

Flight or fight: flexible antipredatory strategies in porcelain crabs

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Autotomy, the voluntary shedding of limbs or other body parts in the face of predation, is a highly effective escape mechanism that has evolved independently in a variety of taxa. Crabs are unusual in that the limb that is typically sacrificed during autotomy, the anterior clawed cheliped, can also be used to ward off attack. During an encounter with a predator, an individual must thus decide between two mutually exclusive strategies: flight or fight. We used experimental predation encounters with two species of porcelain crabs (genus *Petrolisthes*) to examine the factors that influence the decision to flee versus fight and to determine the degree to which this decision is context-dependent. We found that autotomy was highly conditional. The characteristics that best predicted autotomy—smaller body size or female gender—also correlated with a lower escape rate by the alternative escape tactic, struggling and pinching the predator. Variation among individuals in the benefit of autotomy (relative to alternative tactics) appears to drive variation in propensity to autotomize. Porcelain crabs thus demonstrate adaptive flexibility, employing the costly strategy of autotomizing a limb as a last resort, only when their chance at success by struggling is low. *Key words*: autotomy, body size, decapod crustacean, flexible defense strategy, *Petrolisthes*, predation. [*Behav Ecol* 16:1037–1041 (2005)]

Predation is a key selective agent for life-history and behavioral evolution (Harvey and Greenwood, 1978; Lima and Dill, 1990; Reznick et al., 1990; Roff, 1992; Stearns, 1992). Adaptations to reduce predation risk are as diverse as they are ubiquitous and include living in social groups, crypsis, avoidance of predator-rich habitat, use of refuges, protection through armor or noxious chemicals, associations with aggressive species, and speeding up vulnerable life-history stages (Arendt, 1997; Harvey and Greenwood, 1978; Lima et al., 1985; Werner, 1986). Autotomy, or the voluntary shedding of a limb or other body parts, is a particularly intriguing defense against predation because escape comes at the expense of a body part. Autotomy thus involves a particularly clear trade-off—the benefit of reduced mortality from predation versus the fitness costs incurred by coping without the lost body part until it is replaced. Autotomy has evolved in a variety of taxa: for instance, various lizard taxa, rodents, and salamanders autotomize their tails in the face of an attack (Arnold, 1988), crabs shed their chelipeds or legs (Juanes and Smith, 1995; McVean, 1982), spiders drop their legs (Formanowicz, 1990), while brittle stars and sea stars cast off their arms (Lawrence, 1992; Mauzey et al., 1968).

Crabs are unusual among organisms that autotomize in that the limbs that are typically shed during autotomy are also used for active, aggressive defense. Their main defensive weapons, the anterior, claw-tipped appendages, or chelipeds, can thus be used for two distinct but mutually exclusive defensive strategies: flight or fight. Autotomizing a cheliped allows the crab to slip out of the grasp of the predator (Wasson et al., 2002), or the cheliped can be used to pinch or shield the crab from attack. Losing a cheliped thus reduces a crab's ability to escape a future attack either by fighting or autotomizing. In

addition, losing a limb often comes with other costs for crabs, including reduced foraging ability, slower growth, and decreased mating success (Juanes and Smith, 1995). Therefore, the chelipeds are likely only employed for flight by autotomy when this strategy confers a much higher probability of escape than does fighting back with them. Moreover, if the magnitude of costs or benefits of the strategies vary, the decision whether to flee or fight might be a flexible one.

Juanes and Smith (1995) noted that “we have little knowledge of the decision-making process that determines when prey should autotomize a limb” and asked whether it might vary with threat or level of prey vulnerability. For instance, in the blue crab (*Callinectes sapidus*), the costs of autotomy increase with size (larger crabs are more negatively affected by missing limbs) while benefits decrease (larger crabs are better able to defend themselves by fighting), implying that there may be a decreasing propensity to autotomize with increased size (Juanes and Smith, 1995). Likewise for lizards, Arnold (1988) suggested that ease of tail autotomy might be adjusted relative to the threat level and the tail's value. Observations of lizards have revealed that their readiness to shed tails may vary with temperature, age, body condition, and habituation to captivity (Arnold, 1988; Fox et al., 1998). In one of the only experimental studies of autotomy decision making, Fox et al. (1998) demonstrated that male lizards (*Uta stansburiana*) require more applied force to autotomize than do females, and larger individuals require more force than smaller ones. Similarly, Marrs et al. (2000) found that large sea stars (*Asterias rubens*) were slower to detach their arms when stimulated than were small ones. Until now, such variation in autotomy threshold with gender or size has not been investigated empirically in decapod crustaceans.

Porcelain crabs (*Petrolisthes* spp.) are an ideal study system for investigating autotomy as a flexible antipredatory behavior. They can successfully escape a secure hold by a predator either via autotomy or by fighting, making it feasible to search for correlates that predict the occurrence of autotomy (Wasson et al., 2002). In the current study, we examined whether the decision to autotomize was conditional, depending on

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variation in prey or predator attributes. We also assessed the effectiveness of escape without autotomy because crabs with a high probability of escape by other mechanisms should not autotomize. We considered four prey attributes—species, cheliped number, body size and gender—hypothesizing that factors that enable individuals to be better fighters should be negatively correlated with the occurrence of autotomy. We also examined one predator attribute, body size, predicting that porcelain crabs faced with larger predatory individuals opt to autotomize more often because fighting is less effective.

METHODS

Study animals

We collected porcelain crabs (*Petrolisthes cinctipes* and *Petrolisthes manimaculis*) under rocks in the mid-intertidal zone at Baker and Indian Beaches near Trinidad, northern California (41° 06' N, 124° 08' W), during low tides from May to August 1999. We maintained them in flowing seawater at Humboldt State University's Telonicher Marine Laboratory, providing rocks to use as cover and twice weekly enhancing feeding by adding cultured phytoplankton to their containers. We used crabs that had been collected within the previous two weeks for predation trials. Individuals not used for trials and those surviving trials were released back to their original field sites. Prior to each predation trial, we sexed and measured each porcelain crab. Their average size (maximum carapace width) was about 9 mm; crabs ranging from about 4–14 mm were used in trials.

We collected 17 purple shore crabs (*Hemigrapsus nudus*) from the same sites to use as predators on the porcelain crabs. They were maintained individually in buckets supplied with flowing seawater and were released within days of the end of the study. Each crab was measured and then labeled with a number painted on the carapace with nail polish. Their sizes (maximum carapace width) averaged 35 mm (range 20–47 mm). In the analyses, we examined the influence of both absolute predator size (carapace) and relative predator size (ratio of predator carapace to prey carapace).

Experimental design

We videotaped 195 staged encounters between porcelain crabs and larger predatory crabs and prey between June and August 1999 in order to clearly observe the context and outcome of predation attempts and antipredatory behaviors. Each encounter involved a single porcelain crab placed in a bucket with a single larger predatory crab, recorded by a video camera positioned on a tripod directly above the bucket. Later analysis of the time-stamped video allowed us to score various sequential behaviors and the time they occurred. For a porcelain crab that was captured, we determined whether it escaped (was able to completely free itself from the predator and move away), and if so, by what means. The two most common antipredatory mechanisms were autotomy and behavior we categorized as struggling/pinching (hereafter "struggling"). We defined autotomy as "loss of a cheliped when the prey was held only by that cheliped" (Wasson et al., 2002) in order to distinguish autotomy (a voluntary behavior) from involuntary prying off of appendages by the predator, which typically occurs when the predator grasps both the prey body and cheliped. These experiments were within the guidelines for animal experimentation for both the University of California Institutional Animal Care Use Committee and the International Society for Behavioral Ecology.

Statistical analysis

We used logistic regression analysis in JMP (SAS, 2003) to examine the effect of prey and predator characteristics both on the occurrence of autotomy and the probability of escape from a predator once captured. In both sets of analyses, the independent variable was a binary one (autotomized versus not and escaped versus not). For both autotomy and escape, we conducted single-factor logistic regressions for each of the variables as well as a stepwise multiple logistic regression that included all of the independent variables. In the latter, the probability to enter the model was set at 0.25 and the probability to remove from the model at 0.10. In a few cases, where the single-factor logistic regressions yielded poor fit, the data were analyzed with a two-factor contingency table. Although we could have analyzed all the single-factor analyses that entailed categorical independent variables (gender, species) with contingency tables, logistic regressions were used to be consistent with the other comparisons. However, contingency table analyses yielded the same results. Analysis revealed that predator identity did not influence the autotomy decisions of the prey (logistic regression using predator identity as a factor, Wald $\chi^2 = 11.55$, $p = .71$). Therefore, when investigating decisions of prey with respect to predator attributes, we used individual prey as the independent data points. Variance values reported with means are standard errors.

When investigating factors affecting escape by struggling, the main alternative escape mechanism to autotomy (Table 1), we excluded from the analysis all animals that autotomized and then searched for predictors of successful escape among all others that had been captured during the course of an encounter with a predator (including animals never held by the cheliped). For this analysis, we assumed that all captured animals would have tried to struggle or pinch to escape and hence do not limit the analysis to animals held by the cheliped, a criterion used to determine the occurrence of autotomy (see above) but not necessarily relevant to escape by other means. Accordingly, sample sizes differ between analyses of autotomy and escape. Sample sizes for analyses involving gender are slightly smaller than others because we lacked gender for a few animals. Unless noted otherwise, analyses include animals with one and two chelipeds.

RESULTS

Of the 88 animals that were attacked and held by the cheliped (by definition, the prerequisite for autotomy to occur) two-thirds autotomized their chelipeds and successfully escaped the predator (Table 1). Another one-quarter escaped not by autotomy but by struggling and pinching the predator (Table 1). The combination of cheliped autotomy and struggling with the predator as antipredator defenses is very effective—83 of the 88 animals (94.3%) held by the cheliped

Table 1

Escape methods used by the subset of crabs that were held by the predator by one cheliped at some point during the trial

Escape method	<i>Petrolisthes cinctipes</i>	<i>Petrolisthes manimaculis</i>	Both species
Claw autotomy	27	32	59
Leg autotomy	1	1	2
Struggled/pinched	14	10	24
Did not escape	1	2	3
Total	43	45	88

Numbers in the table are numbers of crabs.

successfully escaped by one of these two methods, 2 (2.3%) escaped by other methods, and only 3 animals (3.4%) failed to escape at all (Table 1).

Prey species

The two porcelain crab species did not differ in their frequencies of autotomy; 62.8% of *P. cinctipes* individuals shed a cheliped compared to 71.1% of *P. manimaculis* individuals (single-factor logistic regression, Wald $\chi^2 = 0.69, p = .41$). The two species did not differ significantly in their likelihood of escape by struggling, although there was a trend for a higher escape rate for *P. cinctipes*; 51.7% ($n = 28$) of *P. cinctipes* individuals escaped compared to 34.4% ($n = 32$) of *P. manimaculis* individuals (analysis restricted to individuals with two chelipeds; single-factor logistic regression, Wald $\chi^2 = 3.07, p = .08$). In the multiple logistic regressions that included all possible variables, species affected neither autotomy nor escape (Table 2). For all subsequent analyses, data from the two species were pooled, unless otherwise indicated.

Number of chelipeds

Some of the *P. manimaculis* individuals used in the trials had lost one cheliped prior to the trials. This enabled us to assess whether the number of chelipeds an individual has affects its propensity to autotomize. Number of chelipeds did not affect likelihood of autotomy; 76.5% of *P. manimaculis* crabs with one cheliped ($n = 17$) autotomized compared to 67.9% of animals with both ($n = 28$) (single-factor logistic regression, Wald $\chi^2 = 0.40, p = .54$). Number of chelipeds was also not a significant factor in the multiple logistic regression analysis of autotomy (Table 2).

Probability of escape was not affected by the number of chelipeds when analyzed in a univariate analysis with *P. manimaculis* (17.4% of 23 one-cheliped animals escaped, 34.4% of 32 two-cheliped animals escaped; contingency table $\chi^2 = 1.20, p = .27$). The effect of number of chelipeds on probability of escape was also not significant when analyzed with the multiple logistic regression, although there was a trend for two-cheliped animals to have a higher escape rate (Table 2).

Body size of prey

Body size predicts the occurrence of autotomy (single-factor logistic regression, Wald $\chi^2 = 10.2, p = .0014$). Crabs that autotomized were smaller than those that did not (Figure 1A; 97.3 ± 2.5 mm for the 59 individuals that autotomized versus 112.7 ± 3.4 mm for the 29 that did not).

Body size also affected probability of escape without autotomy, and the pattern was opposite to the size relation with autotomy: bigger animals were far more successful at escaping by struggling than were smaller ones (single-factor logistic regression, Wald $\chi^2 = 11.12, p < .0001$). Crabs that escaped by struggling and pinching were larger than those that did not (Figure 1B; 116.9 ± 3.7 mm for the 27 individuals that escaped versus 98.5 ± 2.4 mm for the 33 that did not). Examining these data in terms of proportions in each size class that autotomized or that failed to escape by struggling revealed strikingly similar patterns for both (Figure 1C). The strong effect of body size on both autotomy and escape remained when analyzed with multiple logistic regressions (Table 2).

Gender

Females were far more likely to shed their chelipeds (82.0% of 39 females) than were males (54.2% of 48 males; single-factor logistic regression, Wald $\chi^2 = 7.09, p = .008$). The effect of gender was also significant in the multiple logistic regression analysis (Table 2); the latter test indicates that gender and body size independently affect the occurrence of autotomy. Gender also had a marginally significant effect on the probability of escape without autotomy; 25.8% of 31 females escaped by struggling compared to 46.9% of 49 males; single-factor logistic regression, Wald $\chi^2 = 2.78, p = .095$. When analyzed with multiple logistic regression, the marginally significant effect of gender on probability of escape remained (Table 2).

To further explore why gender might affect success at escape by struggling, we compared the relative claw size of males and females in both species. Measurements of 308 field-collected individuals showed that males in both species had significantly larger claws for their body sizes than females (ANOVA for the effect of gender on relative claw size $F_{1,294} = 37.23, p < .0001$).

Predator size

The absolute body size of the predator had no influence on the occurrence of autotomy (single-factor logistic regression, Wald $\chi^2 = 0.64, p = .42$) nor did the relative size of the predator (logistic regression, Wald $\chi^2 = 2.64, p = .10$). Absolute predator size did not affect the likelihood of escape by struggling (single-factor logistic regression, Wald $\chi^2 = 0.87, p = .35$). Relative predator size did affect the likelihood of escape when assessed with the single-factor regression (Wald χ^2 for coefficient for relative predator size = 5.71, $p = .017$). However, neither absolute nor relative predator size affected autotomy or escape when assessed with the multiple logistic regression (Table 2).

Table 2

Summary of stepwise multiple logistic regression analysis to determine variables that predict the occurrence of autotomy and factors that predict the probability of escape by struggling and pinching

Variable	Propensity to autotomize		Escape efficiency without autotomy	
	Pattern	Significance	Pattern	Significance
Body size	Higher for smaller crabs	$\chi^2 = 7.94, p < .005$	Lower for smaller crabs	$\chi^2 = 23.71, p < .0001$
Gender	Higher for females	$\chi^2 = 4.80, p = .028$	Marginally lower for females	$\chi^2 = 3.62, p = .057$
Number of chelipeds	None	$p > .25$	Marginally lower for one-clawed animals	$\chi^2 = 3.07, p = .080$
Prey species	None	$p > .25$	None	$p > .25$
Predator size (absolute or relative)	None	$p > .25$	None	$p > .25$

Separate analyses were done for autotomy and escape; $n = 87$ individuals for autotomy, $n = 81$ for escape. Factors that are positively correlated with the occurrence of autotomy are negatively correlated with successful escape by struggling and pinching.

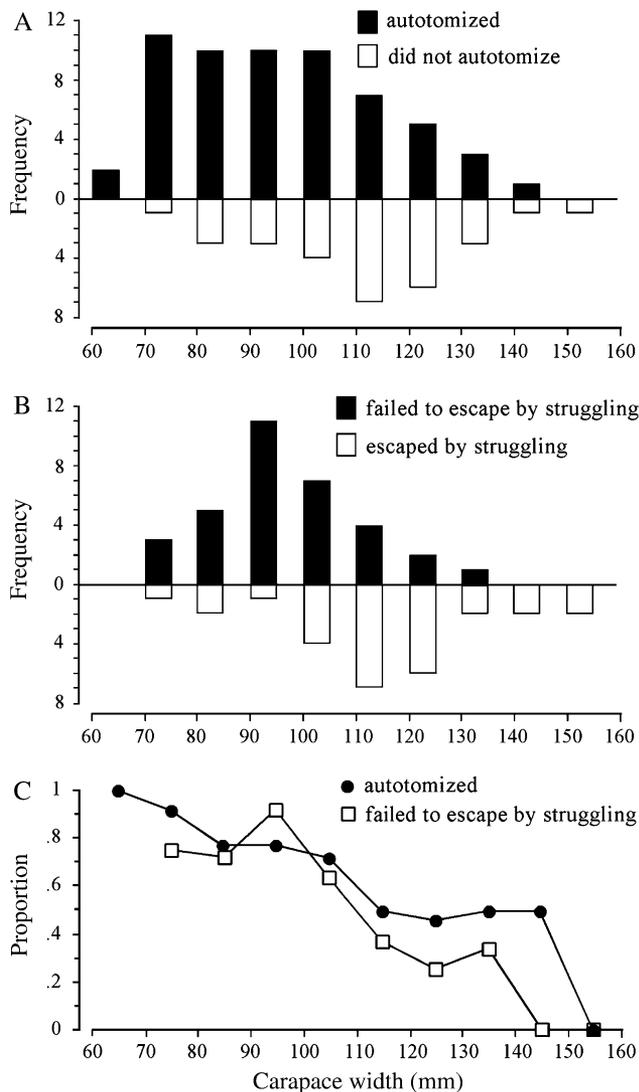


Figure 1 Relationship between body size of *Petrolistes* crabs and their escape strategies. (A) Frequency of cheliped autotomy as a function of body size for those animals that had the opportunity to autotomize (held by cheliped only). (B) Frequency of escape by struggling and pinching as a function of body size, for all captured animals that did not autotomize. (C) Proportions of animals autotomizing and unsuccessfully escaping by struggling as a function of body size; analysis combines data sets from (A) and (B) and illustrates that size-dependent autotomy decisions closely match the likelihood of escape by struggling.

DISCUSSION

Porcelain crabs very effectively employ either a flight or fight defensive tactic once a predator has grabbed them by the cheliped: more than 95% of the individuals captured in this manner in our trials escaped. The decision whether to autotomize or struggle is often made within seconds—autotomy in porcelain crabs is a “hair trigger” response (Wasson et al., 2002). Nevertheless, our results here reveal that this is a subtle behavior, rather than a simple on-off switch: not every crab given the opportunity (held by only the cheliped) autotomizes. We have shown that the propensity to autotomize (versus attempt escape by struggling) varies among individuals, in particular with smaller crabs and females autotomizing more readily than larger ones or males. In addition, individuals do

vary in how quickly they autotomize—in the most extreme cases, some individuals allowed themselves to be held and dragged around the enclosure for 10 min without giving up their claws. Clearly, these animals have exquisite control not only over whether to autotomize but also when to autotomize.

Is the individual variation in autotomy propensity adaptive? If so, this requires that individuals are maximizing their fitness by appropriately tuning their autotomy decisions to context-dependent differences in the benefits or costs of autotomizing. Arnold (1988) has suggested that for lizards, variation in benefits (and not costs) may often drive autotomy decisions. Our findings for porcelain crabs suggest that autotomy is promoted by variation in the benefits of autotomy as well, and that autotomy is part of an adaptively flexible escape strategy that balances the costs and benefits of fight versus flight. Specifically, the fitness benefit of autotomy is best understood as the enhancement of escape efficiency relative to escape by the main alternative, struggling. However, because autotomy always yields a very high probability of escape (98%, Wasson et al., 2002), variation in the success rate of attempting to escape from a predator without autotomizing (i.e., by struggling) must primarily determine the decision to autotomize or not. In support of this view, characteristics of crabs that were associated with less successful escape by struggling—that is, smaller size or female gender—were also associated with higher rates of autotomy (Table 2). That the crabs that were most likely to autotomize were also those that were less likely to escape by the main alternative escape mechanism, struggling (Figure 1C), provides strong evidence that autotomy is condition-dependent and that the flexibility itself is adaptive.

The trade-off between successful escape by struggling and resorting to autotomy was particularly pronounced for body size. This link between small size, reduced escape by struggling, and increased autotomy rate is one of many examples in which body size directly influences strength and determines the outcome of competitive social conflicts within and between species (Austad, 1983; Howard, 1978; Rubenstein, 1984). Further studies with porcelain crabs are required to determine the mechanism by which larger individuals enhance their capacity to escape without autotomy: it may be simply a function of overall increased strength or specifically related to more forceful pinching by the claw. Our results are similar to those of a recent study of a sea star (*A. rubens*) demonstrating that the autotomy propensity declines with size, while mechanical toughness of the body, another type of antipredatory defense, increases (Marrs et al., 2000).

For gender, as with size, our results suggest that variation in benefits drives flexible autotomy decisions. The increased propensity of females to autotomize when held by the cheliped appears adaptive given their decreased likelihood of escape by struggling. Females tend to be somewhat smaller than males, but these gender-related patterns still held when body size was taken into account in the multivariate model—males appear to be superior at struggling even when body size is controlled for. We suggest instead that this fighting ability may be a function of the greater claw size, and thus fighting strength, of males. Similar patterns have been observed in many other crabs (Mariappan, 2000), and porcelain crab males in particular are known to use their claws for territorial defense (Jensen and Armstrong, 1991). If the difference between genders in escape by struggling is due to differences in claw size, then including claw size in the multivariate analysis in place of body size should cause the effect of gender to vanish. Although we did not have claw size data for the individuals used in these experiments (because taking such measurements often results in cheliped autotomy), we used the regression equations obtained from different field-collected individuals to predict the claw size of the experimental subjects, using separate

equations for each gender and each species. As predicted, exchanging claw size for body size caused the effect of gender on struggling success to disappear (gender did not enter in the model; $p > .25$). This provides additional evidence that strength and fighting ability shape autotomy decisions. It would be interesting to compare autotomy thresholds between genders in truly dimorphic species such as fiddler crabs (genus *Uca*), where the enlarged male cheliped is used to ward off predators as well to gain territory and mates (Bildstein et al., 1989). In this case, both decreased benefit (relative to fighting) and increased cost should decrease the propensity of males to autotomize.

Three other factors we examined had no significant effect on the propensity to autotomize or on success at escaping by struggling. These include two prey attributes (species and number of chelipeds) and one predator attribute (predator size) (Table 2). While it is possible that these negative results might reflect low statistical power, this seems unlikely given that other comparisons with identical sample sizes were highly significant. Moreover, the observation that the factors that fail to affect autotomy are the same ones that fail to affect escape by struggling and pinching makes biological sense in terms of the cost-benefit approach we adopt: if the relative benefit of autotomy is determined by factors that influence escape by struggling, then factors that do not affect escape are also predicted to have little influence on autotomy. Nevertheless, behavioral decisions are often based on perceived predation risk (Lima and Dill, 1990), and our study has not exhausted all factors that might affect this perception. With respect to predator attributes, size of the one predatory species we tested appears not to represent important variation in predation threat, but other factors we did not measure may.

While variation (or lack thereof) in benefits to autotomy is sufficient to explain the autotomy decision-making patterns we observed, differing costs of autotomy can of course also shape such strategies. Cost of autotomy, as well as benefits, may vary with prey attributes. For both lizards and crabs, cost of limb loss (in terms of reduced growth rate, mating success, etc.) can vary with size (Arnold, 1988; Juanes and Smith, 1995). Fox et al. (1998) provide an example of differences in costs driving differences in autotomy between sexes of a lizard species (*U. stansburiana*). Significantly more force is required to induce tail autotomy by males than females, apparently due to the greater social cost to males (females but not males can get matings without a tail). Although we propose that variation in the costs of autotomy does not play a major role in determining optimal escape mechanism in our study, autotomy must nonetheless come with high costs. Because these costs are not paid by animals that can escape by struggling, autotomy in porcelain crabs is best considered an example of a “best-of-a-bad-job” type of tactic employed by animals that are likely to have low success with other modes of escape (Dawkins, 1980; Eberhard, 1982). Clearly a full understanding of antipredation decisions in autotomizing taxa requires characterization of both benefits and costs of autotomy and alternative escape mechanisms.

In sum, our study confirms for crabs what Arnold (1988) suggested for lizards: like mimicry, autotomy is a highly complex defensive behavior, rather than a simple adaptation. We have shown that autotomy can be employed as a condition-dependent, adaptively flexible strategy. For the porcelain crabs in our experiments, variation in the benefit of autotomy alone appears sufficient to explain most differences in autotomy threshold between individuals. A framework incorporating the costs and benefits of autotomy versus alternative methods of escape from predators is a powerful way of understanding the evolution of defensive strategies in autotomizing animals.

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REFERENCES

- Arendt JD, 1997. Adaptive intrinsic growth rates: integration across taxa. *Q Rev Biol* 72:149–177.
- Arnold EN, 1988. Caudal autotomy as a defense. In: *Biology of the reptilia*, vol. 16, Ecology B (Gans C, Huey RB, eds). New York: Alan R. Liss; 235–273.
- Austad SN, 1983. A game theoretical interpretation of male combat in the bowl and doily spider. *Anim Behav* 31:59–73.
- Bildstein KL, McDowell SG, Brisbin IL, 1989. Consequences of sexual dimorphism in sand fiddler crabs, *Uca pugilator*: differential vulnerability to avian predation. *Anim Behav* 37:133–139.
- Dawkins R, 1980. Good strategy or evolutionarily stable strategy? In: *Sociobiology: beyond nature/nurture?* (Barlow GW, Silverberg J, eds). Boulder, Colorado: Westview Press; 331–367.
- Eberhard WG, 1982. Beetle horn dimorphisms: making the best of a bad lot. *Am Nat* 119:420–426.
- Formanowicz DR, 1990. The antipredator efficacy of spider leg autotomy. *Anim Behav* 40:400–401.
- Fox SF, Conder JM, Smith AE, 1998. Sexual dimorphism in the ease of tail autotomy: *Uta stansburiana* with and without previous tail loss. *Copeia* 1998:376–382.
- Harvey PH, Greenwood PJ, 1978. Anti-predator defense strategies: some evolutionary considerations. In: *Behavioral ecology: an evolutionary approach* (Krebs JR, Davies NB, eds). Sunderland, Massachusetts: Sinauer Associates; 129–151.
- Howard RD, 1978. The evolution of mating strategies in bullfrogs, *Rana catesbeiana*. *Evolution* 32:850–871.
- Jensen GC, Armstrong DA, 1991. Intertidal zonation among congeners: factors regulating distribution of porcelain crabs *Petrolisthes* spp. (Anomura: Porcellanidae). *Mar Ecol Prog Ser* 73:47–60.
- Juanes F, Smith LD, 1995. The ecological consequences of limb damage and loss in decapod crustaceans: a review and prospectus. *J Exp Mar Biol Ecol* 193:197–223.
- Lawrence JM, 1992. Arm loss and regeneration in Asteroidea (Echinodermata). In: *Echinoderm research 1991* (Scalera-Liaci L, Canicatti C, eds). Rotterdam: Balkema; 39–52.
- Lima SL, Dill LM, 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Can J Zool* 68:619–640.
- Lima SL, Valone TJ, Caracao T, 1985. Foraging efficiency–predation risk trade-off in the grey squirrel. *Anim Behav* 33:155–165.
- Mariappan P, Balasundaram C, Schmitz B, 2000. Decapod crustacean chelipeds: an overview. *J Biosci* 25:301–313.
- Marrs J, Wilkie IC, Skold M, Maclaren WM, McKenzie JD, 2000. Size-related aspects of arm damage, tissue mechanics, and autotomy in the starfish *Asterias rubens*. *Mar Biol* 137:59–70.
- Mauzey KP, Birkeland C, Dayton PK, 1968. Feeding behavior of asteroids and escape responses of their prey in the Puget Sound region. *Ecology* 49:603–619.
- McVean A, 1982. Autotomy. In: *The biology of crustacea*, vol. 4 (Bliss DE, ed). New York: Academic Press; 107–132.
- Reznick DN, Bryga H, Endler JA, 1990. Experimentally induced life-history evolution in a natural population. *Nature* 346:357–359.
- Roff DA, 1992. *The evolution of life histories: theory and analysis*. New York: Chapman and Hall.
- Rubenstein DI, 1984. Resource acquisition and alternative mating strategies in water striders. *Am Zool* 24:345–353.
- SAS, 2003. *JMP statistics and graphics guide*. Cary, North Carolina: SAS Institute, Inc.
- Stearns SC, 1992. *The evolution of life histories*. Oxford: Oxford University Press.
- Wasson K, Lyon BE, Knope M, 2002. Hair-trigger autotomy in porcelain crabs is a highly effective escape strategy. *Behav Ecol* 13: 481–486.
- Werner EE, 1986. Amphibian metamorphosis, growth rate, predation risk and the optimal size at transformation. *Am Nat* 128: 319–341.