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# Limb loss and limb regeneration of crab spiders *Misumena vatia*

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**Abstract.** Limb loss presents an interesting paradox: although it may permit escape from a potentially lethal situation, it may result in subsequent fitness-lowering consequences. Some studies have found costs of limb loss; others have not. If costs are high, they may dictate against retaining the ability to drop an appendage. I use a large data set derived from a long-term study of the crab spider *Misumena vatia* (Clerck, 1757) to investigate the role of several size- and time-related factors in evaluating the cost of losing variable numbers of legs, as well as of growing replacements. Specifically, do limb loss and regeneration affect condition, and do the results differ with sex and age? I focused on adult males because of their high frequency of forelimb loss, including loss of multiple limbs. Numbers of missing adult male forelimbs were correlated with date captured and mass (corrected for number of missing forelimbs), suggesting that the spiders lost forelimbs continually over the summer and that they reached progressively poorer condition than intact individuals, judged by a disproportionate loss in body mass. The frequency of forelimb loss by penultimate males matched that of adult males, but females and juveniles lost less than 1/10th as many forelimbs as males. Males possessed many fewer partially regenerated forelimbs than missing forelimbs, but these frequencies significantly exceeded those for females and younger juveniles. Some information suggested that additional costs arose from the regeneration of forelimbs.

**Keywords:** Male-female difference, male-juvenile difference, predation, sexual dimorphism, Thomisidae

Considerable controversy exists over the consequences of limb loss among many-limbed invertebrates such as spiders and crustaceans. Although some studies have found little or no measurable effect of limb loss on survival or fitness (Guffy 1998; Johnson & Jakob 1999); others have demonstrated such a link, which may have major effects, including both prey capture and escape from predators (Maginnis 2006a; Steffenson et al. 2014). Most limb losses in these forms result from autotomy, a voluntary, nervously mediated defensive response induced by external stimuli (Wilkie 2001; Fleming et al. 2007). A widespread phenomenon, members of at least five invertebrate phyla, 14 classes and 36 orders readily shed limbs (Fleming et al. 2007), and many have retained the ability to regenerate lost parts under certain conditions (Bely & Nyberg 2009; Foelix 2011). Shedding a limb provides a convenient way to escape predation or other contingencies, but the act may have negative future consequences for an individual (Brueseke et al. 2001; Lutzy & Morse 2008). In response to loss, some species regenerate limbs, but this ability is not universal (Randall 1981; Maginnis 2006a), and the utility of this trait is open to question in some species (Maginnis 2006b; Lutzy & Morse 2008). In particular, many of these studies provide little detail that might provide broader insight into the overall advantages of the ability to shed a limb. Although shedding a limb, as opposed to shedding a life, is clearly advantageous in the short term, what success do the survivors enjoy? Do they obtain any fitness benefits that would separate them from those preyed upon, and if so, how much? The data set assembled here allows in-depth evaluation of this question. For instance, do losses of one, two or three limbs change the probability of future success?

Here I present data on limb loss and subsequent regeneration from a large sample of crab spiders, *Misumena vatia* (Clerck, 1757) (Thomisidae) gathered over 13 seasons, which provide insight into the possible relationship of several potentially key variables to limb loss. More specifically, do size (carapace width), mass, mass corrected for limb loss, date of capture, date of death, year, or collection site vary with limb loss? And, what relationship does regeneration have to these variables, any of which might provide insight into the fitness consequences of shedding limbs and attempts to regenerate them? I chose these variables because they allow key insight into the possible effects of size on limb loss and how limb loss affects body condition. The high frequency also provides the opportunity to gather adequate numbers of individuals for analysis. Do these relationships change or do they remain predictable and constant? And, is it worth trying to regenerate a limb?

Male *Misumena* Latreille, 1804 and related species lose limbs with a high frequency (Dodson & Schwaab 2001; Lutzy & Morse 2008). High mobility is an important trait, and the loss of forelimbs seriously compromises the spiders' locomotor capacity (Lutzy & Morse 2008). Although focusing on adult males, I compare them where possible with penultimate males, adult and penultimate females, and younger juveniles. One of the most highly sexually dimorphic of terrestrial animals (LeGrand & Morse 2000; Morse 2007), *Misumena* provides an excellent opportunity to make both intrasexual and intersexual comparisons. Forces acting on individuals of such strikingly different sizes may constrain the opportunity for further change within one sex or the other. To the best of my knowledge, no similar comparisons in extremely sexually dimorphic species have been made (Maginnis 2006a; Fleming et al. 2007). This work also expands on the results of an earlier three-year study (Lutzy & Morse 2008) of adult males. I then comment on the significance of these results for interpreting the present pattern of forelimb loss and regeneration in *Misumena*.

## METHODS

**Study area.**—I collected *Misumena* in an old field at the Darling Marine Center in South Bristol, Lincoln Co., Maine (43°57′N, 69°33′W), and at several other locations along roadsides within 5 km of the Darling Center. These locations are not managed except for being mown yearly. The sample from the Darling field is a probable composite of the other collection sites, because egg masses of females taken from the other sites include those used to rear spiderlings for a wide range of field experiments conducted over the period encompassed by this study (2000–2012). Numbers of individuals from three other collection sites permitted individual treatment as separate samples; those from 14 other locations were pooled into a last sample. These five samples were numbered 1–5.

The sites contain large numbers of flowers upon which *Misumena* hunt as sit-and-wait predators. I inspected flowers and collected spiders as I found them. Principal flower species included common milkweed *Asclepias syriaca*, oxeye daisy *Leucanthemum vulgare*, common buttercup *Ranunculus acris*, black-eyed susan *Rudbeckia hirta*, common St. Johnswort *Hypericum perforatum,* early goldenrod *Solidago juncea* and Canada goldenrod *S. canadensis*. Although this study focuses on adult males, I simultaneously captured penultimate males, penultimate females, adult females and earlier instars. I used many of these spiders in a wide variety of experiments not central to the present study. The data set includes individuals from 2000 and 2001 in Lutzy & Morse (2008), but does not include results from 1999 because those data lack several variables treated here.

**The species.**—*Misumena vatia* is a highly sexually dimorphic sit-and-wait predator that frequents hunting sites in flowers (described in detail in Morse 2007). Males are small and extremely mobile, weighing from 2.5 to 8.0 mg with two pairs of long anterior limbs (forelimbs) over twice the length of the hind limbs. Males do not gain significant amounts of mass as adults; hence, initial weighing of these individuals provides an adequate measure of adult mass. The highly mobile adult males search for unmated females and often guard large penultimate females that will soon molt into adults, at which point they will mate (Hainsworth & Morse 2000).

Penultimate males generally resemble adult males, though with somewhat shorter forelimbs and larger abdomens. Both penultimate and adult females are much larger and more sedentary than the adult males. Large penultimate females weigh 25 mg or more, and gravid adult females weigh as much as 400 mg or more. Most juveniles (early instars) sampled weighed 5–10 mg, near the size range of the males.

**Procedure.**—I captured the spiders during visits to flowers at the various collection sites. I inspected flowers for the presence of crab spiders, captured these individuals and placed them in 7-dram vials (5 cm tall, 3 cm diameter). I used the spiders in a wide variety of experiments, which I have reported elsewhere (e.g., Morse 2007, 2014). I retained approximately half of the adult males in 7-dram vials through senescence, feeding them every 2–3 days with small moths, flies and mosquitoes. I subsequently used the remainder in field experiments in other projects, and often lost these individuals in the process. I gathered all the data presented, other than date of death, at the time of capture; thus, they are not subject to potential changes brought about by retention in the laboratory.

I first categorized males in terms of their number of missing forelimbs, taking care not to include any individuals that had lost limbs during capture. Then I measured the carapace width of each individual to obtain a measure of overall size independent of mass. I also weighed each individual with a Denver Microbalance (Denver Instrument Company Model A-200DS: Arvada, Colorado, USA), then calculated an estimated mass for individuals missing forelimbs, using an earlier measure of the mass of forelimbs, 8.2% of the body mass (Lutzy & Morse 2008). Thus, I added 8.2% to the measured mass of individuals missing one forelimb, 16.4% to those missing two forelimbs, and 24.6% to those missing three forelimbs. Because the mass of the first and second pairs of limbs was similar in an earlier study (Lutzy & Morse 2008), I added the same mass for each missing forelimb. In all, I obtained a sample of 609 adult males with normal-sized forelimbs, including those with one or more missing forelimbs. Seventy (11.5%) of these individuals lacked one forelimb, 32 (5.3%) lacked two forelimbs, and 8 (1.3%) lacked three forelimbs. I also obtained information about capture site, year, date of capture and date of death. I compared forelimb loss of the adult males with that of penultimate males, penultimate females, and adult females captured at the same times as the adult males and used in a wide range of unrelated experiments.

Additionally, 24 adult males had one or more small regenerating forelimbs no more than half the length of normal-sized forelimbs. I collected the same data for these individuals as for those lacking forelimbs. I also calculated expected intact masses for the individuals with short forelimbs, assuming that the mass of these limbs weighed one-fourth of their "normal" weight. Only two individuals lost one of their small posterior limbs, and I did not separate these individuals from the others.

To evaluate the costs of forelimb loss and regeneration I used the above-noted data on date of capture, date of death, year, and capture site. These variables all provide insight into the consequences of forelimb loss. Date of capture provides an opportunity to determine whether losses continue as the season progresses. Date of death provides the opportunity to compare individuals from the field with those spared predation, competition and other contingencies in the laboratory. A decline in numbers infers mortality in the field. Significant differences in year or capture site would complicate the process of pooling data sets.

**Analysis.**—I analyzed the relation of limb loss and presence of short limbs to carapace width and mass with one-way ANOVAs. I also tested capture site, year, date of capture and date of death (in the laboratory) in relation to forelimb loss with ANOVAs. I used analysis of covariance (ANCOVA) to evaluate further the effects of capture site, year, date of capture and date of death on the size of males missing varying numbers of forelimbs. I compared frequencies of forelimb loss and short forelimbs among the different age and sex combinations using *G* tests and the relationship of carapace width and mass with linear regression. Because I lacked data for every variable measured or tested on each individual, *n*'s differ in some of the analyses. Analyses were carried out in R Version 2.13.0 (R Development Core Team 2011).

## RESULTS

**Missing forelimbs.**—A substantial proportion of the adult male spiders lost one or more forelimbs (110 of 609: 18.1%), a

Table 1.—Characteristics of adult male *Misumena vatia* missing 0–3 forelimbs (mean ± SD), and results of ANOVAs. [1] Predicted mass of individual assuming it still possessed all forelimbs; [2] Julian days (30 June = 180); [3] Halfway between 2004 and 2005 = 4.5, etc.; [4] Collection sites numbered 1–5 (see Methods), with non-significance denoting no difference among sites.

| Variable | | | | | *F* | *df* | *P* |
|---|---|---|---|---|---|---|---|
| Number of missing forelimbs (*n*) | 0 (491) | 1 (70) | 2 (32) | 3 (8) | | | |
| Carapace width (mm) | 1.47±0.149 | 1.46±0.151 | 1.43±0.132 | 1.47±0.144 | 2.09 | 1,599 | 0.15 |
| Mass (mg) | 4.58±1.540 | 4.20±1.415 | 3.44±1.010 | 3.06±1.066 | 26.45 | 1,599 | <0.0001 |
| Mass corrected[1] | 4.58±1.540 | 4.54±1.533 | 4.01±1.182 | 3.76±1.357 | 5.1 | 1,599 | 0.024 |
| Date of capture[2] | 172.1±10.66 | 173.2±13.24 | 173.8±10.59 | 181.6±15.05 | 4.53 | 1,599 | 0.034 |
| Date of death[2] | 203.4±18.11 | 201.5±21.96 | 201.6±16.48 | 207.6±25.42 | 0.11 | 1,300 | 0.74 |
| Year[3] | 4.5±4.20 | 4.4±4.25 | 5.6±4.65 | 5.4±4.57 | 1.4 | 1,599 | 0.24 |
| Collection site[4] | 2.7±1.57 | 2.9±1.56 | 2.9±1.68 | 3.3±1.91 | 1.56 | 1,599 | 0.21 |

result that did not significantly exceed the proportion of penultimate males missing a forelimb (6 of 52: 11.5%; $G_1 = 1.84$, $P > 0.1$). The adult male proportion greatly exceeded those of both penultimate (7 of 336: 2.1%; $G_1 = 64.35$, $P < 0.0001$)) and adult females (14 of 862: 1.6%; $G_1 = 97.13$, $P < 0.0001$). The frequency of forelimb loss in the penultimate males also exceeded that of both penultimate and adult females ($G_1 = 8.27$, $P < 0.01$; adults: $G_1 = 11.72$, $P < 0.001$). Numbers of missing forelimbs of unsexed earlier instars closely resembled those of females (4 of 227: 1.8%), significantly less than both adult ($G_1 = 88.89$, $P < 0.0001$) and penultimate ($G_1 = 9.60$, $P < 0.01$) males.

Body size (carapace width) did not differ significantly with the loss of one or more forelimbs, with the four forelimb-loss classes (0 – 3) exhibiting similar carapace widths at all of the sites (Table 1). As predicted, individuals missing progressively more forelimbs weighed less than those with fewer missing forelimbs (Table 1). However, after correcting masses for forelimbs lost, those with missing forelimbs were still significantly lighter than intact ones (Table 1). Although differences in mass between intact individuals and those with a single missing limb (corrected for estimated mass of that missing forelimb) were modest, suggesting a relatively minor effect, those between one and two missing limbs showed a several-fold decrease in mass, which was further extended in those missing three limbs (Table 1). Carapace width and mass (corrected) were nevertheless highly correlated (linear regression: $R^2 = 0.643$, $F_{1,599} = 1083$, $P < 0.0001$), accounting for roughly two-thirds of the total variance.

Among other variables measured, proportions of individuals missing forelimbs increased as the season progressed (date captured) (Table 1), although the majority of forelimb loss had already occurred by the first measure, early in the season. Neither date of death, carapace width, year, nor site of collection differed significantly in relation to forelimb loss (Table 1), allowing me to pool these data sets. Use of date of capture, date of death, year and collection site as covariates resulted in only one change in the relationship between size and forelimb loss: site had a moderately significant effect ($F_{3,298} = 2.81$, $P = 0.040$).

**Short forelimbs.**—Individuals with short forelimbs arise from ones that lost these forelimbs earlier in ontogeny. I encountered individuals with short forelimbs far less frequently than ones missing forelimbs (24 vs. 110; 3.8% vs. 18.1%; $G_1 = 127.08$, $P < 0.0001$, goodness of fit, $n = 633$).

Carapace width did not differ significantly with the presence of short forelimbs (Table 2). Neither mass (Table 2) nor mass corrected for the short limbs (Table 2) differed significantly, the result of a single anomalously large individual regenerating two forelimbs. Of the other variables measured (date of death carapace width, year, site of collection), none was significant (Table 2).

I obtained one penultimate male with a short forelimb (1 of 52 = 1.9%, not differing significantly in frequency from adult males ($G_1 = 0.50$, $P > 0.3$). I have also reared additional penultimate males in the laboratory that lacked a forelimb and subsequently molted into the adult stage with half-length forelimbs similar to those seen on the 24 adult males reported here. I only obtained occasional penultimate and adult females with short forelimbs in much larger samples (penultimate: 1 of 336 = 0.8%; adult: 2 of 862 = 0.2%). These frequencies fall significantly below those of the adult males ($G_1 = 13.85$, $P < 0.001$; $G_1 = 28.84$, $P < 0.001$, respectively). I found no early instars with missing forelimbs (0 of 227).

**Survival in field and laboratory.**—Many confined male *Misumena* lived for periods considerably longer than the

Table 2.—Characteristics of adult male *Misumena vatia* with 0–2 short forelimbs (mean ± SD), and results of ANOVAs. Superscripts 1–4 as in Table 1; [5] After removal of an anomalously large individual of 8.9 mg, mass = 2.93 ± 0.847 mg and mass corrected = 4.08 ± 0.777 mg.

| Variable | | | | *F* | *df* | *P* |
|---|---|---|---|---|---|---|
| Number of short forelimbs (*n*) | 0 (491) | 1 (17) | 2 (7) | | | |
| Carapace (mm) | 1.47±0.149 | 1.45±0.140 | 1.46±0.178 | 0.23 | 1,513 | 0.63 |
| Mass (mg) | 4.58±1.540 | 4.06±1.134 | 4.21±2.222 [5] | 1.71 | 1,513 | 0.19 |
| Mass corrected[1] | 4.58±1.540 | 4.32±1.208 | 4.77±2.516 [5] | 0.03 | 1,513 | 0.87 |
| Date of capture[2] | 172.1±10.66 | 175.1±12.98 | 170.9±9.10 | 0.2 | 1,513 | 0.65 |
| Date of death[2] | 203.4±18.11 | 204.1±18.54 | 215.1±28.27 | 0.63 | 1,262 | 0.43 |
| Year[3] | 4.5±4.20 | 4.9±4.40 | 2.3±3.90 | 0.73 | 1,513 | 0.39 |
| Collection site[4] | 2.7±1.57 | 3.4±1.52 | 2.4±1.81 | 0.27 | 1,513 | 0.60 |

maximum dates I have recorded in the field. During one year that I weekly censused *Misumena* in all flowers at eight sites in the vicinity of the Darling Center (total $= 0.72$ ha), I failed to record adult males after 28 July, a pattern consistent with less systematic observations made over the 2000–2012 period, in which I have rarely found adult males in the field after that date. However, I have frequently maintained males in the laboratory until late August and early September, and 74.6% of the males retained in this study ($n = 303$) survived past 28 July. I did not find significant differences in longevity in the laboratory between intact individuals and those that had lost forelimbs (ANOVA: $F_{1,300} = 0.11$, $P = 0.742$).

## DISCUSSION

**Possible sources of forelimb loss.**—Male *Misumena* lose forelimbs at a highly significantly greater rate than either penultimate or adult females. Forelimb loss of penultimate males is more comparable to that of the adult males than of females or juveniles and provides insight into the frequency of loss among the adult males. Unfortunately, the sample of penultimate males is relatively small, since virtually all of the males since 2002 have molted into the adult stage before our field season begins in early June, part of a pervasive shift in the phenology of several species monitored since 1995 in the main study area (D.H. Morse, unpubl. data).

Adult males engage in aggressive interactions when near each other, but penultimate males, which have a comparable rate of forelimb loss, generally do not undertake high-level interactions (Holdsworth & Morse 2000). A relatively low rate of forelimb loss of adult males even in staged encounters between males at the sites of late-stage penultimate females (3 in 90 encounters, 3.3%: Hu & Morse 2004) and in mating experiments (Morse 2010) makes the putative role of adult male aggression unlikely as a sole or principal source of forelimb loss. Opportunities for these interactions are relatively infrequent in the field, much lower than in the closely related *Misumenoides formosipes* (Walckenaer, 1837) (Dodson & Beck 1993; Dodson et al. 2015). The similar size (carapace width) of individuals with different numbers of missing forelimbs is also inconsistent with aggressive interactions playing the major role in limb loss. Otherwise, one might expect large dominant males to produce higher limb losses in combat than smaller ones, because large individuals initiate attacks more frequently than smaller ones, a pattern seen in other species as well (Jakob 1994; Hu & Morse 2004). Hence, the high frequency of missing limbs in adult males is unlikely to result solely from male aggression.

Mating is a dangerous experience for male spiders, with some species even dying after mating, including instances in which they are killed by their mates (Andrade 1996; Foellmer & Fairbairn 2003; Schneider et al. 2006). Mating takes a less frequent toll in *Misumena*, but aggressive females do regularly capture courting males. However, I have found that in virtually all instances the females strike directly at the body, and the male either escapes intact or is captured and killed (Morse & Hu 2004; Morse 2010). Predators vary in their tendency to strike at a spider's body or limbs (Formanowicz 1990). Thus, male-female interactions also appear unlikely to account for a major part of the observed limb loss.

Male forelimbs are especially long and slender and thus potentially vulnerable to loss. Although not as long as those of adults (Morse 2007), penultimate forelimbs are nevertheless extremely long and slender relative to those of females (Morse 2007) and are thus potentially vulnerable to predators or to entanglement in the vegetation (Maginnis 2006b). On the basis of occasional observations made while collecting males in the field, I predicted that the long, gracile form of male forelimbs would enhance their vulnerability to entanglement in the vegetation (petiole-stem interstices, etc.), especially if suddenly attacked. Analogously, web-building spiders may autotomize limbs if tangled in webs (Johnson & Jakob 1999).

Although spiders may experience difficulty in extracting their limbs from their old molt (Maginnis 2006a; Foelix 2011), male *Misumena* molt successfully in the laboratory, as long as I maintain adequate humidity. Problems of low humidity are probably even less likely to occur in the field. Thus, this potential problem appears unlikely to account for a major part of forelimb loss of the males. The frequency of missing forelimbs in the penultimate males appears adequate to suggest that many of the adults missing forelimbs suffered the loss earlier in ontogeny. Pasquet et al. (2011) and others have reported losses of less than 1% in penultimate males of other species.

**Short forelimbs.**—Adult males with short forelimbs experienced an even greater disadvantage under natural conditions than those completely lacking limbs, in that they performed a number of movements more slowly than even those missing limbs, and most of them also lost condition (Lutzy & Morse 2008). Some spiders held partially regrown limbs away from the body, which therefore did not contribute to locomotion (Vollrath 1990) or prey capture (Wrinn & Uetz 2008). The spiders also expend considerable energy growing these new limbs (Maginnis 2006a; Bely & Nyberg 2009). Thus, it appears that these males would profit from losing their regenerative ability, especially in the later instars. Indeed, one could imagine such selective pressures having driven the loss of regeneration in groups that have lost this ability. Losses of the ability to regenerate limbs have occurred many times among groups that exhibit autotomy and appear related to conditions routinely experienced in the field (Bely & Nyberg 2009).

Since regeneration only produces external limbs at molts, none of the small replacement forelimbs result from losses in the adult stage. Most likely the adult males with partially regenerating forelimbs lost their forelimbs early in their penultimate stage. In some species of spiders, regeneration will occur if limb loss takes place during the first quarter of an individual's penultimate instar (Foelix 2011, citing Bonnet 1930). This prediction is consistent with the statistically similar level of forelimb loss seen in adult and penultimate males.

**Male survival.**—The difference between apparent adult male survival in the field and laboratory suggests that they seldom reach their maximum potential life span in the field. In the field, males spend most of their adult lives vigorously searching for females (LeGrand & Morse 2000). Although adult males do feed (vs. males of many spiders: Foelix 2011) and largely retain their weight over time, their high level of activity (Holdsworth & Morse 2000) presumably takes its toll. Male spiders regularly die before their females (e.g., Dodson & Schwaab 2001). The similar survival in the laboratory between intact individuals and those lacking forelimbs was initially surprising, because individuals lacking forelimbs were significantly lighter (after correction for missing forelimbs) and in poorer condition than intact individuals when captured. This result is probably a consequence of the easily captured food in the laboratory, which permitted feeding to satiation. Thus, the poor condition of individuals lacking one or more forelimbs in the field may result from decreased success in prey capture under complex conditions (Brueseke et al. 2001), as well as compromised locomotor capabilities (Lutzy & Morse 2008). The laboratory-retained individuals lacking one or more forelimbs would presumably have performed poorly in a set of locomotor tasks comparable to those they would experience in the field. In fact, field-captured individuals could not travel on lines as rapidly as intact ones (Lutzy & Morse 2008). If they followed the pattern observed in intact individuals (Lutzy & Morse 2008; Morse 2014), they probably would score poorly in other locomotor activities (running, climbing) as well as in line-crossing. Thus, forelimb loss results in compromised body condition and performance.

**Regeneration and forelimb loss.**—Bely & Nyberg (2009) identify the question of why regeneration persists where it appears to be irrelevant as a major unaddressed question in regeneration studies. Although regeneration of forelimbs appears disadvantageous to penultimate and adult male *Misumena*, it may be advantageous in early instars. However, the earlier *Misumena* instars exhibit significantly lower frequencies of forelimb loss than the penultimate and adult males, which would suggest that selection could not operate as strongly as on the older males. Regeneration might also be advantageous for the females; however, they have strikingly lower frequencies of lost or short forelimbs than the males, making the explanation problematic.

Thus, the results leave a major unanswered question: why are male and female forelimb losses so different? Results presented here and in the literature suggest that this difference involves a conflict between robustness and speed: the difference between the ability of females to manipulate large prey and the ability of males to move quickly when searching for females.

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