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A Comparative Study of Loss and Regeneration of Lizard Tails

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ABSTRACT.—On the basis of degree of adaptation in tail autotomy, five lizard species studied on the same area in northeastern Kansas were arranged in a sequence of specialization. *Eumeces obsoletus* was the most specialized (hatchling tail conspicuously colored and behavior adapted to flaunt it); in *Eumeces fasciatus* also, the hatchling tail was conspicuously colored, but tail flaunting was less developed. In *Cnemidophorus sexlineatus* the hatchling tail was conspicuously colored but there was no tail flaunting. In *Ophisaurus attenuatus*, the tail was easily broken, but there was no special coloration or behavior to direct predator attack. In *Crotaphytus collaris*, the tail was neither conspicuous nor easily broken, and there was no regeneration.

In most lizards, tails break off easily and the detached tail performs lively wriggling contractions that divert the attention of a predator and allow the lizard to escape (Dial and Fitzpatrick, 1983). Depending on the lizard, the tail may have other important functions such as fat storage and locomotion, which also are subject to natural selection. Hence, tail morphology depends on the relative importance of various tail functions (Vitt et al., 1977). In some lizards, juvenile pattern and color seem related to tail autotomy and may be much different from those of adults. Behavior of young, including tail flaunting, has evolved along with adaptations for tail autotomy.

Tail autotomy is known to be effective for predator defense in many lizards (Arnold, 1984, 1988). However, loss of the tail has been shown to hamper locomotion and reduce running speed for escape (*Cnemidophorus sexlineatus*, Ballinger et al., 1979; *Cophosaurus texanus* and *Uma notata*, Punzo, 1982; *Podarcis muralis*, Brown et al., 1995; *Scincella lateralis*, Dial, 1984); lower social status in *Uta stansburiana* (Fox and Rostker, 1982; Fox et. al. 1998; Fox et al., 1998), reduce reproductive success (*Mabuya heathi*, Vitt, 1981; *Coleonyx brevis*, Dial and Fitzpatrick, 1981; *U. stansburiana*, Fox and McCoy, 2000; *Lacerta monticola*, Martin and Salvador, 1993; *Psammodromus algiricus*, Salvador et al., 1996); hinder capture of prey (*Psammodromus algiricus*, Martin and Avery, 1997); and hinder survival in general (*U. stansburiana*, Wilson, 1992; Fox and McCoy, 2000; *S. lateralis*, Clark, 1971). In *Eumeces laticeps*, Vitt and Cooper (1986) found that costs and benefits of tail loss are age-specific and correlated with the striking change in appearance that accompanies growth, from the bright, banded pattern, with conspicuous blue tail in the hatchling, to the dull colored adult.

My purpose was to compare the diverse lizard species of the Fitch Natural History Reservation (FNHR) of the University of Kansas, in frequency of tail loss, location of breaks, and amount and rate of regeneration. The species studied were the Great Plains Skink (*Eumeces obsoletus*), the Common Five-Lined Skink (*Eumeces fasciatus*), the Six-Lined Racerunner (*C. sexlineatus*), the Slender Glass Lizard (*Ophisaurus attenuatus*), and the Eastern Collared Lizard (*Crotaphytus collaris*). Lizards that were present on the reservation, but were not included in the study because of the difficulty of obtaining adequate samples, were the Northern Prairie Skink (*Eumeces septentrionalis*) and the Ground Skink (*S. lateralis*).

MATERIALS AND METHODS

Each of the lizard species in this account has been the subject of a natural history study on FNHR, but over time ecological succession has resulted in habitat changes, populations have dwindled, and some have disappeared. No new material is added for *E. fasciatus*, but pertinent passages are cited from my 1954 account, comparing it with other species, and appropriate information has been extracted from that publication (Fig. 18). For *O. attenuatus*, material from my 1989 account is briefly cited. For the other three species, the facts and ideas set forth are new, but the data were collected in the 1950s, 1960s, and 1970. Captures included 634 for *Eumeces obsoletus*, 3353 for *O. attenuatus*, 581 for *C. sexlineatus* and 834 for *C. collaris*. Measurements of snout–vent length (SVL) and tail length (TL) were obtained from each lizard. In those with regenerated tails, the locations of former breaks were noted. Because the tail constitutes a predictable percentage of the total length for a given age and size category, the lengths of missing tails were estimated by multiplying the SVL by the appropriate percentage. Standard errors of the means are indicated..

RESULTS AND DISCUSSION

Eumeces obsoletus.—The Great Plains Skink was studied on FNHR, 1949–1953. It was confined to several relatively small areas that were the most xeric parts of the reservation, and as succession progressed, its numbers dwindled until none remained (Fitch, 1955). It was especially prominent at Rat Ledge, a limestone outcrop at the top of a south-facing slope where cattle had grazed and at an abandoned limestone quarry on a hilltop edge about 1 km farther north. The species is notable for its fossorial habits. Many were captured in wire funnel traps at the bases of boulders or outcrops. Also, many were captured by hand when they were exposed in burrows beneath sunken flat rocks.

In hatchling Great Plains Skinks the tail is relatively short, averaging 117.9% of SVL (Table 1). The tail becomes proportionately longer as SVL increases, and, in large adults, the intact tail is about 1.5 times SVL. Breaks averaged about halfway from the tail base to the tip (an estimated 45.6 ± 0.03% in 41 males and

TABLE 1. Allometric growth in lizard tails and color pattern of trunk and tail.

Species	N	Sex	SVL range (mm)	Mean relative tail length (tail/SVL) ± SE	Trunk color pattern	Tail color
Eumeces obsoletus	17	juv	35–39	117.9 ± 3.7	Jet black	Indigo
	19	juv	40–79	134.4 ± 2.7	Transitional	Transitional
	10	M	102–123	149.6 ± 1.78	Tan, speckled with black	Trunk color
	12	F	101–122	155.06 ± 2.04	Tan, speckled with black	Trunk color
Cnemidophorus sexlineatus	10	juv	30–39	153.5 ± 2.79	Brightly striped	Bright blue
	19	juv	40–49	181.9 ± 1.60	Transitional	Transitional
	33	juv	50–59	182.2 ± 1.34	Transitional	Transitional
	24	M	60–69	190.3 ± 1.38	Dull stripes	Gray-brown
	17	F	60–69	190.9 ± 1.10	Dull stripes	Gray-brown
	16	M	70–79	194.6 ± 1.01	Dull stripes	Gray-brown
	24	F	70–79	189.2 ± 1.1	Dull stripes	Gray-brown
Ophisaurus attenuatus	20	juv	70–89	189.9 ± 1.26	Tan with black lines	Trunk color
	45	juv	90–109	196.2 ± 1.14	Tan with black lines	Trunk color
	20	juv	120–139	203.3 ± 1.16	Tan with black lines	Trunk color
	24	juv	140–159	206.3 ± 1.82	Tan with black lines	Trunk color
	14	juv	160–179	201.5 ± 1.42	Tan with black lines	Trunk color
	15	juv	180–199	199.4 ± 1.56	Tan with black lines	Trunk color
	8	M	200–224	199.1 ± 2.50	Tan with white speckling	Trunk color
	12	F	200–224	194.2 ± 2.55	Tan with black lines	Trunk color
	8	M	225+	198.5 ± 2.11	Tan with white speckling	Trunk color
	6	F	225+	191.8 ± 3.18	Tan with black lines	Trunk color
Crotaphytus collaris	17	juv	40–49	146.3 ± 1.24	Gray with dark crossbands	Gray
	26	juv	50–59	156.9 ± 1.29	Transitional	Gray
	25	juv	60–69	161.3 ± 1.59	Transitional	Gray
	20	juv	70–79	166.3 ± 1.45	Transitional	Gray
	17	juv	80–89	172.4 ± 1.72	Transitional	Gray
	10	adult	90–99	179.4 ± 2.72	Greenish gray with dark markings and white specks	Gray

TABLE 2. Ontogeny, sex, and tail breakage (number and percent) in three lizard species.

Species	SVL range (mm)	Age and sex	N	Broken tails	
				N	Percent
Eumeces obsoletus	30–39	hatchlings	6	1	16.7
	40–79	juveniles	50	18	36.0
	80–99	larger young	58	31	53.4
	100–133	adult males	40	28	70.0
	100–133	adult females	67	45	67.2
Cnemidophorus sexlineatus	32–39	hatchlings	15	2	13.3
	41–49	small juveniles	15	3	20.0
	50–59	large juveniles	25	3	12.0
	60–69	small adult males	33	7	21.2
	60–69	small adult females	22	6	27.2
	70–79	large adult males	54	17	31.5
	70–79	large adult females	56	17	30.4
Ophisaurus attenuatus	56–79	hatchlings	15	2	13.3
	80–139	1st year juveniles	115	12	9.5
	140–189	large juveniles	76	29	28.6
	190–210	adolescents	22	7	24.0
	211-230	small adult males	18	30	62.5
	211–230	small adult females	13	23	64.0
	231-251	large adult males	6	17	74.0
	231–251	large adult females	2	5	71.5
	>250	largest males	2	15	87.0

47.0 ± 0.04% in 37 females), with no statistically significant difference between the sexes.

The species is notable for its striking ontogenetic change in appearance. The hatchlings are so different that they were long thought to be a different species, "*guttulatus*" (VanDenburgh, 1922, p. 594). They are jet black except for white and orange spots on the supralabials and a deep blue (indigo) tail. When foraging above ground, hatchlings move about with a comically exaggerated "swagger," standing high and swaying from side to side as they walk with the tail performing writhing movements that seem adapted to attract the attention of predators. It is not known how this tail-flaunting affects predators, nor even what kinds of predators are the main ones for the skinks. Tail advertising is even more prominent than in *E. laticeps* as described by Vitt and Cooper (1986).

Eumeces fasciatus.—In this skink, the tail is extremely fragile, and a high proportion of adults have broken and regenerated it. Growth and regeneration of the tail were discussed in Fitch (1954). When there were secondary breaks, these most often occurred on the original tail, proximal to the previous break (regenerated tails lack vertebrae with fracture planes, and consist of tough, fibrous tissue, with a cartilaginous tube replacing the spinal column). The nearer to the tail's base that a break occurred, the longer the regenerated tail; it sometimes grew to approximately two-thirds the length of the original tail. Breaks were relatively infrequent on the basal decile of the tail but were common on the second decile, with the incidence steadily decreasing distally. Tails broken near the base weighed from 16–20% of the skink's total weight, and it seemed that a major part of the total loss consisted of fat (Fitch, 1954). Regeneration was found to be more complete in young that were still growing than in adults. Behavior seems to be adapted to attract attention. As hatchlings move about to forage, the conspicuous blue tail is flaunted by being elevated and made to perform squirming movements. Presumably the lizard benefits by diverting attention, from the body to the tail, which breaks if it is seized, and then wriggles vigorously, holding the attention of the predator. First-hand observations of natural predators catching Five-Lined Skinks and their responses to tail-flaunting are lacking. As a skink nears adult size, the bright blue tail fades, and in old adults it is gray and inconspicuous. Also, the hatchling's body pattern, with contrasting stripes of dark brown and yellow, gradually fades and disappears completely in old males. In old females, the bands are still discernible but have become dull and faint, with but little contrast. The tail flaunting of hatchlings rapidly declines and disappears in larger young.

Cnemidophorus sexlineatus.—Six-Lined Racerunners were common on FNHR when protection as a natural area was initiated, but the successional changes that occurred were not favorable to the species, and it retreated to refugia of xeric habitat, notably the steep banks with bare, sliding soil of a diversion ditch, near the headquarters where it persisted for several years before disappearing (Fitch, 1956a). There are differences between the sexes, and between young and adults, in relative tail length (Table 1). Large adult males have slightly longer tails than those of the largest adult females (194.6 ± 1.01% of SVL in males vs 189.2 ± 1.10% in females). Juveniles have relatively short tails; hatchling tails averaged 153.5 ± 2.79% of SVL). The larger the lizard, the greater its relative tail length. The tail is fragile and subject to breakage. Of 30 racerunners under 50 mm SVL (hatchlings and early young), only five (16.7%) had broken tails (Table 2). In large adults, the percentage of individuals with broken tails increased to 31.5% in males and 30.4% in females (Table 2).

In hatchling racerunners, the tail is bright blue, con-

trasting with the alternating light and dark stripes of the body, and suggesting that, as in skinks, it has evolved to distract predators from the more vulnerable trunk area. However, the hatchling racerunner's tail is not flaunted as it is in skinks, and the blue color fades rapidly as the lizard grows. Recaptures of marked racerunners were frequent, and from these, it was learned that there is no regeneration for the first week or two after a break, but regeneration is rapid during the following weeks. The regenerated tail is much shorter than the original. In 44 adult racerunners with regenerated tails, the average break occurred at 39.9 ± 2.89% of the original tail length from its base. In 25 racerunners with regenerated tails, average length of the regenerated tail was estimated as 51.1 ± 1.9% of the original that was lost. These figures exclude nine individuals with relatively short regenerated tails (2, 3, 4, 5, 6, 6, 7, 13, 16%), but the timing of the breaks was not known. These were apparently captured too soon after the original tail was lost for the new tail to develop fully.

Ophisaurus attenuatus.—In the glass lizard, as in other species, the tail is relatively short in hatchlings and becomes relatively longer as the lizard grows. However, when the growing young have more than doubled their hatching length and have reached about 150 mm SVL, there is a change in the tail's allometric growth, and it becomes relatively shorter in adults (Table 1). In small juveniles, the tail averaged 189.9 ± 1.26% of SVL. The maximum TL/SVL ratio (average 206 ± 1.82%) occurs in the second spring after hatching, when the young are somewhat less than one-fifth of adult weight. Subsequently, as growth proceeds, relative tail length declines to about 195% of SVL in the largest adults.

Maximum regeneration required 22–56 months and the regenerated tail averaged only 15.3% of the length of the missing tail. The detached tail averaged 12.9% of the lizard's weight in 209 instances. Loss of the tail constituted a serious handicap to the lizard by reducing its speed for escape dashes. Thirty-seven of 47 large adults (SVL > 260 mm) all had regenerated tails. There was a decreasing ratio of glass lizards having intact tails as they grew older (Table 2). Tail breaks in males averaged a little farther distally than in females. Comparing adults with intact tails, those of the largest males averaged about 7% longer (± 2%) than those of females of the same size (Table 1). Fragility of the tail in *Ophisaurus* was emphasized by the fact that many of those captured flipped off their tails after they were released. This was especially liable to happen when the lizard was dropped into a cloth bag. If the bag already contained one or more glass lizards, the prospect for autotomy was increased; the presence of other glass lizards seemed to heighten activity.

Crotaphytus collaris.—The Eastern Collared Lizard exemplifies those lizards in which tail autotomy apparently is not a part of defense strategy and the tail does not break easily. In 1949, five of these lizards from the Flint Hills of Kansas near Manhattan were released at the site of an abandoned limestone quarry on FNHR. They thrived and survived through several generations, until ecological succession resulted in a drastic reduction of exposed rock surfaces caused by invasion by shrubs and trees. In all, 43 collared lizards were caught and marked at the quarry. The colony was always confined to the relatively small area of exposed rock at the quarry site (Fitch, 1956b).

Only two of the lizards had damaged tails; these were missing the terminal 55% and 20%, respectively. The latter was found to be missing the terminal 17 mm of its tail on 3 September 1950. During the following year, it was recorded 21 times, and there was no regeneration; the tail remained blunt-ended. The other had lost its tail on 2 September 1949, and in the next 11 months there was no regeneration. Except for the original five, lizards were first caught as hatchlings, and if they were not eliminated at an early age, they were recaptured many times during growth, but only a few survived to maturity.

Conclusions

In the lizard species of FNHR, tail autotomy was found to be developed to varying degrees. It was perhaps most developed in *E. obsoletus* hatchlings; not only was the indigo tail in striking contrast with the conspicuous jet black body, but tail flaunting was a conspicuous aspect of hatchling behavior when the young lizards moved about in the open. Hatchlings stand high and sway from side to side as they walk, with the tail elevated, performing writhing movements. *Eumeces fasciatus* hatchlings also flaunt their tails, which are bright blue, contrasting with a brightly striped body, but the "swagger walk" is less exaggerated than in *E. obsoletus*. In *C. sexlineatus* also, the tail is bright blue, contrasting with the striped body, but flaunting behavior was not observed. The conspicuous tails of the two skinks and the racerunner may be considered adaptations to avoid being eaten by bird predators, because most other predators, including snakes and mammals, probably lack good color vision. In *O. attenuatus*, the tail color does not contrast with that of the body and the pattern in young is not strikingly different from that in adults, but tail autotomy is highly developed, and few survive to adulthood without tail breakage. On many occasions glass lizards were observed to snap off their own tails when they were pursued or captured. The incidence of broken tails increased, from zero in hatchlings to nearly one-third in large adult *C. sexlineatus*, to more than two-thirds in those of *E. obsoletus*, and to about three-fourths in those of *O. attenuatus*. In each species, the incidence of breaks was similar in the sexes but was a little higher in males. In adults of both species of skinks, adult tail length was about 1.5 times SVL In racerunners and glass lizards, the tail/SVL ratio of adults averaged a little more than 1.9. In *C. collaris*, tail autotomy is not developed. The caudal vertebrae do not have cleavage planes, tails do not break easily, and when they do break, there is no regeneration. In all species of this study, tails were relatively short in hatchlings.

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