cruing from it to the organisms is the rapid removal of indigestible matter from their feeding environment. The rapid sinking out of all useless particulate matter eliminates the need to reprocess it repeatedly, an activity that costs energy but yields none. The packaging of useless matter into larger particles may represent a net saving. It appears that, without this activity of the organisms, the fine-particle concentrations in the surface waters of the ocean would build up to much higher levels.

W. G. Deuser, P. G. Brewer
Woods Hole Oceanographic Institution,
Woods Hole, Massachusetts 02543
T. D. Jickells
Bermuda Biological Station for
Research, Ferry Reach 1-15, Bermuda
R. F. Commeau
U.S. Geological Survey,
Woods Hole, Massachusetts 02543

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Lizard Tail Autotomy: Function and Energetics of Postautotomy Tail Movement in *Scincella lateralis*

Abstract. *Handling of autotomized, thrashing and autotomized, exhausted tails of the lizard* Scincella lateralis *by mammals and snakes was tested to examine the function of postautotomy tail movement. Tail movement attracted a mammal's attack to the tail, permitting the lizard to escape and increased the time required for a snake to subdue a tail before swallowing it, increasing the lizard's escape time by 40 percent. Lactate concentrations of autotomized tails after movement were compared to those of intact tails after rest in* S. lateralis, *a species with a high rate of autotomized tail thrashing, and* Anolis carolinensis, *a species with a low rate of thrashing. Postautotomy movement increased tail lactate concentration in both species, but mean tail lactate concentration in* S. lateralis *was 60 percent higher than that in* A. carolinensis, *and a third higher than that reported for whole-body lactate content of the very mobile lizard* Dipsosaurus dorsalis.

Autotomy of body parts has evolved independently in vertebrates (*1, 2*) and invertebrates (*3*) as a predator defense in which mechanical release of the structure facilitates escape (*4*). In general, an autotomous structure is relatively simple in morphology with few interacting variables and has an alternative biological role, such as locomotion or feeding. Thus, autotomy offers a simplified model system for studying several important topics of evolutionary biology—for example, the costs of predator defense mechanisms, apportionment of resources to somatic versus reproductive components, and the evolution of predator-prey interactions (*5, 6*). A postautotomy phenomenon characterized by an extended period of muscle contraction in the autotomized structure occurs in several groups: decapods, arachnids (*7*), salamanders (*1*), and lizards (*8*) are examples. The tail in some species of lizards may thrash rapidly from side to side immediately after autotomy (*8*). Although postautotomy tail movement has been of interest for nearly a century (*9*), neither the function nor energetics involved is clear (*10–12*). We report experimental evidence indicating that postautotomy tail movement either distracts predators from escaping lizards or increases handling time of the released tail, allowing more time for prey escape (or both), and that such tail movement is supported by anaerobic metabolism, the capacity of which is greater in species that use autotomy as a principal predator escape tactic.

Lizards constitute an important dietary component of mammals (*13, 14*) and snakes (*15*). Because the feeding mechanics and behavior of these predators differ considerably (*14, 16*), the effects of autotomized tail movement on predator handling might vary among predator types. Because capturing prey for many mammal species involves manipulation with forelimbs before ingestion, prey are periodically free from a mammal's grip, and a mammal's attention is focused on the most active part of the prey (*14*). We thus hypothesized that movement of an autotomized tail should function to attract and maintain a mammal's attention on a tail and away from an escaping lizard. In contrast, a prey item is rarely free from a snake's grip. In addition, many snake species, in particular those that subdue prey by constriction, do not manipulate prey before prey movement has subsided (*16*). We hypothesized that autotomized tail movement should increase the time required for a snake to handle a tail, thereby allowing more time for prey escape.

To examine whether postautotomy tail movement distracts predators, we staged encounters between lizards of two species and a feral cat (*Felis catus*, 5.5 kg). We chose the lizards *Scincella lateralis* and *Anolis carolinensis* (*17*) because of their high and low rates of tail thrashing (*18*). Tail autotomy is the principal escape tactic of *S. lateralis*, which relies on autotomy to a greater extent than does *A. carolinensis* (*18*); *A. carolinensis* uses several alternative escape tactics. We recorded the cat's reaction to lizards of both species plus their autotomized and thrashing tails and their autotomized and exhausted tails (*19*). To examine whether postautotomy tail movement increases predator handling time, we staged encounters between *S. lateralis* and a snake, *Lampropeltis triangulum*, again using both autotomized and thrashing tails and autotomized and exhausted tails (*20*). For each tail, we measured total handling time and two of its components: subdue and ingestion time (*21*). To examine whether postautotomy tail movement is supported by anaerobic metabolism and is greater in species that chiefly use autotomy, we compared lactate concentrations of autotomized tails after thrash-

Table 1. Responses of a feral cat to simultaneous presentation of autotomized tails and live tailless bodies of *A. carolinensis* ($N = 14$) and *S. lateralis* ($N = 13$). Attacks on exhausted as opposed to thrashing tails in *A. carolinensis* were not significantly different, but those for *S. lateralis* were ($P < .001$; $\chi^2(1) = 14.01$).

Tail	Number of responses		
	Attack to tail	Attack to body	Escape of lizard
	Anolis carolinensis		
Exhausted	0	8	3
Thrashing	0	6	1
	Scincella lateralis		
Exhausted	0	6	0
Thrashing	7	0	7

ing to those of intact tails after rest for both species of lizards (*22*).

All of the lizards in the mammal experiments immediately attempted to escape. In 100 percent of the trials with *A. carolinensis* (both thrashing and exhausted tails), the cat pursued the lizards and ignored the tails (Table 1). In 100 percent of the trials with exhausted *S. lateralis* tails, the cat pursued and captured the lizards, whereas in 100 percent of the trials with thrashing *S. lateralis* tails the cat was attracted to and attacked the tails. Lizard escape occurred in all thrashing tail trials with *S. lateralis*. Thus, in an encounter with a mammal, postautotomy tail movement appears to be a successful escape tactic for *S. lateralis*, whereas the modest tail movement in *A. carolinensis* is not.

In snake-lizard encounters with *S. lateralis*, total handling time was significantly longer for thrashing tails than that for exhausted tails ($P < .02$) (*23*), primarily because the subdue time was significantly longer (Fig. 1) ($P < .01$); ingestion times were not significantly different. The time required for a snake to subdue a thrashing tail—the handling component affected most by prey movement (*16*)—before it could be manipulated and swallowed averaged 23 percent of the total handling time; exhausted tails required only 2 percent of the total handling time for what could be called subduction. Snakes required an average of 37 seconds longer to handle thrashing tails than exhausted tails, increasing the total time available for a lizard's escape by 40 percent. Snakes constricted 44 percent of the thrashing tails, a behavior associated with prey subduction (*16*), but none of the exhausted tails. Although snakes attacked all exhausted tails, they immediately released 43 percent of them and returned to their original foraging behavior. Perhaps tail movement also mimics captured lizard movement, relaying to the snake a message of successful capture.

Lactate concentration was significantly higher in autotomized tails after thrashing than in intact tails after rest for both species (Fig. 2) ($P < .001$). Mean lactate concentration in autotomized *S. lateralis* tails (2.71 mg/g) was significantly higher than that of *A. carolinensis* (1.61 mg/g) ($P < .001$), and was one-third higher than the maximum whole-body concentration reported for lizards (*24*). Although thrashing significantly increased lactate content in *A. carolinensis* tails, the increase reflects only the normal whole-body capacity of anaerobic metabolism for this species; mean autotomized tail lactate concentration was not significantly different from that of exhausted whole-body *A. carolinensis* (*t*-test) (*25*). In contrast, mean lactate concentration of autotomized *S. lateralis* tails was twice that reported for exhausted whole-body *S. lateralis* (*25*). However, because other values reported (*25*) are for whole animals, and many lizards use intact tails in locomotion (*5, 11, 26*), it is possible that concentrations in *S. lateralis* reflect the anaerobic metabolic capacity of intact tails, an adaptation that may facilitate rapid-burst locomotion during escape (*27*). We tested this by comparing lactate concentrations of autotomized tails after thrashing with those of intact tails taken from lizards after escape behavior (*28*). Mean lactate concentration of autotomized *S. lateralis* tails after thrashing was eight times higher than that of intact tails after escape behavior (Fig. 2). Thus, the high anaerobic metabolic capacity of autotomized *S. lateralis* tails appears to be an adaptation for the postautotomy aspect of this defense (*29*).

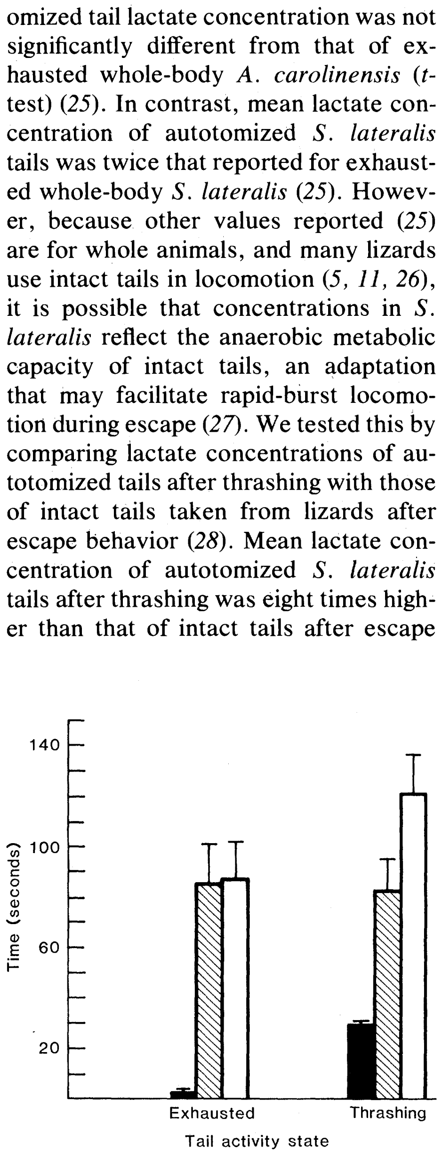

Fig. 1. Subdue time (S_t, solid bars), ingestion time (I_t, striped bars), and total handling time (H_t, open bars) for *L. triangulum* with autotomized and exhausted or autotomized and thrashing tails of *S. lateralis*. Sample sizes for exhausted and thrashing tails, respectively, are S_t ($N = 12$ and 16), I_t ($N = 12$ and 13), and H_t ($N = 12$ and 13). Data are reported as means ± standard errors of the mean.

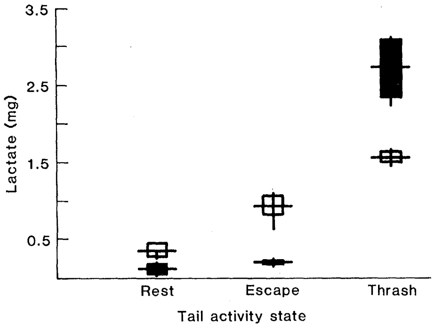

Fig. 2. Lactate concentration of intact tails at rest, intact tails after escape behavior, and autotomized tails after 60 seconds of thrashing for *A. carolinensis* (open bars) and *S. lateralis* (solid bars). For *A. carolinensis*, $N = 6$, 4, and 6, respectively, and for *S. lateralis*, $N = 6$ in all three cases. Horizontal lines represent mean values; vertical lines, ranges; and rectangles, 1 standard deviation.

In many lizard species, such as *A. carolinensis*, tail autotomy represents a secondary line of defense to alternate primary tactics (*5, 30*), functioning simply as a mechanical release that facilitates escape from a predator's grip; after autotomy has occurred, the autotomized tail is not important to the success of this defense. In contrast, in those species that use tail autotomy as a principal escape tactic, such as *S. lateralis*, our results suggest that postautotomy tail thrashing supplements mechanical release and that its function differs among various predator types: to attract a predator's attention or to increase the predator's handling time of the autotomized tail. Studies of postautotomy muscle contraction in autotomized structures of other vertebrates and many invertebrates (*1, 3, 7*) may demonstrate convergence of both the functional and biochemical bases of this novel predator defense tactic.

BENJAMIN E. DIAL
Department of Biology, Texas A&M University, College Station 77843
LLOYD C. FITZPATRICK
Department of Biological Sciences, North Texas State University, Denton 76203

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10. Clark (*8*) showed experimentally that postautotomy tail movement propels tails through leaf litter and suggested that the tail may therefore move away from a predator and be retrieved by its owner. However, in more than 50 snake-lizard encounters that resulted in tail autotomy, we did not observe a snake to loose its grip on a tail. In addition, many lizard species with active autotomized tails, such as most eublepharine and gekkonine lizards, occur in relatively open, litter-free habitats.
11. C. M. Pond [*Annu. Rev. Ecol. Syst.* **9**, 519 (1978)] suggested that autotomized tail movement might mimic snake movement, and, presumably, frighten predators. However, many predators that encounter autotomized tails are themselves snakes or predators of snakes.
12. Most accounts simply suggest that autotomized tail movement distracts a predator [for example, (*9*); H. B. Cott, *Adaptive Coloration in Animals* (Methuen, London, 1944), pp. 160–161; A. Bellairs, *The Life of Reptiles* (Universe Books, New York, 1969)]. However, there have apparently not been experimental studies of this proposal nor has a mechanism been reported.
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17. Adults of both species were collected in the spring of 1980 in Dallas and Harris counties, Texas. Only specimens with original (nonregenerated) tails were used in experiments.
18. Thrash rates: *S. lateralis* > 300 per minute; *A. carolinensis* < 50 per minute. Mean frequency of tail break: *S. lateralis*, 64 percent ($N = 31$); *A. carolinensis*, 38 percent ($N = 32$).
19. Autotomy was induced by gripping tails at the basal caudal fracture plane (*2*) with forceps. In thrashing tail trials, lizards and their autotomized tails were placed in front of the cat immediately after autotomy. In exhausted tail trials, tails were allowed to thrash to exhaustion (> 5 minutes), after which lizards and their autotomized tails were placed in front of the cat.
20. In thrashing tail trials, intact tails were presented to snakes, base first; snakes attacked tails, after which autotomy and thrashing occurred. In exhausted tail trials, autotomy was induced with forceps. After tails had thrashed to exhaustion, they were presented with forceps, base first to snakes. Thrashing and exhausted tails were not significantly different in mass, length, or maximum diameter. *Lampropeltis triangulum* is a natural predator of *S. lateralis* [F. N. Blanchard, *U.S. Natl. Mus. Bull.* **114**, 1 (1921)]. Specimens (three subadults) were obtained from a commercial dealer.
21. For thrashing tails, subdue time (S_t) is the time from autotomy to manipulation of the tail in the snake's jaws. For exhausted tails, it is the time from attack to the tail to manipulation. Ingestion time (I_t) is the time from manipulation to completion of ingestion. Total handling time (H_t) = $S_t + I_t$. All times were measured to the nearest 0.01 second with an electronic stopwatch.
22. To establish resting lactate content of intact tails, we maintained lizards at rest for 24 hours, froze them in liquid nitrogen, removed tails, and measured lactate concentration. To establish lactate content after autotomy and thrashing, we induced autotomy at the basal caudal fracture plane, allowed tails to thrash for 60 seconds, froze them in liquid nitrogen, and measured lactate concentration. Data from our experiments with predators handling autotomized tails suggest that 60 seconds is the most ecologically important time span after autotomy; in most trials the predator had begun tail manipulation before 60 seconds had expired. However, *S. lateralis* tails may thrash for 4 to 5 minutes. Thus, our data may in fact underestimate total lactate production of an autotomized tail. Tails were homogenized in five to eight times their mass in 0.6N perchloric acid in a tissue grinder. Samples were centrifuged for 10 minutes at 3000 rev/min. The supernatant was removed and filtered with a syringe filter. Samples were analyzed for lactate content with an enzymatic test kit (Single Vial Lactate, Bio-Dynamics/bmc Co.) and a spectrophotometer. All samples were read at 340 nm.
23. Unless otherwise noted, we used the Mann-Whitney U test [S. Sigel, *Nonparametric Statistics for the Behavioral Sciences* (McGraw-Hill, New York, 1956), pp. 116–127.
24. The maximum concentration (2.07 mg/g) was reported in the extremely mobile *Dipsosaurus dorsalis* after 2 minutes of activity [A. F. Bennett and W. R. Dawson, *J. Comp. Physiol.* **81**, 289 (1972)].
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28. To estimate lactate concentration of intact tails after escape behavior, we chased lizards through leaf litter (*S. lateralis*) and among wooden perches (*A. carolinensis*) for 60 seconds, froze them in liquid nitrogen, removed tails, and measured lactate content (*22*).
29. Tail lactate content will depend at least partly on the proportion of the tail that is muscle versus skeletal and fat tissue. Thus, a higher lactate concentration in the autotomized tail of one species might reflect proportionally more muscle tissue in that tail [R. W. Putnam, *Physiol. Zool.* **52**, 509 (1979)].
30. See L. J. Vitt and J. D. Congdon [*Am. Nat.* **112**, 595 (1978)] for some examples.
31. We thank C. L. Simmons, H. W. Greene, M. E. Feder, A. F. Bennett, and G. W. Ferguson for comments on the study and the manuscript, and H. E. Rawlins, Jr., R. E. Gatten, J. B. Murphy, D. Barker, B. Tryon, R. G. Coghill, J. Norwood, and T. Faulkner for assistance during the study. Supported in part by grants to B.E.D. from the Theodore Roosevelt Memorial Fund (American Museum of Natural History), the Gaige Fund (American Society of Ichthyologists and Herpetologists), and Sigma Xi, and to L.C.F. from the Faculty Research Fund. Funds for manuscript preparation were provided by the Department of Biology, Texas A&M University.

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A Bean α-Amylase Inhibitor Formulation (Starch Blocker) Is Ineffective in Man

Abstract. *A commercial α-amylase inhibitor with potent inhibitory activity in vitro was used in a randomized double-blind, cross-over clinical trial in six nonobese, healthy adult males. In these subjects, this inhibitor had no effect on the response of blood glucose, insulin, or breath hydrogen to a standardized starch meal. It is concluded that this formulation has no effect on starch digestion in humans.*

A large number of α-amylase inhibitor formulations (starch blockers) derived from kidney bean have recently become available to the general public as dietary supplements. Advertisements for these products claim that they decrease starch digestion and absorption, resulting in weight loss. In June 1982, consumption of these starch blockers in the United States was estimated to be 10 million tablets per week (*1*). We have studied the effects of one of several apparently similar commercial inhibitor formulations on starch digestion and absorption in humans.

In vitro, α-amylase inhibitors prevent hydrolysis of the α-1,4-glycosidic linkages of starch by noncompetitive binding to the enzyme; however, their effect in humans is unknown (*2*). Marshall and Lauda isolated and characterized the inhibitor derived from kidney beans and developed an in vitro assay for inhibitor activity (*3*). Other reports have described similar inhibitors derived from other plant sources (*4*). These inhibitors appear to be glycoproteins specific for mammalian amylase of either salivary or pancreatic origin. They appear to have no other physiologic activity, for example, trypsin inhibition or hemagglutination.

Effective inhibition of starch digestion in vivo would diminish glucose formation and absorption by the small intestine and increase the amount of undigested starch reaching the colon. We tested the effect of the inhibitor on glucose formation and absorption by measuring changes in the concentrations of glucose and insulin in the serum of human volunteers after they had consumed a starch meal. We simultaneously measured breath hydrogen levels that would rise if greater than 6 to 10 g of unabsorbed carbohydrate reached the colon (*5*). If α-amylase inhibitors were effective, we would expect a reduced increase in glucose and insulin and elevated breath hydrogen production.

We obtained α-amylase inhibitors from four commercial sources. The inhibitors were assayed (*6*) for inhibitory activity in vitro by the method of Marshall and Lauda (*3*). We selected the most active of these commercially available inhibitors for study and used two tablets containing 16,666 units of total activity. This dose was compared to a calcium phosphate placebo which exhibited less than 5 percent of the inhibitor's activity and was physically indistinguishable from the inhibitor (*7*).

We studied six, healthy, nonsmoking