.K., personal observation)—a hallmark of conventional sex roles in systems where sexual selection on males strongly shapes male traits. Despite evidence of male preference for and choice of virgin females (Table 2, Table 3), the coupling of male mate choice with intense inter-male competition and female-imposed sexual selection suggests this is “partial” rather than “complete” role reversal (Bonduriansky, 2001). This is reinforced by our finding that male preference is focused on female mating status, and this preference is expressed only during initial mate searching (Fig 2). As appears to be the case for other species listed in Table 1, there is little opportunity for male-imposed sexual selection to affect females. This key result is predicted by our measurement of Bateman slopes for redbacks, which are steeper for males than females, although the apparent existence of some females that do not mate makes female Bateman slopes non-zero (Fig. 1). Selection imposed by the risk of not mating likely explains the production of attractive sex pheromones by receptive females. We conclude that non-promiscuous mating effort alone, even of the extreme form found in these species, does not necessarily cause sex role reversal.

Our results support the idea that high non-promiscuous mating effort predisposes males to choosiness. A high cost of mating imposes a constraint on male mating frequency, which increases selection for maximizing the reproductive payoff from each mating (Bonduriansky, 2001; Parker, 1983). Male preferences depend on the relative reproductive value of females, but choice in nature is shaped by factors that can reduce the expected reproductive payoff of attempting to find and mate with a given female (Parker, 1983; Jennions and Petrie, 1997). In redbacks and many other invertebrates, virgin females are reproductively valuable, but non-virgins are much less so (Bonduriansky, 2001). For redbacks, many males that mate with non-virgin females will gain no paternity (Snow and Andrade, 2005). As predicted, our data show males are able to make fine-grained discrimination of female reproductive status in the laboratory (Table 2), and males preferentially seek out virgin females during mate searching (Table 3). The latter is interesting as it might be predicted that a high risk of mortality during mate searching (Andrade, 2003) would reduce the likelihood that males would express choice at this stage (*e.g.*, Fromhage *et al.*, 2005). It seems that redback

TABLE 3. Number (percent) of males attracted to webs produced by females of different age and mating status in a randomized block experiment in the field.

	Female age/mating status			
	Juvenile	Virgin	Non-virgin	Control
Trial 1	1 (12.5)	7 (87.5)	0 (0)	0
Trial 2	0 (0)	13 (86.7)	2 (13.3)	0
Total	1 (4.3)	20 (87.0)	2 (8.7)	0

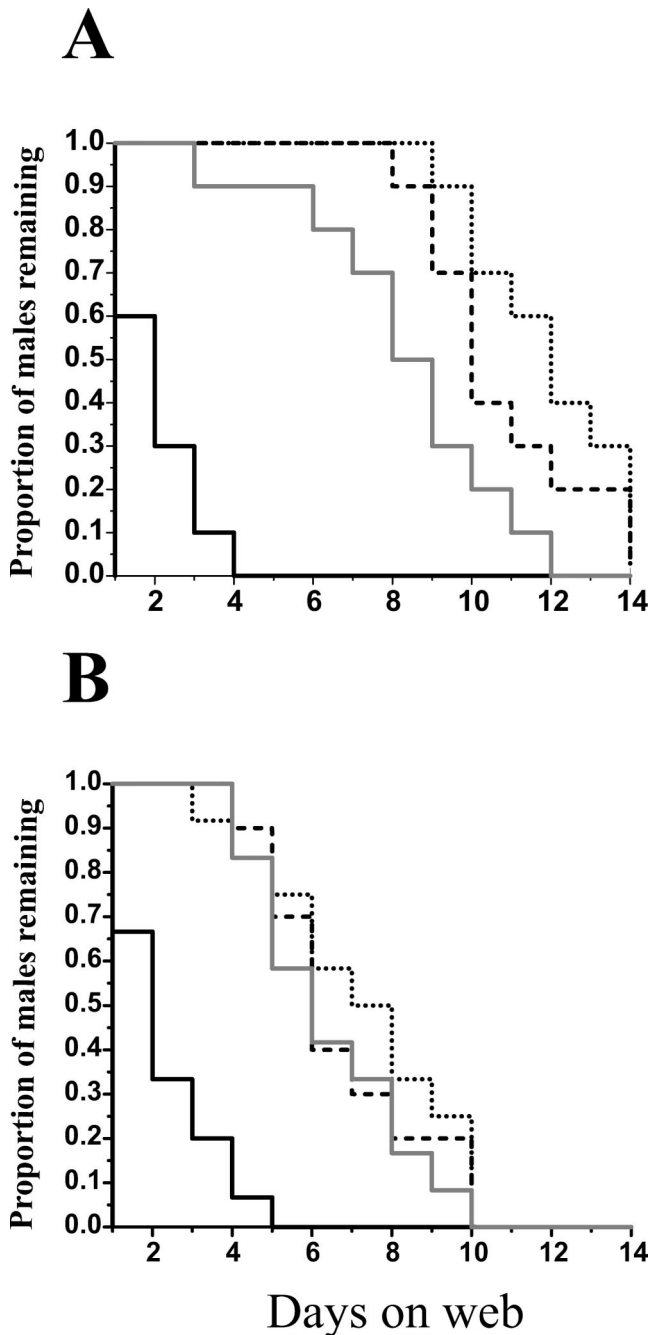


FIG. 2. Kaplan-Meier survival function for the proportion of males with a given tenure (days) on webs of females in four age/mating status categories in the field. Males were placed on webs with resident females (A) that were juveniles (n = 10, solid black), penultimate instar (n = 10, dashed black), virgin adults (n = 10, dotted black) or non-virgin adults (n = 10, solid gray). (B) In a second experiment, males were placed on webs from which juvenile (n = 15), penultimate (n = 10), virgin adult (n = 12) or non-virgin females (n = 12) had just been removed (line coding as in A).

males are able to detect valuable females at a distance (likely using airborne pheromones, e.g., Kasumovic and Andrade, 2004), and this ability may be common for terminally-investing male web-building spiders (e.g., Gaskett *et al.*, 2004). However, male choice ap-

parently manifests only during searching, as once males reach webs, they do not discriminate mated from virgin females (Fig. 1B). This may be because the expected value of a non-virgin female (even incorporating the high likelihood of first male precedence) is greater than the expected value of other potential mates (given the high mortality rates during mate-searching; M.C.B.A., unpublished data). Generally, for species in which terminal investment may arise as a male mating strategy (e.g., Andrade, 1996, 2003; Fromhage *et al.*, 2005), levels of male choosiness in nature may be similarly constrained. In contrast, in species where terminal investment arises out of conflict with voracious females, even though non-promiscuous mating effort is similarly high, males may exercise choice over a wider range of conditions. Further studies of fitness effects of terminal investment and male mate choice in *Argiope keyserlingi* might be particularly useful for understanding links between mating effort, male strategies and male mate choice. Recent data suggest *A. keyserlingi* males are choosy on their first mating (after which males attempt to escape female cannibalistic attacks), but not choosy on their second mating (when males succumb to females with little or no resistance, Gaskett *et al.*, 2004).

In other contexts, it may not be necessary to distinguish between cases where high levels of non-promiscuous mating effort increase male fitness (and thus may be considered a male mating strategy) and those where high mating costs are imposed by females with little fitness benefit for males. For the species surveyed in table 1, we included as ‘terminal investment’ a variety of processes that lead to or suggest male monogamy. These included frequency of mortality during mate searching (e.g., *Latrodectus hasselti*), frequency of cannibalism arising from conflict with females (e.g., *Nephila* species), and mechanistic indicators of monogamy (e.g., sperm exhaustion and sterility in *Nephila clavipes*). These processes all suggest a high cost of mating and significant constraint on potential reproductive rates of males. The frequency with which these result in male monogamy determines the expectation of multiple mating for males which should in turn affect the evolution of the mating strategies in that species. Thus, for our assessment of the effect of male mating effort, they were taken to be functionally equivalent.

Considering these as functionally equivalent in this critical way may be instructive for future studies. First, a focus on “terminally investing” species may be useful for comparative tests of the variety of other concepts that have been proposed for predicting the strength and effect of sexual selection (see Jones *et al.*, 2000). One of the key differences among current models for the control of sexual selection is the value of the operational sex ratio (OSR; Emlen and Oring, 1977). Although originally proposed to control sexual selection by determining which sex was in excess (Emlen and Oring, 1977), the OSR has been challenged as being difficult to measure and an unreliable

predictor of sexual selection (*e.g.*, Andersson, 1994; Andersson and Iwasa, 1996). Suggested replacements include the potential reproductive rates of males and females (Clutton-Brock and Vincent, 1991), variance in reproductive success (Wade and Arnold, 1980), and variants of the OSR that focus on only those individuals that mate at least once (*e.g.*, breeding sex ratio; Arnold and Duvall, 1994). Web-building spiders are perhaps unusual in the relative ease with which many of these quantities could be estimated in nature. Female's webs can be intensively observed, males can generally be found as juveniles before initiating mate searching, and only those males who arrive at a female's web have the opportunity to mate. Since males generally appear to detect females at a distance and may cluster on webs of valuable females (*e.g.*, Gaskett *et al.*, 2004; Kasumovic and Andrade, 2004; Robinson and Robinson, 1980; Andrade, 1996), the operational sex ratio may show spatial or temporal variation within species (*e.g.*, Foellmer and Fairbairn, 2005), and may be different from the breeding sex ratio, particularly if some females never mate, and those that do mate copulate with only one or two males (*e.g.*, Fromhage *et al.*, 2005). These features may provide some power to unravel the relative value of different models for assessing the strength of sexual selection.

Terminal investment system may also be useful because, regardless of the origins of this pattern of investment, males of these species have available a similar, limited range of mating strategies for maximizing fitness. These strategies are likely to be largely focused on ensuring success in a single (or relatively few) matings. Thus conjecture about trade-offs of current *versus* future reproductive effort are not necessary, facilitating precise predictions and empirical tests of the influence of ecology and demography on male mating strategies.

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