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Experimental evidence that high population frequencies of lizard tail autotomy indicate inefficient predation

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Frequency of autotomized tails in lizard populations has been taken as an indicator of predation pressure upon those populations. However, recent correlational evidence points to autotomy as reflecting lizards' escape efficiencies and/or predators' attack inefficiencies. We report experimental evidence on the relative inefficiencies of three predator species (a teiid, a snake, and a falcon) as autotomy-producing agents, and on the relative escape efficiencies of three congeneric lizard species under laboratory conditions. The falcon was the least inefficient lizard predator (100% of successful attacks) whereas the teiid and snake were more inefficient (10–20% of the lizards escaped by autotomizing their tail). Lizards that successfully escaped predation by the widely-foraging teiid had relatively longer tails than unsuccessful ones. No difference in this feature was detected between successful and unsuccessful lizards attacked by the sit-and-wait snake. All three lizard species were equally efficient at escaping the three predators through tail autotomy. Our observed differences of comparative inefficiencies of lizard predators give experimental support to assertions that tail-loss frequencies do not adequately serve as indices of presumed predation pressure. High rates of tail-loss among lizard populations could instead reflect attempts at predation by inefficient predators.

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Introduction

Autotomy, the voluntary tail shedding shown by many lizard families, may occur as a consequence of intra- and inter-specific agonistic encounters (Vitt et al. 1974), or as the result of predator attacks. Frequency of broken and/or regenerated tails in lizard populations has often been taken as an indicator of predation pressure upon those populations, particularly in comparative contexts (Rand 1954, Pianka 1967, 1986, Turner et al. 1982, among many others). Schoener (1979), Jaksić and Núñez (1979), Schoener and Schoener (1980), and Jaksić and Fuentes (1980), however, cautioned that the population frequencies of autotomy may in fact be negatively related with the effectiveness of injury-producing agents (predators included). Indeed, Jaksić and Greene (1984) and Jaksić and Busack (1984) documented that there was a negative correlation between population frequency of autotomy, and respective incidence of lizards in diets of sympatric predators. This information, albeit correlational, points to autotomy somehow reflecting the lizards' escape efficiencies and/or the predators' attack inefficiencies, and consequently cautions against the widespread belief that population frequencies of autotomy index predation pressures upon lizards. In the same vein, Morin (1985) documented experimentally that a negative correlation exists between the population frequency of autotomy in tadpoles and the population density of their predators.

Previous laboratory studies of lizard autotomy have evaluated its physiological (Clark 1971, Vitt et al. 1977, Ballinger and Tinkle 1979, Vitt 1981, Dial and Fitzpatrick 1983), reproductive (Vitt 1981, Dial and Fitzpatrick 1981), locomotor (Ballinger 1973, Punzo 1982,

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Daniels 1983), and social costs (Fox and Rostker 1982). Also, benefits derived from autotomy as an escape tactic have been evaluated in laboratory situations (Congdon et al. 1974, Dial and Fitzpatrick 1983, 1984, Cooper and Vitt 1985, Daniels 1985, Vitt and Cooper 1986, Daniels et al. 1986). However, these studies focused on individual-level responses, rather than on population consequences of autotomy.

Here we report relative inefficiencies of three predator species as autotomy-producing agents, and relative escape efficiencies of three lizard species under laboratory conditions.

Materials and methods

Species

Three predator and three lizard species were subjected to experimental treatment. Predators were: a) two individuals of *Callopistes maculatus* (Sauria: Teiidae), the only saurophagous lizard in Chile (Donoso-Barros 1966); b) five individuals of *Philodryas chamissonis* (Serpentes: Colubridae), one of two Chilean snake species that prey on lizards (Jaksić et al. 1982); and c) four individuals of *Falco sparverius* (Falconiformes: Falconidae), the Chilean avian predator with the highest incidence of lizards in its diet (Yáñez et al. 1980).

Prey lizards were: a) 40 individuals of *Liolaemus lemniscatus* (Sauria: Iguanidae), a ground-dwelling species of mean = 44.6 mm snout-vent length; b) 50 individuals of *L. monticola,* a rock-dweller of 54.3 mm; and c) 53 individuals of *L. altissimus,* a rock- and ground-dweller of 67.5 mm. None of these species is sexually dimorphic (Jaksić and Fuentes 1980). All predators and prey were collected between January and May 1986 (austral summer and fall), around Santiago (33°30'S, 70°40'W), Chile.

Experimental setting

Staged encounters between lizards and their reptile predators (the teiids and snakes) were observed in a 2.0 × 1.0 × 0.8 m terrarium. The encounter chamber walls were wooden except for the glass front; the substrate was carpeted with soil and dead leaves, the roof was of wire mesh, and a 100 W lamp provided both light and heat. The temperature of the terrarium was monitored with a dry bulb thermometer placed at mid-distance on one of the lateral walls. Snakes and teiids were maintained in the same cages where the encounters were run.

Before each encounter, the following measurements on each lizard were taken with calipers (precision 0.1 mm): snout-vent length and tail length (only individuals with intact tails were used in the experiments). Subsequently, the lizard's body temperature (as well as that of a teiid or snake predator) was elevated to its normal field activity temperature (see Fuentes and Jaksić 1979) by placing a lamp above the storage cage, and was monitored with a Schultheis cloacal thermometer. In the case of the falcons, a 4.0 × 3.5 × 2.5 m room with soil and leaves as substrate, and a blind for observations, was used. Each individual lizard prey was used in one staged encounter only, all of which were conducted between 1100 and 1700 hours from January to May, 1986.

Observations recorded

We noted whether an encounter resulted in autotomy or not, and whether lizards that autotomized tails actually escaped predation or not. The following two situations were recognized: a) sucessful autotomy: when the lizard escaped predation by shedding its tail, and was not caught for at least 10 s after the encounter occurred; b) capture: when the lizard was captured before autotomizing, or when autotomy was unsuccessful, that is, the autotomized lizard was captured within 10 s of having lost its tail.

The inefficiency of each predator species was computed as the number of successful autotomies elicited over the total number of predator attacks. Relative inefficiency across predator species could then be determined: the most inefficient predator species was that which caused the largest percentage of successful autotomies. Conversely, escape efficiencies of the different lizard species were computed as the number of individuals that escaped through tail autotomy (versus those captured) over the total number of prey lizards subjected to predation encounters.

Statistical significance of relative inefficiency of predators, relative escape efficiency of lizards, and attack sites on the prey, was evaluated by means of Williams' continuity-corrected G-tests (Sokal and Rohlf 1981).

Shortcomings of the experimental design

Because the teiids and snakes were kept in the same cages where the encounters were staged, whereas the lizards were introduced from a different cage, the latter were at a definite disadvantage as per familiarity with their surroundings. The same happened with the falcon-lizard encounters. Consequently, predator inefficiencies at capturing lizards in the encounter chambers may be grossly (though systematically) underestimated in comparison to natural situations. Also, because the substrate in the encounter cages was only of soil and dead leaves, it may have been more favorable (in terms of escape) for the fully terrestrial *L. lemniscatus,* and the rock-and-ground dweller *L. altissimus,* than for the fully saxicolous *L. monticola.* Consequently, relative escape efficiencies measured for the different lizards may be artificially low estimates of their escape success in the wild.

Tab. 1. Outcomes of the attack of three predator species on lizards: either capture or escape by autotomy. The location of the attack on the lizards' body is also presented. n1 = individuals of predators tested; n2 = individuals of prey lizards tested. Figures in table are frequencies by number and by percentage (in parentheses).

Predators	n1	n2	Attack outcome				Attack location					
			Capture		Escape		Head		Trunk		Tail	
Teiid	2	65	58	(89.2)	7	(10.8)	21	(32.3)	38	(58.5)	6	(9.2)
Snake	5	41	33	(80.5)	8	(19.5)	10	(24.4)	23	(56.1)	8	(19.5)
Falcon	4	37	37	(100.0)	0	(0.0)	0	(0.0)	37	(100.0)	0	(0.0)

Results and discussion

All three predator species were efficient at capturing lizards in the experimental cages (80–100% of the lizard individuals were killed during encounters; Tab. 1). The falcon was the most deadly predator: lizards did not have a chance to autotomize, whereas 10–20% of the lizards subjected to encounters with teiids and snakes were able to escape predation by autotomy (Tab. 1). Overall, there was a significant difference in the relative inefficiencies of the three predators (G = 10.6; d.f. = 2; $P < 0.01$). However, there was no significant difference in the inefficiency of teiids and snakes as lizard predators (G = 1.49; d.f. = 1; $P > 0.10$), but the difference was significant in the comparison of teiids with falcons (G = 6.11; d.f. = 1; $P < 0.025$), and of snakes with falcons (G = 10.45; d.f. = 1; $P < 0.005$).

Relative inefficiencies may be related to perceptual differences between predators: teiids and snakes appeared to detect and approach lizards by olfaction, directing their attack to the bulk of the lizard, oftentimes to the tail (Tab. 1). In contrast, visually-oriented falcons appeared to direct their attack specifically to the lizard's trunk, never to the head or tail (Tab. 1). There was no significant difference between teiids and snakes in attack frequency on different parts of the lizard's body (G = 2.45; d.f. = 2; $P > 0.10$), but the difference was significant in the comparison of teiids with falcons (G = 27.98; d.f. = 2; $P < 0.001$), and of snakes with falcons (G = 26.41; d.f. = 2; $P < 0.001$).

A distinction may be made between the snakes and teiids tested: the former are ambush predators whereas the latter are widely-foraging predators (pers. obs.). These different foraging modes may be reflected on the lizards attacked (Huey and Pianka 1981); long-tailed terrestrial lizards have been hypothesized to have evolved this feature as a means to reduce the attack success of widely foraging predators (Vitt 1983). We tested this hypothesis by comparing tail length (as standardized by snout-vent length) of lizards attacked on the tail versus the body (head and trunk combined) by either snakes or teiids. Lizards attacked by snakes on the tail versus the body did not differ in relative tail length (mean = 1.73 ± 2SE 0.2, n = 8; versus 1.62 ± 0.2, n = 33; Student t test for heterogeneous variances: t = 0.52; $P > 0.50$). Instead, lizards attacked by widely foraging teiids on the tail versus the body had relatively longer tails (1.90 ± 0.2, n = 6; versus 1.55 ± 0.1, n = 59; Student t test for heterogeneous variances: t = 2.14; $P < 0.05$). This result supports the hypothesis of Vitt (1983).

All lizard species were equally efficient at escaping the three predators through tail autotomy (G = 1.80; d.f. = 2; $P > 0.10$). This is intriguing because the three prey species do differ in the population frequencies of broken/regenerated tails as recorded in the field. Jaksić and Fuentes (1980) reported the following figures: *L. lemniscatus* (49.0%), *L. monticola* (68.0%), and *L. altissimus* (52.9%). These, however, are frequencies uncorrected for longevity and subsequent cumulative exposure to predators, and may be misleading as indices of predation pressure or inefficiencies. In addition, population tail break frequencies may differ for the same lizard species. In a different site, Núñez and Yáñez (1984) reported the following figures: *L. lemniscatus* (51%), *L. monticola* (24%), and *L. altissimus* (59%). The discrepancy for *L. monticola* is large.

Our observed differences of comparative inefficiencies of lizard predators lend experimental support to correlational evidence that tail-loss frequencies may not adequately serve as indices of presumed predation pressure (Jaksić and Greene 1984, Jaksić and Busack 1984). High rates of tail-loss among natural populations of lizards could instead reflect multiple attempts at predation by an inefficient predator, e.g., *C. maculatus* of our study. Predator inefficiency (from laboratory studies) as well as its diet (from field studies) must be known to evaluate its impact on tail-loss frequencies among lizard prey. Even though *C. maculatus* is an inefficient predator, it may not often hunt lizards in nature, preferring alternative insect prey. Tail-loss frequencies in nature are a complicated property of predator electivity and inefficiency and prey longevity and conspecific-induced autotomy. Our study stresses the importance of evaluating the relative inefficiency of lizard predators, especially in studies that include comparisons of predation pressure between sites with different predator or prey composition.

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