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LEG AUTOTOMY AND ITS POTENTIAL FITNESS COSTS FOR TWO SPECIES OF HARVESTMEN (ARACHNIDA, OPILIONES)

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ABSTRACT. Leg autotomy often confers immediate benefits on the animal losing its legs, such as escape from a predator, while costs are usually less obvious and accrue long after the leg is lost. I conducted a survey to determine the prevalence and characteristics of leg autotomy in two species of harvestmen, *Leiobunum nigripes* Weed 1892 and *L. vittatum* Say 1821, from May-December 1996 at Chicot State Park, Evangeline Parish, Louisiana. Nearly half of all individuals found were missing at least one leg. There was no significant difference in the median number of legs between months for *L. nigripes,* but differences were found among several months for *L. vittatum.* Either of the second legs was most likely to be lost in both species. These results indicate that leg autotomy is common in harvestmen. Furthermore, these results suggest that the second legs are not as crucial to the survival of harvestmen as previously believed. Leg autotomy may result in a reduction of potential fitness for individuals, but harvestmen may choose to incur these costs rather than risk a catastrophic loss of fitness (e.g., death); that is, leg autotomy may be a bet-hedging strategy for harvestmen.

Autotomy of appendages is widely known for a variety of animal groups, including molluscs (Edmunds 1966), crustaceans (Juanes & Smith 1995), arachnids (e.g., spiders: Formanowicz 1990; harvestmen: Kaestner 1968), insects (Carlberg 1994), echinoderms (e.g., *Thyone briareus* LeSueur 1824: Smith & Greenberg 1973), salamanders (Wake & Dresner 1967), and lizards (Arnold 1984). The effect that autotomy has on the fitness of an individual depends on the sum of the benefits and costs of appendage loss. Benefits may be immediate or nearly so and include distraction of predators (Arnold 1984), escape from a predator's grasp (Arnold 1984), and escape from traps (e.g., spider webs). Costs are spread over a longer period of time and include loss of mobility or balance, reduced ability to escape subsequent encounters with predators, decrease in social status, divergence of energy resources to replacement of the lost appendages, decrease in mating success, and even death in some instances (reviewed in Edmunds 1974; Arnold 1984, 1988; Juanes & Smith 1995).

Harvestmen autotomize their legs but do not regenerate them as either juveniles or adults (Comstock 1920; Kaestner 1968); therefore, there are no costs associated with regeneration, such as allocation of nutrients to new tissue. However, harvestmen also are not able to recover the benefits that they originally had with the full complement of eight legs. Because harvestmen do not regenerate their legs, when confronted with predators they should be under natural selection to weigh the benefits of leg autotomy against the future costs associated with autotomy, such as subsequent encounters with predators, loss of mobility, loss of foraging ability, or loss of mating opportunities.

The second pair of legs is the longest in *Leiobunum* (Kaestner 1968; Edgar 1990), and these legs are believed to contain the main sensory organs of these animals (Comstock 1920; Edgar 1963; Cloudsley-Thompson 1968). In one study, harvestmen that had lost the second pair of legs were reported to be more reluctant to move, eat, drink, or mate (Sankey & Savory 1974). Cloudsley-Thompson (1968) wrote that the loss of both of the second pair of legs quickly results in death. Given the reported importance of the second pair of legs, I predict that harvestmen should be particularly reluctant to autotomize this pair compared to the other pairs.

In general, three different life histories can be found in Opiliones (Todd 1949). (1) Eggs laid the previous autumn hatch in the spring.

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The animals mature over the summer and lay eggs in the autumn, then adults may or may not die at the first frost (e.g., *Leiobunum nigripes* Weed 1892). This results in an overlap of generations in some species (e.g., *Phalangium opilio* Linnaeus 1758: Clingenpeel & Edgar 1966). (2) Eggs hatch in the autumn and the young overwinter. The young mature during the following summer, lay their eggs, then die before the clutches hatch. Clingenpeel & Edgar (1966) used populations of *Leiobunum politum* Weed 1889 and *L. vittatum* Say 1821 from Michigan as examples, but the latter species appears to follow pattern 1 in south central Louisiana (pers. obs.). (3) As in the previous case, the eggs hatch in the autumn and the young overwinter. Eggs are laid the following autumn, but the adults do not die until after the eggs hatch, resulting in an overlap of generations (e.g., *L. townsendi* Weed 1893: Cokendolpher et al. 1993). Harvestmen are ametabolous, and the young undergo 5–8 molts before reaching adulthood (Edgar 1971; Kaestner 1968) with the first molt taking place within hours of hatching (Edgar 1971).

Both *L. vittatum* and *L. nigripes* were collected throughout the year at Chicot State Park, Evangeline Parish, Louisiana; but it was common to find only adult *L. vittatum* from late November to early January and to find only juvenile *L. nigripes* from early January to mid-February. *Leiobunum nigripes* emerged 1–2 months earlier than *L. vittatum*.

In this study, I conducted field observations of *L. nigripes* and *L. vittatum* to determine the prevalence of leg autotomy in these species, which legs are most likely to be autotomized, and what costs might be associated with leg autotomy. I predicted that: (1) the proportion of individuals missing legs should increase with age, (2) the second legs should be the least likely to be autotomized, and (3) individuals found mating should be more likely to have all eight legs than those individuals found alone.

METHODS

Study animals.—I observed juveniles and adults of *L. nigripes* and *L. vittatum* at Chicot State Park, Evangeline Parish, Louisiana between May and December 1996. Individuals were collected from cabins, vegetation, and 10.2 × 10.2 × 50.0 cm wooden posts. I recorded location, number of legs, which legs were missing, and whether or not collected individuals were found in the copulatory position. Both species in this study are sexually dimorphic, but the characters used to identify the sexes of *L. nigripes* (size, color; pers. obs.) are not as reliable as that used for *L. vittatum* (size of pedipalps; Davis 1935). Any animals for which the sex was uncertain were removed from comparisons based on sex. I released all animals near the sites at which they were collected. A previous mark-recapture study indicated that $<10\%$ of marked animals were caught at the site at which they were marked after 24 h and $<1\%$ were recaptured after two weeks (unpubl. data); therefore, pseudoreplication due to resampling should have been negligible.

Comparisons between months.—I used a Kruskal-Wallis one-way ANOVA by rank (Siegel & Castellan 1988) to determine if there was any significant difference for each species in the number of legs present among months. When a significant difference was detected, I used a multiple comparisons test (Siegel & Castellan 1988) to locate significant differences between months. These tests were two-tailed and the test statistics were adjusted for ties with $\alpha = 0.05$.

Comparisons of leg pairs.—I summed the number of times that either leg of a particular pair was autotomized and compared these observed values to an expected value obtained by assuming that each pair was equally likely to lose a member. The probability (P) that either leg of any particular pair would be lost was 0.25. This value was calculated as follows

$$P(X_L \text{ or } X_R) = P(X_L) + P(X_R) = \tfrac{1}{8} + \tfrac{1}{8} = \tfrac{2}{8} = 0.25$$

where X is any particular leg pair, L indicates left, and R indicates right. This null hypothesis was evaluated for both species with a Chi-square goodness of fit test (Freund & Simon 1992) and compared to $\alpha = 0.05$.

I compared the number of individuals missing both legs of the second pair to an expected probability of 0.036 (again assuming an equal likelihood that any leg would be autotomized). This probability was calculated as follows

$$P(X) = P(\mathrm{X}_1) \text{ and } P(\mathrm{X}_2) = P(X_1)P(X_2) = (\tfrac{2}{8})\,(\tfrac{1}{7}) = 0.036$$

where X is any particular leg pair. I used a

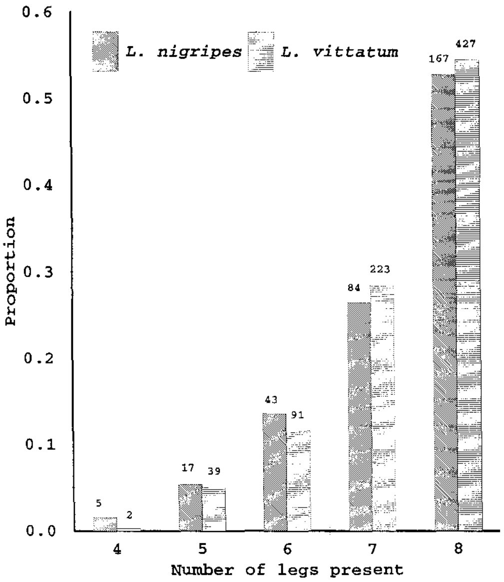

Figure 1.—The incidence of leg autotomy in two species of harvestmen from Evangeline Parish, Louisiana, May-December 1996. The proportion of individuals with a given number of legs was not significantly different between the two species. The numbers above the bars indicate sample sizes.

one-tailed binomial test (Siegel & Castellan 1988) to evaluate the null hypothesis that the observed values for the loss of the second pair of legs came from a binomial distribution with $P = 0.036$. I compared the test results to $\alpha = 0.05$.

Comparisons of mating pairs with lone individuals.—I counted the number of legs of those individuals of *L. vittatum* found in the copulatory position and those found alone on 24 and 31 October 1996. Copulation in both *L. nigripes* and *L. vittatum* occurs when the male grasps the female's prosoma with his pedipalps and repeatedly attempts to insert his penis under the genital operculum of the female (*L. nigripes*: pers. obs.; *L. vittatum*: Edgar 1971; Macías-Ordóñez 1997). I compared the number of legs of those animals found alone to those found in the copulatory position; but because of the small sample sizes of those animals with seven or fewer legs, I pooled all of those animals and compared them to animals with eight legs in my statistical analyses. I tested the null hypothesis of no significant difference with a G-test of independence with the Williams correction (Sokal & Rohlf 1995). The test statistic was compared to $\alpha = 0.05$.

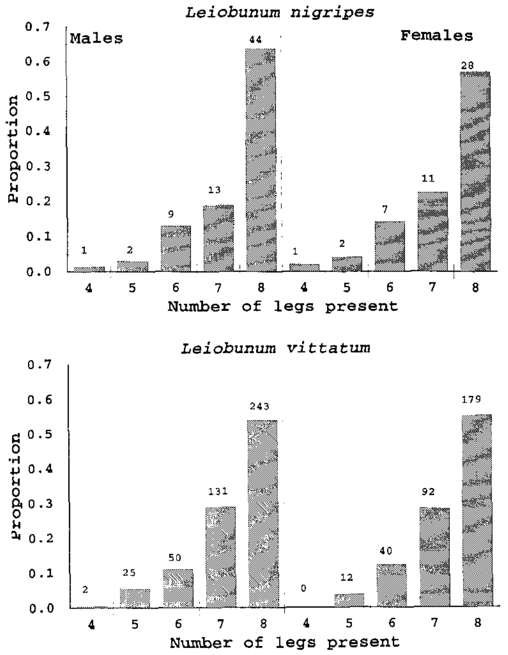

Figure 2.—A comparison of leg number by species and sex. There was no significant difference in proportions between the sexes for either *Leiobunum nigripes* or *Leiobunum vittatum*. The dashed vertical line separates the data for males from that for females in each graph. The numbers above the bars indicate sample sizes.

RESULTS

Nearly half of all harvestmen found were missing at least one leg (Fig. 1). There was no significant difference between *L. nigripes* and *L. vittatum* in the proportion of individuals at each level of leg loss ($\chi^2 = 5.65$, $P = 0.226$). Likewise, there was no significant difference between the sexes in the proportion of individuals missing a particular number of legs within either *L. nigripes* (Fig. 2A; $\chi^2 = 0.53$, $P = 0.768$) or *L. vittatum* (Fig. 2B; $\chi^2 = 1.77$, $P = 0.621$). The ratio of males to females was 1.3:1 ($n = 136$) for *L. nigripes* and 1.4:1 ($n = 897$) for *L. vittatum*.

There was no significant difference in the median number of legs among months for *L. nigripes* (Table 1; $df = 7$, $KW = 10.07$). A significant difference was detected among months in the median number of legs for *L. vittatum* (Table 2; $df = 7$, $KW = 43.01$). A multiple comparisons test indicated that those

Table 1.—Leg number for *Leiobunum nigripes* by month. A Kruskal-Wallis one-way ANOVA by rank, adjusted for ties, yielded $P = 0.186$.

Month	*n*	Mean (± SE)	Median
May	109	7.1 (0.10)	7.0
June	42	7.0 (0.16)	7.0
July	46	7.4 (0.12)	8.0
August	39	7.4 (0.15)	8.0
September	31	7.5 (0.17)	8.0
October	24	7.2 (0.23)	8.0
November	21	7.4 (0.19)	8.0
December	4	7.8 (0.25)	8.0

Table 2.—Leg number for *Leiobunum vittatum* by month. A Kruskal-Wallis one-way ANOVA by rank, adjusted for ties, yielded $P < 0.001$. Like superscripts indicate no significant difference in medians between those months as detected by a multiple comparisons test.

Month	*n*	Mean (± SE)	Median
May	100	7.6 (0.07)	8.0^{A}
June	31	7.4 (0.14)	8.0^{AB}
July	119	7.5 (0.07)	8.0^{A}
August	45	7.4 (0.10)	8.0^{AB}
September	173	7.4 (0.06)	8.0^{A}
October	58	7.2 (0.14)	8.0^{AB}
November	102	7.2 (0.09)	7.5^{AB}
December	156	6.9 (0.08)	7.0^{B}

animals found in December had significantly fewer legs than those in May, July, and September (Table 2).

For both *L. nigripes* and *L. vittatum,* I determined that legs were not equally likely to be lost (Fig. 3; *L. nigripes*: $\chi^2 = 19.93$, $P < 0.001$; *L. vittatum*: $\chi^2 = 42.06$, $P < 0.001$). A leg was most likely to be missing from the second pair in both species (Fig. 3). The second pair of legs was missing significantly more often than expected for both *L. nigripes* ($n = 26$, $k = 6$, $P < 0.001$) and *L. vittatum* ($n = 86$, $k = 6$, $P = 0.034$).

I found no significant difference in leg number for those males of *L. vittatum* found in a copulatory posture ($n = 21$) compared to those found alone (Fig. 4A; $G = 0.015$, $P = 0.902$). Likewise, there was no significant difference in leg number for those females found in the copulatory position ($n = 20$) and those found alone (Fig. 4B; $\chi^2 = 3.10$, $P = 0.078$). There was no significant difference between the sexes of *L. vittatum* in the numbers of animals with eight legs found alone ($G = 3.006$, $P = 0.083$).

DISCUSSION

Because *Leiobunum* is typically univoltine (Clingenpeel & Edgar 1966; Cokendolpher et al. 1993) and does not regenerate autotomized legs, I predicted that the average number of legs per individual would decrease with time. Contrary to expectations, the median number of legs did not decrease in *L. nigripes* over the course of the study period. However, *Leiobunum vittatum* found in December had significantly fewer legs than those found in May, July, and September.

The second pair of legs plays an important role in sensing the surrounding environment of individuals of *Leiobunum* (Comstock 1920; Sankey & Savory 1974). Therefore, I predicted that harvestmen are under pressure from natural selection to protect those legs. However, the results presented here indicate that when only one leg is autotomized, the lost limb is most likely to be from the second pair

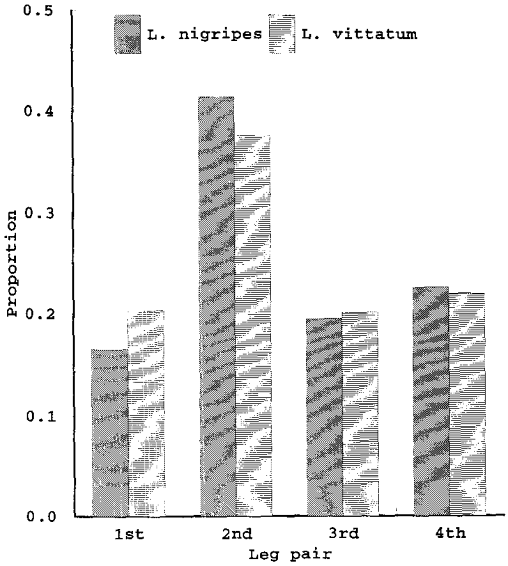

Figure 3.—The proportion of each pair of legs represented in the sample of those harvestmen missing at least one leg. The observed numbers were significantly different from the values expected given an equal chance of autotomy for all legs. The expected proportion is represented by a solid horizontal line across the middle of the graph. The numbers above the bars indicate sample sizes.

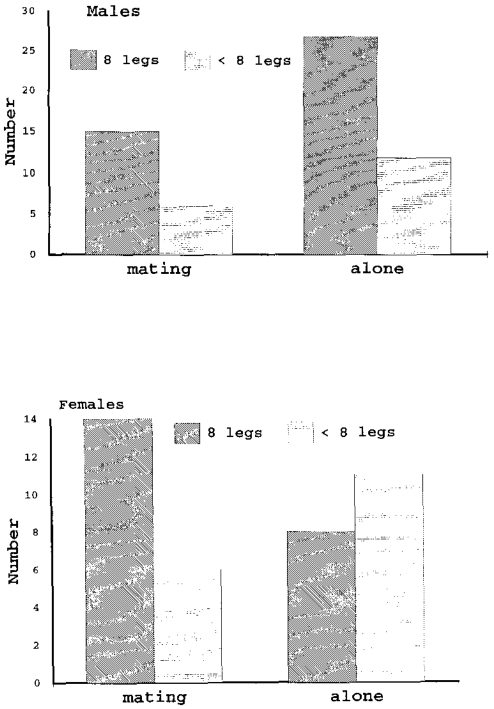

Figure 4.—A comparison of leg numbers of those individuals of *Leiobunum vittatum* found either mating or alone on 24 and 31 October 1996. There was no significant difference in the number of animals found either mating or alone for males or females.

of legs. Also, the second pair of legs is significantly more likely to be lost than expected if one assumes that all legs have an equal probability of being lost.

My final prediction was that significantly more individuals of *L. vittatum* found mating would have all eight legs than those individuals found alone. This would be expected if legs are important for finding mates or in intrasexual contests. I found no significant difference in the proportions of individuals with eight legs found mating compared to those found alone for either sex.

Leg autotomy is common in *L. nigripes* and *L. vittatum*. Leg loss may be caused by (1) intraspecific or intrasexual battles, (2) poor nutrition resulting in loss of legs during molting, or (3) different types of predation pressures such as direct attack or loss in webs. Males of *L. vittatum* fight over access to oviposition sites by shoving one another with their bodies, only rarely grasping one another by the legs (Macías-Ordóñez 1997). Therefore, intraspecific or intrasexual combat do not appear to be significant causes of leg autotomy.

If nutrition is responsible for a significant degree of leg loss, then the average number of legs present per animal should decrease during juvenile stages (January-July) but should not change significantly after the final molt (*ca.* July). My data do not cover the earliest molts, but I found no significant differences in leg number between the later instars and adults, suggesting that nutritional state is not the primary cause of loss of legs in older juveniles.

If the risk of predation is equal between species and between sexes within species, then this would explain why there is no significant difference in leg number between these groups. Furthermore, because the second legs are longer than any others in *Leiobunum* (Kaestner 1968; Edgar 1990) and these legs are the first part of the harvestman to move when individuals are disturbed (Comstock 1920; Sankey & Savory 1974), these legs are most likely to come into contact with predators or traps and thus to be autotomized. Spivak & Politis (1989) found that the longest and most exposed limbs of crabs were the most likely limbs to be autotomized. If the second legs are the most important sensory organs of harvestmen, then autotomy may result in a substantial cost to these animals in terms of loss of sensory ability.

Though the data presented here indicate that there was no significant difference in leg number between *L. vittatum* found mating and those found alone, I did not have enough individuals missing two or more legs to make comparisons at specific levels of leg autotomy (e.g., eight legs *vs.* six legs). There may be a cost in fitness due to reduced mating success as a result of leg autotomy, especially when two or more legs are missing. Such costs may be caused by a reduced ability (1) to find mates because of lessened mobility or diminished sensory capacity, (2) to find oviposition or mating sites, or (3) to prevail during intrasexual encounters. Mates and oviposition sites are apparently identified only through direct contact with the legs (Macías-Ordóñez 1997). Therefore, leg autotomy has the potential to impose a significant cost on the future fitness of both males and females of *L. vittatum.*

Males of *L. vittatum* with more legs than their opponents win significantly more male-male contests when both males have equal territorial status, but the contest winners do not achieve increased mating success (Macías-Ordóñez 1997). Macías-Ordóñez (1997) conducted his research at a site in which oviposition (and hence, mating) sites were not limited. Therefore, contest losers were soon able to find other mating sites. The outcome of contests, and thereby leg number, might be more important in those areas in which oviposition sites and access to females are limited or when male-male contests involve individuals with unequal territorial status. I could not determine if the oviposition sites for the populations in this study are limited.

Bet-hedging strategies are those behaviors that decrease the expected fitness of an individual but with the benefit of reducing the risk of a total loss of fitness; that is, lower potential fitness is offset by a reduction in the variance of fitness (Seger & Brockmann 1987). Leg autotomy may reduce an individual's expected fitness by decreasing its sensory capabilities (unpubl. data). It is also possible that individual fitness may decrease as a result of autotomy due to reduced mobility or increased risk of capture during subsequent encounters with predators. Harvestmen that autotomize their legs presumably benefit by avoiding being eaten by spiders or other predators. The interaction between the immediate benefits obtained from leg autotomy and its later costs fits the model for a bet-hedging strategy (Seger & Brockmann 1987).

To this point, I have considered only the hypothesis that leg autotomy imposes a cost on those harvestmen that lose legs. An alternative hypothesis is that harvestmen have enough legs such that loss of one or a few of them does not cause any substantial reduction in the expected fitness of an individual—in other words, harvestmen may have spare legs. Most of the data presented above show only the potential for a reduction in fitness. Within each sex, there was no significant difference in the proportions of individuals found alone or mating. The spare-leg hypothesis would lead to the prediction that when animals are divided into groups with either all eight legs present or those missing one or a few legs, as reported in this study, there would be no significant differences detectable. Instead, differences would only be detectable after a certain number of legs are lost, requiring a finer resolution of the categories compared.

It remains to be determined (1) if leg autotomy at any level is costly to harvestmen and, if it is costly, (2) at what point leg loss becomes so costly that a harvestman would be just as well off risking a catastrophic failure of reproduction (e.g., because of death by predation). While the present study does not quantify the costs associated with leg autotomy, it suggests that such costs exist and leads to an expectation that there is some level of leg autotomy at which harvestmen obtain a greater payoff for not losing any additional legs.

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