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## Effect of Caudal Autotomy on Locomotor Performance of Wall Lizards (*Podarcis muralis*)

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**ABSTRACT.**— We examined the effects of caudal autotomy on terrestrial and arboreal locomotor performance using European wall lizards (*Podarcis muralis*) from an established population in Cincinnati, Ohio. Tail loss significantly increased running speed and distance travelled but markedly decreased arboreal locomotor performance (speed and distance). The effects of tail type (original, unbroken vs. regenerated, previously broken) seldomly were significant before autotomy but became more markedly apparent following tail removal. Significant interactions between tail type and autotomy indicated that individuals possessing original or regenerated tails responded differently to tail loss. Whereas original tails were associated with superior locomotor performance before tail loss, individuals that had possessed regenerated tails before autotomy ran fastest and farthest and traversed an arboreal substrate fastest after their tails were removed. These results suggest that lizards that have been previously subjected to caudal autotomy are able to learn by experience how to compensate for the absence of a tail and, accordingly, traverse an arboreal substrate faster—even after their tail has regenerated and is subsequently autotomized again. The importance of these trends is discussed in light of foraging and escape mode postulates.

Studies of lizard anti-predator tactics have focused on many complex behavior patterns (Schall and Pianka, 1980) including fleeing (Ballinger et al., 1979; Bauwens and Thoen, 1981; Punzo, 1982; Daniels, 1983), crypsis (Vitt and Congdon, 1978), biting and defecation (Bustard, 1971), and caudal autotomy (Vitt et al., 1977; Bauwens and Thoen, 1981; Punzo, 1982; Daniels, 1983; Vitt, 1983; Vitt and Cooper, 1986; see Arnold, 1984, 1988 and Ballairs and Bryant, 1985 for reviews). The ability of a lizard to shed its tail (caudal autotomy) during an attack allows for escape by distracting predator attention away from vulnerable body parts and by facilitating escape when the tail is grasped (Dial, 1981; Daniels, 1983; Arnold 1984, 1988; Vitt and Cooper, 1986). Caudal autotomy is an anti-predator adaptation that should be selectively favored in both habitat-generalists that forage widely and rely primarily on running for predator escape, and in the habitat-specialists, the so called “sit-and-wait” ambush foragers that rely primarily on crypsis for predation avoidance (Vitt and Congdon, 1978; Huey and Pianka, 1981; Vitt, 1983; see also Bauwens and Thoen, 1981).

The adaptive significance of this mechanism is suggested by records of high tail breakage and regeneration frequencies from lizards surviving high intensity predation (Vitt et al., 1977; Vitt, 1983; but see Schoener, 1979), and by experiments showing that tailless lizards are less

able to escape capture by predators as compared to their tailed counterparts (Daniels, 1981 as cited in Daniels, 1983; Dial and Fitzpatrick, 1981; Vitt and Cooper, 1986). The importance of caudal autotomy as an escape mechanism is also confirmed by records of large numbers of detached tails found in the stomachs of lizard predators (McKinney and Ballinger, 1966).

Tails serve many other important functions and autotomy may be physiologically disadvantageous and energetically costly (Arnold, 1984, 1988; Bellairs and Bryant, 1985). For example, tail loss may result in decreased growth rates (Ballinger and Tinkle, 1979), loss of lipid energy reserves (Avery, 1974; Vitt et al., 1977), decreased reproductive capacity (Dial and Fitzpatrick, 1981; Vitt and Cooper, 1986) and decreased probability of future survival (Wilson, 1992). Tail loss may also reduce social status within lizard species that use the tail for intraspecific displays (Fox and Rostker, 1982; see Schall et al., 1989). Several studies have shown tail loss to be costly in terms of locomotion; in bipedal lizards, the tail has been shown to act as an important traction providing counterbalance (Ballinger et al., 1979) and its loss may result in marked decreases in running speed (Punzo, 1982). The tail may also be an important balancing organ for climbing species (Ballinger, 1973), which may use it as a counterpoise or coil it around branches while climbing; even unspecialized climbers may depend on the tail to more evenly distribute weight over flimsy vegetation (Arnold, 1988; see also Sinverno and Losos, 1991).

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The present study stems from observations of a population of urban European wall lizards, *Podarcis muralis* (Lacertidae), that developed from a small number of individuals introduced to Cincinnati, Ohio from northern Italy in 1951 (Vigile, 1977; Heeden, 1984). This population has thrived for more than forty years in total isolation from its native source and has spread throughout much of Cincinnati's east side along the Ohio river (Vigile, 1977; Hedeon, 1984; Kwiat and Gist, 1987). Tail breakage occurs at frequencies between 40–60% ( $N = 203$ ; RMB, unpubl. data) and predation pressures on Cincinnati populations are almost entirely attributed to omnipresent feral cats (RMB, pers. obs.; no avian predation has been observed). When approached by a potential predator (cat or investigator), Cincinnati wall lizards do not employ crypsis, but instead retreat immediately into adjacent cover (preferred habitat is south facing containment walls bordered with vegetation; Gruschwitz and Bohme, 1986) and often traverse horizontally through underbrush before dropping to the substrate for retreat into burrows or similar refugia (RMB, pers. obs.).

We examined both terrestrial and arboreal locomotion in an attempt to elucidate the importance of the tail for two classes of locomotor performance in *P. muralis*. Because tail breakage is such a prevalent phenomenon in this population and since predation pressures would not be expected to change following autotomy, the experimental design incorporated lizards with unbroken original tails as well as lizards with regenerated tails in order to test whether tail type (original vs. regenerated) affects performance (terrestrial or arboreal) before and/or after autotomy.

#### MATERIALS AND METHODS

We employed a  $2 \times 2$  experimental design to examine the effects of tail loss (caudal autotomy) and tail type (original unbroken vs. regenerated) on terrestrial and arboreal locomotor performance in *Podarcis muralis*.

To minimize sampling biases, ten male wall lizards, five with original tails and five with tails regenerated were nonselectively chosen from 46 comparably sized wall lizards collected by noosing from Cincinnati, Ohio in July 1991. Prior to locomotion trials, all lizards were housed outdoors in 76 L aquaria within a screened enclosure in direct sunlight and provided with basking sites and refugia. The animals were fed a diet of mealworms and crickets ad libitum and were also provided with small dishes of water. Experiments were undertaken within one week of capture.

Before locomotor behavior of individual lizards was tested, snout-to-vent length (SVL), tail

length, and total body mass were measured to the nearest 0.1 mm or 0.1 g, respectively. In an effort to control for any potential effects of temperature or time of day (i.e., activity level) all locomotion trials were conducted under identical conditions within the wire enclosure in the late afternoon at temperatures ranging from 32–34 C. A fiberglass-walled track ( $2 \times 0.35 \times 0.35$  m) with a porous press-board floor, marked with 1 cm increments, and equipped with a sliding-door starting gate, was used for all tests.

Terrestrial locomotion was initiated by flicking wall lizards across the base of the tail with a dissecting needle and simultaneously opening the starting gate as sprints were recorded with a Sony Video-8 camera at 30 frames per sec (calibrated by filming a running stopwatch). Arboreal locomotion was recorded in a similar manner by filming wall lizards forced to horizontally traverse a braid of heavy nylon cord 2 cm in diameter (also marked with 1 cm increments) suspended above the sprint arena and attached to far ends of the track. The cord braid was pulled tight enough to prevent it from looping down but loose enough to allow for some swinging from side to side. Five trials were recorded for each lizard per test with a 5 min recuperation period between each trial. The best sprint for each lizard (maximum velocity and distance) was used in subsequent analyses after examining the data from each set of five trials for patterns in performance that might indicate training or fatigue effects.

Tails were then autotomized by pinching at the tail base (the mass of tailless lizards and of the tails were recorded immediately to the nearest 0.1 g). Wall lizards were then housed individually in  $15 \times 30 \times 9$  cm plastic storage boxes that minimized running and climbing and possible associated learning effects during the period of injury recovery. Locomotor performance tests were repeated 48–50 h later and tailless body mass was again recorded (identical conditions and methods).

Video-8 films of locomotor performance trials were transferred to a VHS Toshiba SVF 9-90 VCR which has a digital read-out and a frame-per-frame advance feature enabling analyses to be carried out by counting frames during the determination of sprint velocity ( $\Delta d/\Delta t$  expressed in m/sec) and sprint distance (m).

Following initial confirmations of normality (Sokal and Rohlf, 1981) we used one-factor analyses of variance (ANOVA) to analyze the morphological data, and two-factor repeated measures ANOVAs for performance variables factored by autotomy and tail types. Student's *t*-tests (with protected alpha levels;  $\leq 0.025$ ) were used to examine for group differences within each level of the ANOVA factors.

TABLE 1. Morphological characteristics of ten male wall lizards utilized in sprint studies. Measurements included snout-to-vent length (SVL), tail length, total body mass, autotomized body mass, tail mass, and tail percentage of total body mass. Presented are means ( $\pm 1$  SD) based on  $N = 5$  lizards per group and a summary of findings of one-way ANOVAs carried out separately on each variable.

Source	Original tail	Regenerated tail	F-value	P-value
SVL (mm)	59.3 ( $\pm 2.73$ )	60.2 ( $\pm 2.87$ )	4.86	0.068
Tail length (mm)	126.0 ( $\pm 4.18$ )	90.0 ( $\pm 9.27$ )	62.6	0.0001*
Total body mass (g)	6.7 ( $\pm 0.91$ )	6.9 ( $\pm 0.61$ )	0.17	0.693
Tail mass (g)	1.9 ( $\pm 0.67$ )	1.7 ( $\pm 0.41$ )	5.97	0.058
Autotomized body mass (g)	4.8 ( $\pm 0.66$ )	5.3 ( $\pm 0.44$ )	1.34	0.281
Tail (% of total body mass)	28.0 ( $\pm 4.24$ )	23.6 ( $\pm 1.82$ )	4.54	0.065

\* Statistically significant at the  $P \leq 0.05$  confidence level.

## RESULTS

Original tails were significantly longer than were regenerated tails (Table 1). No statistically significant differences in tail type (original vs. regenerated) were found with respect to SVL, total body mass, or autotomized body mass. Tail type differences in tail mass and tail mass expressed as % of total body mass were marginally significant.

Video records of lizard sprint trials per individual were examined for non-random distribution within the five repeated runs. Due to the difficulties associated with inducing lizards to run continuous, uninterrupted, unidirectional trajectories, usually only one (but occasionally two) out of the five trials was suitable for the calculations of velocity and distance. On the occasion when two trials could be transcribed, calculations of velocity and distance were used to pick the one which would be used in subsequent data analyses. The trial that was the fastest invariably was the longest and was chosen for scoring; individuals were not observed to either improve performance (ruling out training effects) or decrease in performance (i.e., no fatigue effect) with successive trials.

Table 2 shows the results of four repeated measures ANOVAs used to analyze the terrestrial (Fig. 1) and arboreal (Fig. 2) performance data. When wall lizards were first induced to run on a horizontal terrestrial surface, individuals with original tails ran slightly faster than did their regenerated tail-possessing counterparts (Fig. 1a). In addition, lizards with original tails ran farther than those with regrown tails (Fig. 1b). However, no significant differences were detected between tail types with respect to sprint velocity (Unpaired  $t = 0.71$ ,  $df = 8$ ;  $P = 0.50$ ) or distance run (Unpaired  $t = 0.38$ ,  $df = 8$ ;  $P = 0.72$ ).

Following autotomy all lizards ran significantly faster on average than they had prior to tail loss (pooled tail types: Paired  $t = -9.305$ ,  $df = 9$ ;  $P < 0.001$ ) and lizards that had previously possessed regenerated tails ran faster than

lizards that had possessed original unbroken tails before experimentally induced autotomy but these differences were marginally significant (Unpaired  $t = -2.247$ ,  $df = 8$ ;  $P = 0.050$ ). Autotomy was associated with farther running distances for all lizards on average (pooled tail type groups: Paired  $t = -4.707$ ,  $df = 9$ ;  $P = 0.0011$ ) and lizards with regenerated tails ran farthest, although these differences were not statistically significant (Unpaired  $t = -1.27$ ,  $df = 8$ ;  $P = 0.24$ ). An interaction term was significant (Table 2) between autotomy and tail type with regards to running speed ( $P = 0.03$ ) but not for distance ran ( $P = 0.50$ ).

When wall lizards with unbroken tails were first forced to traverse the locomotor performance arena on the arboreal substrate, subjects with original unbroken tails traversed faster (Fig. 2a) and farther (Fig. 2b) than lizards with regenerated tails. Significant differences were detected between tail types with respect to arboreal velocity (Unpaired  $t = 3.13$ ,  $df = 8$ ;  $P = 0.01$ ) but not distance traversed (Unpaired  $t = 0.87$ ,  $df = 8$ ;  $P = 0.41$ ).

Tail loss resulted in significantly reduced mean arboreal velocity (pooled tail types: Paired  $t = 5.621$ ,  $df = 9$ ;  $P < 0.001$ ) and distance (pooled tail types: Paired  $t = 6.543$ ,  $df = 9$ ;  $P < 0.001$ ) for all lizards. Lizards that had previously possessed regenerated tails traversed significantly faster (Unpaired  $t = -3.046$ ,  $df = 8$ ;  $P = 0.020$ ) but not significantly farther (Unpaired  $t = -2.239$ ,  $df = 8$ ;  $P = 0.05$ ) after autotomy than did those that had experienced the loss of an original unbroken tail. Significant interaction terms (Table 2) were detected between autotomy and tail type in both arboreal performance variables ( $P_s \leq 0.05$ ).

## DISCUSSION

There is uncertainty in the literature as to whether *P. muralis* suffers tail loss during intra-specific conflicts (Arnold et al., 1978; Gruschwitz and Bohme, 1986; Arnold, 1988). Further, observations of 168 agonistic encounters (RMB,

unpubl.) have produced no evidence to suggest that this is so. Thus, the possibility of autotomy resulting from intraspecific conflicts will not be further discussed here.

Vitt (1983) found no significant differences in tail breakage frequencies between groups of lizards employing two primary lizard foraging modes (active foragers vs. sit-and-wait ambush foragers; Huey and Pianka, 1981) but asserted two important predictions: (1) long and slender tails may be selectively advantageous due to their utility as traction weight-loading counterbalances and allow for quick acceleration by positioning weight over the powerful rear limbs (Ballinger et al., 1979; Arnold, 1984, 1988). Long tails may also increase distance between a pursuing predator and susceptible lizard body regions (Vitt, 1983), and ameliorate losses suffered to fat reserves when only small distal portions of the tail are lost during an attack (Arnold, 1984, 1988). Because the tail is not "offered" as a distraction, but instead serves as an attack buffer, selection should not favor the evolution of tails that thrash about after autotomy in these species (Vitt, 1983). (2) In contrast, Vitt (1983) argued that selection should favor relatively shorter, more robust tails in lizards that are sit-and-wait foragers. For example, in geckonid species in which crypsis is the primary anti-predator mechanism, shorter, more robust tails that thrash wildly after autotomy may be selectively advantageous both because of the lizard's lesser dependence on locomotory performance for escape and the tail's relatively high distractive value before and after autotomy (Vitt, 1983). The ability of these tails to incite the attention of a predator may be attributed to post-autotomy wiggling, conspicuously bright coloration, and/or distinctive morphology. Tails of greater caloric value due to larger autotomized sections associated with more proximal fracture planes may also be favored by predators optimizing foraging efficiency in terms of calorie intake per unit time (Vitt and Cooper, 1986; Bellairs and Bryant, 1985). Also, lizards that rely primarily on crypsis may allow a predator to approach closely before attempting to flee (Bauwens and Thoen, 1981) at which point the costs associated with energy reserve loss may be minimal when compared to the possibility of unsuccessful predator avoidance (i.e., serious injury or death).

Unexpectedly, and in contrast both to predictions based on foraging mode (Vitt and Congdon, 1978; Huey and Pianka, 1981; Vitt, 1981) and other experimental evidence concerning quadrupedal lizards (Ballinger et al., 1979; Punzo, 1982; Arnold, 1984), wall lizards in this study exhibited a dramatic increase in terrestrial locomotor performance with the re-

TABLE 2. Analysis of variance tables summarizing results of four separate Type III expected mean square repeated measures ANOVAs employed to examine the effects of tail type (original vs. regenerated) and autotomy (tail loss) on the performance variables velocity and distance for running on a horizontal terrestrial substrate and climbing performance on a horizontal arboreal substrate.

Substrate	Source	Velocity						Distance					
		Type III MS	df	MS	F-value	P-value	Type III MS	df	MS	F-value	P-value		
Terrestrial	Tail type	0.02178	1	0.0123925	1.758	0.2215	0.00242	1	0.02393	0.101	0.7586		
	ID (tail)	0.0123925	8	0.0070225	1.765	0.2196	0.02393	8	0.02393	0.512	0.8183		
	Autotomy	1.02152	1	0.0070225	145.46	0.0001*	0.99458	1	0.04670	21.30	0.0017*		
	Interaction	0.05	1	0.0070225	7.120	0.0284*	0.03042	1	0.04670	0.651	0.4429		
Arboreal	Tail type	0.0004513	1	0.0004887	0.923	0.3648	0.004805	1	0.00985	0.488	0.5048		
	ID (tail)	0.0004887	8	0.0001038	4.711	0.0210*	0.009855	8	0.00361	2.734	0.0882		
	Autotomy	0.0214512	1	0.0001037	206.75	0.0001*	0.285605	1	0.00361	79.23	0.0001*		
	Interaction	0.0052812	1	0.0001037	50.90	0.0001*	0.031205	1	0.00361	8.656	0.0186*		

\* Statistically significant at the  $P \leq 0.05$  confidence level.

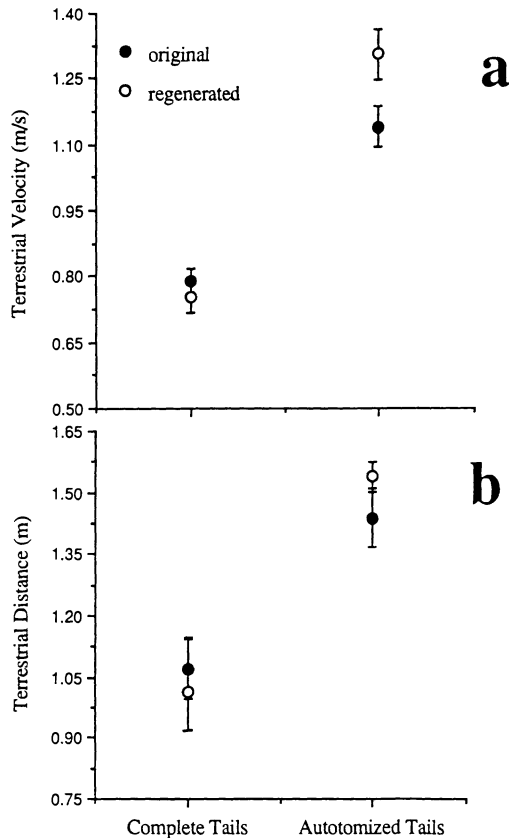


FIG. 1. The effects of tail loss and tail type on terrestrial locomotor performance. Shown are mean ( $N = 5$ ) running velocities (a) and running distances (b); error bars indicate one standard error of the mean. An interaction term was detected between autotomy and tail type sources for velocity but not for distance (Table 2). See text for significance levels between groups at each level of the autotomy factors.

removal of their tails. These observations are inconsistent with studies emphasizing the counterpoising role of the tail as a traction increasing weight load above the rear legs (Ballinger et al., 1979; Arnold, 1984, 1988). Our results are concordant with one study involving the gecko *Phyllodactylus marmoratus*, a sit-and-wait forager and cryptic defense specialist (Daniels, 1983; see also Congdon et al., 1974). Daniels (1983) interpreted post-autotomy running speed increase as a possible indication of differences between cursorial and quadrupedal lizards. He argued that the tail's counterbalancing action was of less importance for quadrupedal species and further that intact tails may reduce running speed by means of drag induced friction with the substrate. Daniels (1983) also suggested that *P. marmoratus* may employ a post-autotomy compensatory escape tactic (i.e., a behavioral modification) by increasing running speed. This

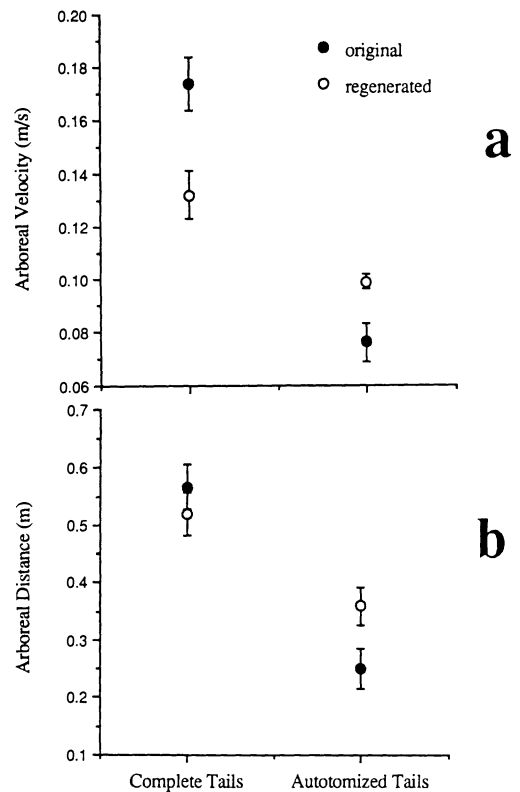


FIG. 2. The effects of tail loss and tail type on arboreal locomotor performance. Shown are mean ( $N = 5$ ) traversing velocities (a) and traversing distances (b); error bars indicate one standard error of the mean. Interaction terms were detected between autotomy and tail type sources for both performance variables (Table 2). See text for significance levels between groups at each level of the autotomy factors.

suggests that reliance on fleeing may become critical during the period of regeneration immediately following tail loss when the effectiveness of autotomy is reduced due to small or absent tails. We believe that such a suggestion may also apply to *P. muralis*. In fact, some characteristics of Cincinnati wall lizards are more reflective of sit-and-wait strategists than widely-foraging species. These include heavy reliance on autotomy, inferred from frequent naturally occurring tail breaks, distractive tails that thrash when autotomized, and a low mobility suggested by extremely small home range sizes (relative both to records of other species and European members of the same species; Brown et al., *in press*). Thus, it appears that not all escape behavior patterns observed in the Cincinnati population of wall lizards conveniently fit into either groups of correlates postulated by Huey and Pianka (1981, see their Table 8). These authors did predict short-term shifts in other-

wise fixed foraging mode postulates due to food availability; we suggest that the high predation intensities and low optimal habitat availability which are characteristic of this species' range in Cincinnati may also influence foraging mode correlates in a similar manner.

Arnold (1988:249) lists *P. muralis* as an example of an unspecialized climber reliant upon its tail for arboreal locomotion. This reliance is demonstrated by *P. muralis*' habit of coiling the tail around branches and of using it as a counterpoise aiding in the distribution of body weight over flimsy vegetation while climbing. Arboreal locomotor performance trials carried out in this study confirmed Arnold's (1988) categorization and showed that tail loss has a significant negative effect on arboreal performance. If wall lizards in Cincinnati depend on their tails for arboreal locomotor performance, autotomy may reduce chances of escape or require alternative behavioral tactics. However, decreased locomotor performance in arboreal settings does not necessarily indicate that autotomized lizards will suffer higher mortality. Although gravid female lacertids (Bauwens and Thoen, 1981) and scincids (Cooper et al., 1990) have been shown to exhibit marked reductions in terrestrial sprint velocity and activity, behavioral escape mode switching from fleeing to crypsis (and/or maintenance of close proximity to retreats) may offset actual mortality (see Schall and Pianka, 1980, for a discussion of possible learning effects on escape behavior diversity). Because lacertids are alert, diurnal, actively foraging species (Arnold et al., 1978; see Avery, 1978), the foraging mode of Vitt and Congdon (1978) predicts that the primary means of predator avoidance in *P. muralis* should be locomotion as opposed to crypsis maintained by immobility. While *P. muralis* in Cincinnati have not been observed to employ crypsis, small home range sizes (Brown et al., *in press*) may allow them to maintain close proximity to retreats.

While tail type (unbroken original vs. regenerated) did not often have a significant effect on locomotor performance, significant interactions were detected between tail type and autotomy sources with respect to terrestrial velocity, arboreal velocity, and arboreal distance performance variables. This suggests that lizards possessing original tails and those possessing regenerated tails responded differently to autotomy when forced to run and/or traverse horizontally. Original tails were associated with superior performance in the above mentioned variables before autotomy, whereas lizards that had previously possessed regenerated tails performed best following autotomy. This may reflect familiarization or learned ability, which may enhance locomotor performance in lizards

that have previously experienced autotomy and/or have become accustomed to shorter tails and reduced distribution of body weight (Table 1; note marginal tail type effects on tail mass and tail % of total body mass) during climbing. Lizards that have lost tails before may be experienced in locomotion without the advantages of this structure and may have developed a superior locomotor ability that is reflected in performance.

Illustration of our interpretation of the interaction between caudal autotomy and tail type sources may best be facilitated by the case of arboreal velocity performance: when lizards were tested with complete tails, individuals possessing significantly longer original tails traveled fastest across the arboreal substrate, possibly due to superior counterpoise capabilities. While all lizards on average demonstrated decreased locomotor performance upon subsequent removal of the tail, the above mentioned trends in tail type associated performance were reversed; wall lizards that previously possessed regenerated tails climbed fastest following autotomy. This may be due to learning effects associated with a history of previous tail loss discussed above. Also, while original tails were not significantly heavier, we feel that the observed strong trend ( $P = 0.058$ ) may have biological significance and reinforce the greater utility of complete unbroken tails as counterbalancing agents if they are longer ( $P < 0.001$ ) and constitute a marginally greater percentage of total body mass ( $P = 0.065$ ).

These findings contribute to a growing body of empirical evidence accentuating the importance of the tail for locomotor performance in lizards. Because of the complexity of morphological, energetic, behavioral, and historical factors influencing locomotion, further studies are necessary to elucidate the adaptive significance of the kind of interactions discussed here. It seems clear that foraging mode postulates will not account for all interspecific variation in model correlates and that species must be examined individually under varying conditions. Introduced populations provide unique opportunities if native and introduced populations are geographically separate and exposed to differing environments. This may be especially true if the history of isolation is known as in the case of these Lacertids. Future studies of anti-predator behavior that quantify actual controlled interactions between prey and their predators may best elucidate compensatory and alternative escape tactics of the kind alluded to here. Cooper and Vitt (1991) have presented a predictive model that may aid future studies by generating conditional probabilities of escape after detection by predators. The authors tested

their model with conspicuously-tailed scincids, but stressed that any conspicuous trait (e.g., behavior) can be experimentally manipulated for testing of the model's postulates (Cooper and Vitt, 1991). Successive performance/escape trials conducted over periods of tail regeneration may serve as particularly valuable repeated measures in conjunction with studies of this type.

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## Geographic Variation of Serum Albumin in the Monotypic Snake Genus *Diadophis* (Colubridae: Xenodontinae)

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**ABSTRACT.**— The ringneck snake, *Diadophis punctatus* (Colubridae [s.l.]: "Xenodontinae"), is one of the most widespread snake species in North America. Thirteen subspecies currently are recognized based upon variation in several morphological characters. An antiserum prepared against the serum albumin of the eastern subspecies, *D. p. edwardsii*, revealed very high levels of variation in albumin across the range of this species. The immunological distances (direct estimates of amino acid differences) range from 0 to 25; this degree of albumin divergence typically is found between congeneric species in other vertebrates, including snakes, and indicates substantial genetic differentiation within *D. punctatus*. The primary division within this genus appears to separate eastern and western (including midwestern) subspecies and dates to approximately the Miocene. These data indicate that *Diadophis* may not be a monotypic genus, but instead contains at least two genetically distinct species.

Molecular techniques have proven to be invaluable in detecting genetic variation between taxa having no obvious or consistent morphological differentiation (Highton, 1979; Donnellan and Aplin, 1989; Hedges and Thomas, 1991). Some workers have suggested that investigations of genetic variation at the species level is the province of isozyme, cytogenetic, and, most recently, DNA sequence data (Hillis and Moritz, 1990). However, estimates of amino acid sequence divergence between proteins obtained using the immunological technique of micro-complement fixation (MCF) have helped to reveal a number of cryptic species (Maxson, 1978; Scanlan et al., 1980; Maha et al., 1983). Although MCF primarily has been applied to problems of inter-specific and inter-generic

variation, this technique has proven useful in intra-specific studies of geographic variation within widespread species (i.e., *Plethodon glutinosus*; Highton et al., 1989). Sequence divergence in serum albumin has been shown to increase in an approximately linear manner with time across a wide diversity of vertebrate taxa; an average of 10 amino acid substitutions between taxa accumulate every 6 million years (Maxson, 1992). This relationship indicates that data generated through MCF can provide insights on divergence times between lineages.

The "xenodontine" snake genus *Diadophis* (Baird and Girard, 1853), currently recognized as a monotypic species (*punctatus*), is one of the most widely distributed North American snakes, ranging from southern Canada into Mexico, and