The energetic consequences of tail loss to juvenile lizards

by

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(ABSTRACT)

I evaluated the hypothesis that juveniles of species whose tail is important for predator deflection should allocate energy preferentially to tail growth at the expense of body growth. Relative linear tail growth (linear tail growth/linear body growth) and relative mass tail growth (tail mass growth/body mass growth) were measured for juveniles of two species of skinks: Eumeces fasciatus that use the tail for predator deflection, and Chalcides ocellatus that does not use the tail for predator deflection. Experimental conditions produced an energy limiting situation under which the priority of energy allocation to tail regeneration should be exhibited. For E. fasciatus, relative linear tail growth was higher for the energy limited than control group and for the tail-removal than the tailed lizards. For C. ocellatus, relative linear tail growth was not affected by energy level but was lower for tail-removal than tailed lizards. For both species, relative tail mass growth was lower for the tail-removal than tailed lizards. The greater relative linear tail growth of regenerating than normal tails of E. fasciatus supports the hypothesis that rapid tail regeneration is important for a species whose tail is used for predator deflection. However, the low rate of tail regeneration in mass suggests that mass gains occur late in the regeneration process. In contrast, lower relative linear and mass tail growth of C. ocellatus that were regenerating tails suggests that tail regeneration has a low priority for this species.

Acknowledgements

"Mountains should be climbed with as little effort as possible and without desire. The reality of your own nature should determine the speed. If you become restless, speed up. If you become winded, slow down. You climb the mountain in an equilibrium between restlessness and exhaustion. Then, when you are no longer thinking ahead, each footstep isn't just a means to an end but a unique event in itself. This leaf has jagged edges. This rock looks loose. From this place the snow is less visible, even though closer. These are things you should notice anyway. To live only for some future goal is shallow. It's the sides of the mountain which sustain life, not the top. Here's where things grow."

Robert M. Pirsig <u>Zen and the Art of Motorcycle Maintenance</u>

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LITERATURE REVIEW

Functions of the tail in lizards.

The tails of lizards (order Squamata) vary considerably in their function (Etheridge 1967, Vitt et al. 1977, Arnold 1984). Four non-exclusive functions are: locomotion, energy storage, social cues, and predator deflection.

Locomotion is generally aided by the tail. The tail reduces the lateral swing of the hindquarters during quadrupedal locomotion. Tail loss in <u>Cophosaurus</u> <u>texanus</u> <u>scitulus</u> (Iguanidae) results in a 32% decrease in running speed (Punzo 1982). Among those lizards adapted for climbing in flimsy vegetation, the tail provides an additional large surface area over which to distribute the body mass, acting as a counterpoise (Arnold 1984). The tails of some lizards show specialized adaptations for climbing. For example, most Chamaeleontidae have prehensile tails, and <u>Lygodactylus</u> <u>klugei</u>, a small gecko, has an adhesion pad on the tip of its tail (Vitt and Ballinger 1982). Aquatic species have laterally compressed tails that increase their propulsive force while swimming. A less common adaptation for locomotion is stablization and lift during gliding flight by the agamid <u>Draco</u>, the geckonid <u>Ptychozoon</u>, and the lacertid <u>Holapsis</u> <u>guentheri</u> (Arnold 1984). In contrast, when large quantities of fat are

stored in the tail, locomotion may be aided via tail loss. For example, Phyllodactylus marmoratus runs faster following tail loss apparently because of the reduced weight and drag (Daniels 1983).

A second function of the tail is as a site of fat deposition. In Eumeces laticeps (Scincidae) the tail contains approximately half the animal's total lipid store (Vitt and Cooper 1986a). Several Gekkonidae have short, thick tails also used for lipid storage (Congdon et al. 1974, Dial and Fitzpatrick 1981, Daniels 1984). Coleonyx variegatus (Gekkonidae), a desert species, depends on caudal lipid reserves as an energy source during periods of food and water shortage (Bustard 1967). Congdon et al. (1974) showed that metabolism does not increase as a result of tail loss in Coleonyx brevis.

The third function of the tail is as a social cue which facilitates obtaining and maintaining dominance. Juvenile Uta stansburiana that had intact or regenerated tails were able to dominate juveniles of equal snout-vent length (SVL) that had lost more than 1/3 of the tail. Dominant juveniles, however, consistently lost their status following tail loss (Fox and Rostker 1982). In Sauromalus obesus, tails of at least 65% of SVL were necessary for males to maintain possession of a territory. As in Uta stansburiana, loss of the tail resulted in loss of dominance (Berry 1974). An intact tail may be associated with social dominance because the tail increases apparent body size and/or mass. Tail size is further exaggerated in some species by the presence of spines or a crest on the tail (Arnold 1984).

A fourth function of the tail is as a defense mechanism. Many large-bodied lizards thrash the tail to ward off predators (Arnold 1984, Arnold 1988). The presence of spines in some species may increase the effectiveness of tail thrashing. Small-bodied lizards use the tail to deflect predator attacks away from the head and body. Such deflection may be facilitated by contrasting body and tail coloration and tail movement (Arnold 1984). For example, the brightly colored tails and tail waving of juveniles of the skink genus Eumeces deflect predator attention and increase the probability of escape (Cooper and Vitt 1985, Vitt and Cooper 1986a).

Tail autotomy.

Tail autotomy is an important predator deflection mechanism in many lizard species (Congdon et al. 1974, Vitt et al. 1977, Arnold 1984, Cooper and Vitt 1985, Vitt and Cooper 1986a). In encounters with predators, lizards capable of autotomy will be better able to escape attacks when the predator grasps the tail and not the body. Selective pressures due to predation may have maintained autotomy in many lizard groups and in some cases resulted in tail waving displays and coloration that draw predator attention to the tail. Species exposed to weak predation pressure may exhibit a less developed autotomic ability (Vitt et al. 1977). In some species tail autotomy has been completely lost (Arnold 1984, Arnold 1988).

The mechanism and systematic distribution of autotomy

Autotomy of the tail generally occurs at intra-vertebral fracture planes, between septa of muscle and fat, and in areas of epidermal weakness in the caudal region (Etheridge 1967, Bellairs and Bryant 1985). These morphological features facilitate loss with minimal damage and blood loss. Such intravertebral autotomy is considered the primitive state in Squamata (Etheridge 1967, Arnold 1984, Arnold 1988). The capability for autotomy is lost via fusion of the caudal fracture planes. A new mechanism of autotomy involving intervertebral separation has evolved in the Agamidae and Amphisbaenidae. However, this form of autotomy is not followed by regeneration of a new tail (Arnold 1988, Etheridge 1967, Arnold 1984).

Families in which all members have intravertebral autotomy are the Anelytropsidae, Cordylidae, Dibamidae, Lacertidae, Teiidae, Xantusiidae, and Gekkonidae, with the exception of the gekkonid Nephrus asper which has a reduced tail (Arnold 1984). Families that have lost autotomy (fracture planes are no longer present) include the Chamaeleontidae, Helodermidae, Lanthanotidae, Varanidae, and Xenosauridae (Etheridge 1967, Arnold 1984). The remaining families, the Anguidae, Scincidae, and Iguanidae, contain both autotomic and non-autotomic genera.

Loss of autotomy is correlated with large body size and/or use of the tail for locomotion (Arnold 1984). For example, the non-autotomic Varanids and Helodermidae are large powerful lizards and have few predators as adults. This correlation is also seen in non-autotomic genera of families that include both autotomic and non-autotomic members. For example, many large bodied Iguanidae use the tail as a weapon or for locomotion [Amblyrhyncus (swimming), Basilicus (bipedal), and Phenacosaurus (prehensile)]. Smaller iguanids that have reduced and/or spiny tails, such as Phrynosoma, may move too slowly for autotomy to be an effective means of predator deflection (Arnold 1988).

Some functional correlates of autotomy

Among autotomic families and the autotomic members of mixed families there are differences in the ease with which tail autotomy occurs. Tails capable of autotomy but possessing some other function, tend to be lost less readily than those used primarily as escape mechanisms. Much of the research on tail autotomy centers around the balancing of costs and benefits of tail loss (Vitt et al. 1977). Thus, the morphology and specific use of the tail may give some indication of the relative importance of autotomy in different species.

Tails of some species thrash following autotomy and, therefore, maintain the predator's attention. A comparison of the rates of tail thrash between the terrestrial skink, Scincella lateralis, and the arboreal Anolis carolinensis (Dial and Fitzpatrick 1983) showed that the former had a high rate of tail thrash and that predator attention was predominately directed to the tail. The low rate of tail thrash in A. carolinensis resulted in predator attention directed toward the lizard rather than the tail. Thus, the amount of tail movement determines the maintenance of predator attention. Increased motion should increase the effectiveness of autotomy for terrestrial lizards where the tail is not displaced from the lizard following autotomy. Thrashing may carry the tail away from the area of attack and/or cause the tail to disappear into the ground cover directing predator attention away from the lizard.

Temperature may also affect the ease of autotomy in individual lizards. The ease of loss across a temperature gradient is bimodal for one species of gecko, Gehyra variegata. The ease of loss in the active temperature range (T_a=18-29°C) is relatively high, which would be expected due to the increased potential risk of predation while foraging. At 11°C, lizards are mobile enough to escape if necessary, and autotomy seldom occurs. At very low temperatures (4°C) lizards are sluggish and autotomize readily if confronted by a predator (Bustard 1968).

Energetic consequences of tail loss

The energy requirement of growing a new tail following autotomy may reduce energy allocation to other processes such as body growth and reproduction (Congdon et al. 1974, Maiorana 1977, Vitt et al. 1977, Ballinger and Tinkle 1979, Dial and Fitzpatrick 1981, Arnold 1984, Daniels 1984, Vitt and Cooper 1986a). Tail loss does not reduce clutch size in Coleonyx brevis, but energy content of individual eggs is reduced. This reduction results in smaller hatchlings that may have reduced survival (Dial and Fitzpatrick 1981). The negative effect of tail regeneration on body growth in the field was demonstrated in several Sceloporus species. Individuals without tails had a lower growth rate (mm SVL/day) than tailed individuals (Ballinger and Tinkle 1979). Vitt et al. (1977) point out that juveniles should allocate large amounts of energy to body growth, as size is important in determining the age of sexual maturity, in social rank, and in territorial aquisition and defense. Thus, the energetic drain due to tail regeneration following loss may delay sexual maturation and thus reduce overall fitness. However, in a lab study where food was available ad libitum, body growth in Eumeces juveniles was not affected by tail loss (Vitt and Cooper 1986a).

"Economy of autotomy", the loss of only a portion of the tail, should occur when tails are used for functions in addition to predator deflection. For example, because of stored lipids, survival during starvation was higher for Phyllodactylus marmoratus with intact tails com-

pared to tailless individuals. In the laboratory, P. marmoratus did practice "economy of autotomy" when grasped with forceps, but in actual predator encounters the entire tail was consistently lost (Daniels 1985). Thus, "economy of autotomy" seen in the laboratory may have been the result of a non-predatory situation. Loss of the complete tail in a predator en-counter may be necessary for distracting and holding the predator's attention while the lizard escapes. Total tail loss is common among geckos. In several geckos the autotomic mech-anisms are restricted to the basal caudal autotomic vertebrae, lending further support to the theory that the whole tail is important in predator distraction (Etheridge 1967, Arnold 1984).

INTRODUCTION

Tail autotomy is a common predator deflection mechanism in some juvenile lizards (Vitt et al. 1977, Arnold 1984, Arnold 1988). Predator attention is drawn away from the head and body by exaggerated tail movement. Deflection of the predator's attention is often facilitated by bright coloration of the tail (Cooper and Vitt 1985, Vitt and Cooper 1986a). The importance of autotomy is supported by regeneration of a new tail similar in size and color to the original tail.

Regeneration is important in several contexts (e.g. tail use in predator defense, locomotion, social status). Thus, the regeneration rate appears to be subject to conflicting selective pressures. On one hand, Vitt et al. (1977) point out that juveniles should allocate large amounts of energy to body growth as size is important in determining the age of sexual maturity, rank obtained, and in territorial aquisition and defense. On the other hand, the probability of escape following future predator encounters is reduced during the interim between tail loss and regeneration of a new tail (Congdon et al. 1974, Cooper and Vitt 1985, Vitt and Cooper 1986a). Thus, rapid regrowth of the tail will reduce the time a lizard is exposed to an enhanced predation risk.

Energy requirements of tail regeneration may reduce energy allocation to other processes such as body growth and energy storage (Congdon et al. 1974, Vitt et al. 1977, Ballinger

and Tinkle 1979, Dial and Fitzpatrick 1981, Arnold 1984, Daniels 1984, Vitt and Cooper 1986a). The amount of energy available for growth and lipid storage depends on food intake (Derickson 1976, Andrews 1979). Energy above maintenance is typically allocated to growth. Thus, regeneration of a new tail is an added energy cost. Because metabolic rate does not increase during regeneration (Congdon et al. 1974), allocation to tail regeneration reduces the energy available for growth and lipid storage.

The relative amount of energy that is allocated to tail regeneration may differ between species based on the importance of the intact tail. When the intact tail serves to deflect predators, loss of the tail increases mortality during subsequent predator attacks (Congdon et al. 1974, Daniels 1983, Dial and Fitzpatrick 1984, Cooper and Vitt 1985, Daniels et al. 1986, Vitt and Cooper 1986a). Under these conditions, selective pressures should favor rapid re-generation even at the cost of body growth and energy storage. In contrast, when the intact tail does not enhance survivial, selective pressures should favor body growth at the expense of tail regeneration.

The object of this study was to evaluate the hypothesis that species whose tail is impor-tant for predator deflection should allocate energy preferentially to tail regeneration. To test this hypothesis, observations were made on tail regeneration by juveniles of two species of skinks.

Eumeces fasciatus is a widely foraging species (Fitch 1954, Cooper and Vitt 1985, Vitt and Cooper 1986b). Invertebrate prey are located through both vision and olfaction (Vitt and Cooper 1986b). The bright blue tail of juveniles, in conjunction with tail waving, effectively diverts predator attacks away from the head and body, allowing escape by tail autotomy (Vitt and Cooper 1986a). Regenerated tails of juveniles are blue, although not as bright as the or-iginal tail, suggesting that color is an important part of predator deflection. The tail clearly serves as an important defense mechanism for juvenile E. fasciatus. Tail regeneration should therefore be rapid and might occur at the expense of body growth.

Chalcides ocellatus is a fossorial desert species native to the Middle East and North Africa. It has a small head, elongated trunk, and reduced limbs which allow it to burrow

through sand. Unlike juvenile E. fasciatus the tail and body are uniform in color and there is no tail waving display. Tails of fossorial species do not appear to facilitate locomotion (Gans 1986, Arnold 1988). Thus, tail regeneration should not occur at the expense of body growth.

METHODS AND MATERIALS

Source of experimental animals.

To obtain juvenile E. fasciatus, eggs were collected from William B. Umstead State Park, Raleigh, North Carolina (35°78′N, 78°65′W), in June and July 1987 and 1988. Eggs were found below the bark or in the top layer of wood of partially rotted logs. In the laboratory, each clutch was housed in a plastic container lined with moist rotting wood and enclosed in a plastic bag to maintain high moisture levels. Juveniles were transferred to glass aquaria upon hatching. To meet the required sample size in 1987, additional juveniles were captured by hand from the study area. Juvenile C. ocellatus were obtained in July 1987 and 1988 from a breeding colony at VPI&SU. Juveniles of both species were permanently marked by toe clipping.

Initially, C. ocellatus juveniles were larger than E. fasciatus juveniles. Initial snout-vent lengths (SVLs) of E. fasciatus ranged from 26.5 to 34.0mm with a $\overline{X}$ of 29.3±0.36mm. Total tail length (TTL) ranged from 36.0 to 51.0mm with a $\overline{X}$ of 43.4±0.71mm. Total tail length (TTL) is related to SVL as TTL=-12.54+1.93SVL (N=16, R^2=0.99, P<0.001). Mass ranged from 0.33 to 0.95g with a $\overline{X}$ of 0.53±0.03g. Mass is related to SVL as Mass=$2.6 \times 10^{-6}(SVL)^{3.61}$ (N=34, R^2=0.89, P<0.001). Initial SVLs of C. ocellatus ranged from 40.0 to 51.0mm with a $\overline{X}$ of 45.4±0.38mm. Initial TTL ranged from 31.0 to 60.0mm with a $\overline{X}$ of 52.3±0.74mm. Total tail

length (TTL) is related to SVL as TTL=10.64+0.94SVL (N=18, R^2=0.86, P<0.001). Mass ranged from 0.92 to 2.36g with a $\overline{X}$ of 1.44±0.05g. Mass is related to SVL as Mass=$6X10^{-7}(SVL)^{3.85}$ (N=45, R^2=0.84, P<0.001).

Experimental design.

To evaluate the priority of energy allocation to tail regeneration, I measured tail growth relative to body growth in juvenile lizards. The priority of energy allocation to tail regeneration or body growth should be exhibited under energy stress. Therefore, lizards were subjected to two levels of food intake by manipulating access to heat sources for thermoregulation. Food intake is increased by behavioral thermoregulation due to increased foraging activity and through increased metabolism (Avery 1984).

The experimental design was a 2X2 factorial with two temperature treatments and two tail conditions. Cages with and without heat lamps provided the two temperature regimes (cold and warm=control). Lizards with manually autotomized tails and lizards with intact tails provided the two tail conditions (tail-removal and tailed=control).

Cages were provided with a sand (C. ocellatus) or a sand and bark (E. fasciatus) substrate, water dishes, and wooden boards for hiding places. All cages were illuminated from 0900 to 1500 (EST) by fluorescent vita-lites (Duro-test) hung 50cm above the cage substrate. Heat lamps (75 watt) suspended 22cm above the substrate (warm cages only) allowed behavioral thermoregulation from 0900 to 1500.

Tails were autotomized 2-3mm from the base by grasping the tail with the thumb and forefinger, applying slight pressure, and allowing the lizard to break free.

All lizards were provided food (live crickets dusted with vitamin powder for the Eumeces and catfood supplemented with live crickets for the Chalcides) and water ad libitum. Lizards were fed at the start of the lighting period (0900) three days a week (Monday, Wednesday, Friday).

Individuals were assigned to one of two temperature treatments and one of two tail manipulation treatments: warm-tailed, warm-tail-removal, cold-tailed, cold-tail- removal. Forty E. fasciatus were divided evenly among 8 cages and 48 C. ocellatus were divided evenly among 6 cages. Juveniles from the same clutch were divided among cages. Assignment of lizard treatments (tailed or tail- removal) was done within each cage separately. Lizard toe-clip numbers were drawn at random (from an envelope) and assigned to treatments alternately. Two Chalcides and 7 Eumeces died during the experimental period and were omitted from all analyses. The experiment ran for 84 days (Eumeces, August 4 to October 27, 1987 and Chalcides, August 18 to November 10, 1987).

Daily temperature fluctuations within the two temperature treatments were determined by measuring cage substrate temperatures (directly under heat lamps in the warm cages and in the corresponding area of the cold cages) hourly for a period of 12 hours. All substrate temperatures were measured using either a digital reading thermometer or a thermocouple thermometer. Temperatures were monitored for three days each month during the experiment [September 1,4,11, 1987, and October 14,21,27, 1987 (Eumeces and Chalcides)].

Cloacal temperatures were also taken when cage substrate temperatures were measured. All measurements were made using a thermocouple thermometer. Only one measurement per lizard was taken per day to avoid damage and stress. As a result cloacal measures were made every third hour of the cage monitoring sequence, and staggered on the three days to cover the whole 12 hour period.

Air temperature was measured hourly for a period of 12 hours on the same days as the cage substrate temperatures. Temperature was measured at the center of the room at a height of 1m with a digital reading thermometer.

Scat production was used as a measure of food intake. Given a constant absorption efficiency and passage rate, scat production differs from food intake by a constant factor (Andrews and Asato 1977). Scat production was measured twice during the experimental period: sample 1, September 17-19, 1987 and sample 2, October 23-25, 1987. Lizards were removed from their cages at 1500 following feeding at 0900. They were held individually in plastic bags for 48 hours at 30°C and all scat (fecal + urinary) material was collected. Scats were washed from the bags with 95% ethanol into pre-weighed aluminum ashing pans, dried to constant weight (24 hours at 60°C), and weighed to the nearest 0.0001 gram. Samples were ashed in a muffle furnace for 30 minutes at 550°C, cooled in a dessicator and weighed. Ash weight was subtracted from the scat weight and, to correct for differences in lizard size, divided by lizard mass to provide a measure of ash free scat mass (mg) per gram lizard (AFSMmg/g) for each sampling period. Because of the high ash content of C. ocellatus scats due to sand ingestion, it was not possible to separate fecal and urinary portions of the scats.

Apparent absorption efficiencies.

To determine if absorption efficiency was affected by the experimental conditions, food intake and fecal production were measured during July-August (C. ocellatus) and September-October (E. fasciatus) 1988. Lizards were assigned a 2x2 factorial design identical to that used in 1987 observation except that 1) only one lizard was assigned to each cage (E. fasciatus N = 16, and C. ocellatus N = 16), 2) cages were provided only with water dishes and plastic cup halves as hiding places (no substrate was added), and 3) lizards were fasted for 4 days before and 4 days following the experimental period. Cage temperatures were the same as those in September and October, 1987.

Lizards were given weighed amounts of food every other day at 0900 (catfood, C. ocellatus, and crickets dusted with vitamin powder, E. fasciatus) and water ad libitum. The uneaten portion of the catfood (Chalcides) was removed at 1500, dried for 48 hours at 60°C,

Lizards were given weighed amounts of food every other day at 0900 (catfood, C. ocellatus, and crickets dusted with vitamin powder, E. fasciatus) and water ad libitum. The uneaten portion of the catfood (Chalcides) was removed at 1500, dried for 48 hours at 60°C, cooled in a dessicator and weighed. Eumeces fasciatus were fed weighed crickets one at a time until satiated. One additional cricket was left in the cage. Cages were checked at 1500 and if uneaten, the cricket was removed.

Wet masses of food placed in the cages were converted to dry masses by multiplying wet mass by the average proportion dry mass. The proportion dry mass of food was determined at each feeding from samples of catfood and individual crickets. Samples were weighed and dried for 48 hours at 60°C, cooled in a dessicator, and weighed. The proportion of dry mass was obtained by dividing the dry mass by the wet mass for each sample. These values were averaged for each food type.

Fecal portions of scats were collected from each cage every other day during the experimental period and then daily during the final fasting period. Feces were dried for 48 hours at 60°C, cooled in a dessicator, and weighed. Urinary portions of scats were excluded from analysis because they represent food that has been absorbed and, if included, would bias estimates of absorption efficiency. Because no substrate was used in the cages Chalcides scats did not contain sand and could easily be separated into fecal and urinary portions.

To obtain the proportion of ash in ingested and egested material, dried samples of food and feces were weighed, ashed in a muffle furnace for 30 minutes at 550°C, cooled in a dessicator and weighed. Ash mass was divided by total dry mass to give the proportion of ash in each sample.

Two methods from Speakman (1987) were used to estimate absorption efficiency. First, apparent dry mass absorption for each lizard was estimated from the total dry mass of food ingested and the total dry mass of feces egested using the formula:

$A_{dm} = (M_i - M_f)/M_i$

A_{dm} - apparent dry mass absorption

M_i - mass ingested

M_f - mass egested

Second, apparent absorption for each lizard was estimated from the proportion of ash in the ingested mass and the egested mass using the formula:

$A_{am} = 1 - [P_{xi}/P_{xf}]$

$\quad A_{am}$ - apparent absorption of ash free

$\qquad$ dry mass

$\quad P_{xi}$ - ash per gram ingested

$\quad P_{xf}$ - ash per gram egested

Growth measurments.

Body and tail sizes were measured at the beginning and end of the 84 d experimental period. Snout-vent length (SVL) was measured to the nearest mm along the midline of the body. Total tail length (TTL) was measured to the nearest mm from the vent to the tip of the tail for both the tailed and tail-removal groups. Total mass was measured to the nearest milligram. Wet mass of bodies and tails were measured initially for the tail-removal group and for all individuals at the end of the experiment. Regression equations from known body and tail masses (initial tail-removal measures and final measures of the tailed controls) were used to estimate the initial body (M) and tail masses (TM) for the tailed group. The resulting equations were $TM = -0.026 + 0.199M$ ($N = 34$, $R^2 = 0.97$, $P < 0.001$) and $TM = 0.009 + 0.170M$ ($N = 45$, $R^2 = 0.94$, $P < 0.001$) for E. fasciatus and C. ocellatus, respectively. All wet masses were converted to dry mass (body dry mass = BDM and tail dry mass = TDM) by multiplying wet mass by percent dry mass for each individual. Growth rates (mm/day or mg/day) were obtained by subtracting the first measurement from the last and dividing that difference by 84 days.

Relative tail growth was calculated as

$$\Delta TTL/\Delta SVL \;=\; \frac{TTL_2 - TTL_1}{SVL_2 - SVL_1}$$

and

$$\Delta TDM/\Delta BDM \;=\; \frac{TDM_2 - TDM_1}{BDM_2 - BDM_1}$$

Expected normal tail lengths for the tail-removal groups were estimated from the previous regression equations relating TTL to SVL. Percent regeneration of estimated normal tail length was obtained by dividing regenerated length by estimated normal tail length and multiplying by 100.

Lipid extraction.

Because lipid storage could be altered by the experimental conditions, lipid content of bodies and tails was measured at the end of the experiment. Lipids were extracted in four soxhlet apparati. Each Soxhlet unit consisted of a glass extractor, a 250ml solvent flask in contact with a constant heat source, and a condenser. A 2:1 chloroform to methanol mixture (boiling point of 32°C) was used as the solvent. Each extractor held two 19x90mm cellulose extraction thimbles containing the samples.

Individual glass dessicator tubes were used to reduce absorption of atmospheric water during weighing. These dessicator tubes consisted of a 25x150mm glass test tube with a cloth sack containing dessicant in the bottom. The tubes were sealed with #4 rubber stoppers. Tubes were kept at room temperature and rubber gloves were worn during handling. All weights obtained of the extraction thimbles were taken while enclosed in the glass dessicator tubes.

Extraction thimbles were initially dried to constant weight (24 hours at 60°C). Extraction samples consisted of lizard bodies with the gut contents removed and lizard tails. Each sample was finely shredded with scissors and placed in a preweighed extraction thimble. The samples were then dried to constant weight (48 hours at 60°C) and weighed. The thimbles were then soaked in 95% ethanol for 10-15 minutes to denature protein, preventing its removal by the solvent (Sawicka-Kapusta 1975). Thimbles were placed in the Soxhlet unit and run for 10 hours (pre-determined by a standardization run on 0.5g lizard samples). Extracted samples were dried for 12 hours and weighed. Tails were too small to use for individual extraction, and were therefore pooled and an overall mean obtained for each experimental group.

Water content of bodies and tails.

To determine if mass was affected by differential water retention or loss due to the treatments, percent dry mass of bodies and tails was determined from wet and dry weights of dead individuals at the end of the experiment. Percent dry mass was used to convert wet mass to dry mass for all mass measurements.

Temperature selection.

Selected temperatures on a thermal gradient may reflect active body temperatures under field conditions. Temperature selection was measured on a thermal gradient consisting of a 68x96cm copper sheet heated from below by resistance wires running across the width of the sheet at intervals of 10cm. One end was cooled by an ice bath. Six wooden runways (9x89cm) with thin cloth bottoms and plexiglass tops were placed on top of the copper sheet and covered with a plexiglass top to reduce air flow. The gradient was housed in an environmental chamber set at 18-20°C. Gradient substrate temperature was measured from 16 thermocouple

wires attached at 6cm intervals down the center, and 3 wires attached at 36cm intervals down each side. Adjustment of the current to the resistance wires made it possible to obtain a uniform temperature gradient ranging from 22-40°C down the length (0.22°C/cm) and temperature consistancy across the width of the gradient (a mean difference of 0.01°C/cm across the width).

Observations were made (October 7 to November 10, 1987). Lizards were placed in a runway and allowed to acclimate for 30 minutes. Six lizards were observed simultaneously with only one observation period per lizard. Any observation in which a lizard was not on the floor of the gradient was omitted. Lizard position at mid-body on the gradient was then recorded every two minutes for a total of 31 observations. Following the observation period, the lizard was captured and cloacal temperature measured within 30 seconds using a thermocouple thermometer.

The prior protocol provided a direct measurement of body temperature (T_b). T_b was also measured indirectly from observations of location on the gradient. The following observations allowed me to convert substrate temperatures (TS) corresponding to lizard position to estimated body temperatures (EBT). Lizards were confined to a small region of the gradient over which substrate temperature did not vary by more than 0.5°C. Substrate temperatures of the areas tested ranged from 27.0-37.0°C. After a 30 minute equilibration time (time to equilibration was determined by preliminary experiments), substrate temperature and lizard cloacal temperature were measured. The resulting regression equations were EBT = 4.11 + 0.77TS ($N = 34$, $R^2 = 0.93$, $P < 0.001$) for E. fasciatus and EBT = 4.8 + 0.78TS ($N = 45$, $R^2 = 0.96$, $P < 0.001$) for C. ocellatus. The mean selected temperature was calculated by dividing the sum of EBTs by the total number of observations.

Statistical analysis.

One and two-way ANOVAs were used to compare treatment effects. Pair-wise comparisons were used if there were significant interactions between main effects. A three- way ANOVA was used to analyse the scat data using time as the third main effect. All analyses were carried out on the Statistical Analysis System (SAS, 1988) at Virginia Polytechnic Institute and State University. Descriptive statistics are given as $\overline{X} \pm 1SE$.

RESULTS

Cage and lizard temperatures.

Ambient lab temperatures ranged from a monthly mean low of 19.5°C to a monthly mean high of 26.0°C (Fig. 1a). Mean ambient temperature dropped about 3°C between September and October. This drop was reflected in lowered cage substrate and lizard cloacal temperatures. However, the drop did not change the magnitude of the temperature difference between warm and cold cages.

Temperatures within cold cages ranged from 18.0 to 26.5°C with daily fluctuations parallel to ambient lab temperature (Fig. 1b, and c). Warm cages paralleled ambient lab temperature except during and for 1 hour after the six hour heating period, when substrate temperatures averaged 10-20°C above ambient.

Lizard cloacal temperatures for animals housed in the cold cages ranged from 17.2 to 28.3°C (C. ocellatus) and 17.7 to 27.8°C (E. fasciatus). These temperatures were similar to ambient lab temperature. Lizard cloacal temperatures for animals housed in the warm cages ranged from 19.9 to 33.2°C (C. ocellatus) and 17.7 to 32.7°C (E. fasciatus). These temperatures followed ambient except during the heating period when temperatures ranged from 30.1-32.7°C (E. fasciatus) and 28.7-33.2°C (C. ocellatus) (Fig. 2a, and b).

Scat production.

Eumeces. Scat production by E. fasciatus was affected by the temperature treatment (Fig. 3a, see Tables 1 & 2 for statistical summaries for this and the following analyses which are given as $\overline{X}\pm SE$). The warm group ($\overline{X}=10.9$ AFSMmg/g) had significantly higher scat production than the cold group ($\overline{X}=6.8$ AFSMmg/g). Scat production was not affected by the tail manipulation treatment. Scat production was significantly higher in September ($\overline{X}=11.8$ AFSMmg/g) than in October ($\overline{X}=6.1$ AFSMmg/g). There were no interactions for the three-way ANOVA.

Chalcides. Scat production by C. ocellatus was affected by the temperature treatment. The warm group ($\overline{X}=4.2$ AFSMmg/g) had a significantly higher scat production than the cold group ($\overline{X}=2.6$ AFSMmg/g) (Fig. 3b). Scat production was not affected by the tail manipulation treatment. Scat production was significantly higher in September ($\overline{X}=4.5$ AFSMmg/g) than in October ($\overline{X}=2.4$ AFSMmg/g). There were no interactions for the three way ANOVA.

Apparent absorption efficiencies.

Apparent absorption efficiencies were not affected by the temperature or tail manipulation treatment in either species (Fig. 4). Mean A_{dm} for E. fasciatus was 82% and for C. ocellatus was 71%, and mean A_{am} for E. fasciatus was 77% and for C. ocellatus was 67%.

Food intake [dry mass (mg) ingested during the experimental period per gram lizard] for E. fasciatus was affected by the temperature treatment only. The warm controls ($\overline{X}=385\pm12$mg/g) had a significantly higher food intake than the cold group ($\overline{X}=317\pm9$mg/g). However, for C. ocellatus food intake was not affected by either the temperature or tail manipulation treatment ($\overline{X}=316\pm29$mg/g). Most scats were collected within the first two days of fasting, and there was no apparent difference between the warm and cold groups.

Growth.

Eumeces absolute growth rates. Snout-vent length (SVL) growth rates of E. fasciatus were affected only by the temperature treatment (Fig. 5a). The warm controls ($\overline{X} = 0.19 \pm 0.008$mm/day) had a significantly higher SVL growth rate than the cold group ($\overline{X} = 0.14 \pm 0.007$mm/day). The tail manipulation treatment affect was not significant.

Growth rate in body dry mass was affected only by temperature treatment (Fig. 5b). The warm controls ($\overline{X} = 3.63 \pm 0.23$mg/day) had significantly higher rates of mass gain than did the cold group ($\overline{X} = 2.68 \pm 0.16$mg/day).

Total tail length (TTL) growth rates were not significantly affected by either the temperature or tail manipulation treatments. However, tail-removal lizards had consistently higher TTL growth rates than the tailed lizards (Fig. 6a). Percent regeneration of estimated normal tail length was not affected by the temperature treatment ($\overline{X} = 50.7 \pm 1.34\%$).

Growth rate in tail dry mass was affected only by the tail removal treatment (Fig. 6b). Tail-removal lizards ($\overline{X} = 0.42 \pm 0.032$mg/day) had significantly lower rates of tail mass gain than did the tailed lizards ($\overline{X} = 0.73 \pm 0.099$mg/day).

Chalcides absolute growth rates. Snout-vent length (SVL) growth rates of C. ocellatus were affected by both the temperature and the tail manipulation treatments (Fig. 7a). The warm controls ($\overline{X} = 0.11 \pm 0.006$mm/day) higher SVL growth rates than the cold group ($\overline{X} = 0.06 \pm 0.005$mm/day). The tailed lizards had significantly higher SVL growth rates ($\overline{X} = 0.10 \pm 0.008$mm/day) than the tail-removal lizards ($\overline{X} = 0.06 \pm 0.006$mm/day).

Body growth in dry mass was affected only by the temperature treatment (Fig. 7b). The rate of mass gain was greater by the warm controls ($\overline{X} = 2.27 \pm 0.12$mg/day) than by the cold group ($\overline{X} = 1.12 \pm 0.08$mg/day). However, there was a significant interaction between the treatments. Within the warm controls, tailed lizards had significantly higher mass gains than did the tail-removal lizards ($P < 0.05$, Pairwise Comparison). In contrast, within the cold group tailed and tail-removal lizards did not differ in mass gains.

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Total tail length (TTL) growth rates were affected by both the temperature and tail manipulation treatments (Fig. 8a). The warm controls had significantly higher TTL growth rates ($\overline{X} = 0.45 \pm 0.06$mm/day) than the cold group ($\overline{X} = 0.40 \pm 0.06$mm/day). The tail-removal lizards had significantly lower TTL growth rates ($\overline{X} = 0.17 \pm 0.01$mm/day) than the tailed lizards ($\overline{X} = 0.70 \pm 0.02$mm/day). Percent regeneration of estimated normal tail length was affected by temperature ($P < 0.001$, Ttest). Warm lizards ($\overline{X} = 36.5 \pm 1.6\%$) had a higher percent regeneration than the cold lizards ($\overline{X} = 19.1 \pm 0.9\%$).

Growth rate in tail mass was affected by both the temperature and tail manipulation treatments (Fig. 8b). The warm controls ($\overline{X} = 0.46 \pm 0.05$mg/day) had a greater rate of mass gain than the cold group ($\overline{X} = 0.15 \pm 0.03$mg/day). Tailed lizards ($\overline{X} = 0.40 \pm 0.05$mg/day) had a greater rate of mass gain than the tail-removal lizards ($\overline{X} = 0.21 \pm 0.03$mg/day).

Eumeces relative growth rates. The ratio $\triangle$TTL/$\triangle$SVL was affected by the temperature treatment and by the tail manipulation treatment (Fig. 9a). Relative tail growth was higher for the cold group ($\overline{X} = 2.47 \pm 0.12$) than for the warm controls ($\overline{X} = 2.05 \pm 0.14$). Relative tail growth of the tail-removal lizards ($\overline{X} = 2.52 \pm 0.12$) was higher than that of the tailed lizards ($\overline{X} = 1.88 \pm 0.12$).

Relative tail growth in dry mass was affected by the tail-removal treatment only (Fig. 9b). Relative tail mass growth of tail-removal lizards ($\overline{X} = 0.13 \pm 0.01$) was lower than that of the tailed lizards ($\overline{X} = 0.23 \pm 0.03$).

Chalcides relative growth rates. The ratio $\triangle$TTL/$\triangle$SVL was affected by the temperature treatment and by the tail manipulation treatment (Fig. 10a). Relative tail growth was higher for the cold group ($\overline{X} = 6.27 \pm 0.90$) than for the warm controls ($\overline{X} = 3.96 \pm 0.40$). Relative tail growth of the tailed lizards ($\overline{X} = 7.79 \pm 0.65$) was higer than that of the tail-removal lizards ($\overline{X} = 2.68 \pm 0.29$). There was a significant interaction between treatments ($P < 0.001$, Pairwise Comparison). The interaction resulted from a strong response to tail removal; relative tail

growth of tail- removal lizards in cold and warm groups did not differ, although the tailed lizards responded strongly to temperature (Fig. 10a).

Relative tail growth in dry mass was affected by the tail-removal treatment only (Fig. 10b). Relative tail mass growth of tail-removal lizards ($\overline{X}$ =0.13±0.02) was higher than that of the tailed lizards ($\overline{X}$ =0.23±0.02).

Body composition.

Percent lipid in the bodies was not affected by the temperature or tail manipulation treatment for either species (Tables 1&2). The overall means for tail lipids were 16.54% (E. fasciatus) and 4.66% (C. ocellatus).

Percent water in the bodies of both species was affected by the temperature treatment only. Cold groups (E. fasciatus, $\overline{X}$ =76.13% and C. ocellatus, $\overline{X}$ = 75.71%) had a higher per-cent water than the warm controls (E. fasciatus, $\overline{X}$ =75.82% and C. ocellatus, $\overline{X}$ = 74.27%). These differences can probably be attributed to a higher evaporative water loss in the warm cages and are so slight that they will not be considered further.

Percent water in the tails of E. fasciatus was affected by the tail manipulation treatment but not the temperature treatment. Tailed lizards ($\overline{X}$ =63.4±1.3%) had a higher percent water than the tail-removal lizards ($\overline{X}$ =56.8±1.2%). In contrast, percent water in the tails of C. ocellatus was affected by the temperature treatment but not the tail manipulation treatment. The warm controls ($\overline{X}$ =71.1±0.64%) had a higher percent water than the cold group ($\overline{X}$ =73.1±0.75%). There was a significant interaction between treatments (P<0.05, Pairwise Comparison).

Temperature selection (observations on the thermal gradient).

Selected body temperature of E. fasciatus estimated from their position on a thermal gradient (EBT) and cloacal temperatures (T_b) were affected only by the temperature treatment. The cold group had EBTs and Tbs ($\overline{X}$ = 30.7 and 30.7°C, respectively) higher than those of the warm controls ($\overline{X}$ = 28.0 and 28.2°C, respectively). Thus, selected body temperatures in the gradient of lizards from cold cages were very similar to body temperatures exhibited by lizards in the warm cages during the lighting period. In contrast, selected body temperatures in the gradient of lizards from warm cages were lower than those exhibited in the cages during the lighting period.

Selected body temperature of C. ocellatus estimated from their position on a thermal gradient (EBT) and cloacal temperatures (T_b) was not affected by the temperature treatment or the tail manipulation treatment (Table 1&2). Selected temperatures averaged 32.0°C T_b and 31.8°C EBT. Thus, selected body temperatures in the gradient were similar to those of lizards in the warm cages during the lighting period.

DISCUSSION

Eumeces faciatus and C. ocellatus juveniles responded differently to the experimental treatments (Fig. 11). E. fasciatus juveniles were affected largely by temperature whereas C. ocellatus juveniles were affected by both temperature and tail removal. Moreover, as predicted, E. fasciatus exhibited enhanced relative tail growth in response to autotomy and C. ocellatus exhibited reduced relative tail growth in response to autotomy.

Food Intake.

Scat production by both species was significantly lower for the cold groups than the warm controls. Scat production for E. fasciatus was reduced by 36% and for C. ocellatus by 25%. Differences in scat production were presumably a consequence of the temperature treatment; body temperatures in the cold groups averaged about 7°C lower than in the warm controls during the 6h/d when thermoregulation was possible.

Scat production is directly proportional to food intake given a constant absorption efficiency and passage rate. In this study, absorption efficiency did not differ between the cold and warm groups for either species. Thus, the experimental conditions resulted in differences

in food intake between lizards in the cold and warm cages. This is also supported by the lower food intake by cold E. fasciatus during the absorption experiment.

Performances such as locomotion, growth, metabolism, and digestion are temperature dependent (reviewed by Huey 1982). However, these functions tend to show weak thermal dependence around the individual's normal activity temperatures (Bennett 1980, Huey 1982). In this study, the lizards in cold and warm cages were exposed to less than 1 Q_{10} difference in temperature for only 25% of experimental period. Thus, large differences in performance on the basis of temperature per se would not be expected. For example, absorption efficiencies of lizards did not differ in the cold and warm cages.

Growth.

Body growth in both SVL and mass was lower for the cold groups than the warm groups of both species. Low body growth of the cold groups was presumably a consequence of reduced food intake. In contrast, tail removal had no effect on body growth of E. fasciatus but it reduced linear body growth of C. ocellatus. Lipid contents of E. fasciatus or C. ocellatus bodies did not vary as a function of the treatments, suggesting that differences in body growth were not a function of differential lipid storage but were related to differences in food intake. However, for both species, lizards that were regenerating tails tended to have higher body lipids, suggesting that additional lipids are stored in the body during the period of tail regeneration.

In contrast to the comparable changes in body growth, the two species responded differently to the treatments with regards to tail growth. For E. fasciatus, tails grew linearly at the same rate irrespective of treatment ie. regenerating tails grew at the same rate as normal tails for both cold and warm groups. This rate was very similar to that observed by Vitt and Cooper (1986a) for juvenile E. fasciatus. However, regenerating tails had a slower dry mass gain than did the normal tails. In contrast, for C. ocellatus, linear and dry mass tail

growth was affected by both food intake and tail condition; under reduced food intake tail growth was reduced and regenerating tails grew slower than normal tails.

Tails were not totally regenerated during the 84 days of observation. E. fasciatus regenerated an average of 50.7% of estimated normal tail length with no difference between warm and cold treatments. This proportional tail regeneration rate is lower than those reported for some other lizards. For example, adult Lacerta dugesii regenerated 90% of the portion lost in 84 days (Bryant and Bellairs 1967). However the reason for the rapid regeneration by L. dugesii is that observations were on adults which not have had energy costs of body growth in addition to tail regeneration. In contrast, C. ocellatus regenerated 19.1% and 36.5% of estimated normal tail length in the cold and warm groups, respectively. This is consistent with the slow regeneration rate reported for other fossorial species (Bryant and Bellairs 1967).

Relative tail growth.

Juvenile E. fasciatus and C. ocellatus responded differently to both the temperature and tail removal treatments with regard to relative linear tail growth. For E. fasciatus relative linear tail growth was higher for lizards in the cold than the warm group. Thus, when food intake was reduced, linear tail growth was enhanced. Moreover, relative linear tail growth for lizards regenerating their tails was higher than for lizards with normal tails. Thus, greater linear tail growth relative to body growth by E. fasciatus under both experimental treatments supports the hypothesis that a species whose tail is important for predator deflection should allocate energy preferentially to tail regeneration.

For C. ocellatus, there was no difference in the relative linear tail growth of lizards that were regenerating tails between the cold and warm conditions although the overall effect of reduced food intake was statistically significant. The overall effect was due to the very large response to reduced food (cold) by the tailed controls (Table 2). Moreover, the relative linear tail growth of lizards regenerating their tails was considerably lower than the tailed controls.

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Thus, as predicted, relative linear tail growth of C. ocellatus juveniles that were regenerating their tails was not at the expense of linear body growth.

Juvenile E. fasciatus and C. ocellatus responded similarly to the tail manipulation treatment with regard to relative mass tail growth. For both E. fasciatus and C. ocellatus, relative tail mass growth was lower for the tail-removal than the tailed lizards, irrespective of temperature. Thus, energy was not allocated to tail mass growth at the expense of body growth for either species.

The process of tail regeneration in E. fasciatus and C. ocellatus is clearly quite different. E. fasciatus regenerated their tails rapidly, at least, in length. During the 84 day observation period E. fasciatus regenerated 50.7% of estimated normal tail length. Functionally this means a partial tail is present relatively soon after loss even though it does not have the mass of a normal tail. In contrast, C. ocellatus regenerated the tail slowly in both length and mass. This supports the hypothesis that the tail is not important for predator deflection, and that tail growth is not favored over body growth for this species.

Evaluation of alternative hypotheses.

Tails have other functions than predator deflection. Could these functions be responsible for the differences exhibited by E. fasciatus and C. ocellatus in relative tail growth and regeneration? Normal tails are necessary for social dominance in some iguanid lizards (Berry 1974, Fox and Rostker 1982). Such a role for tails is not known for skinks. Moreover, Vitt and Cooper's studies (1987) suggest that social interactions for E. fasciatus are based on olfactory cues and not on visual cues. The social biology of C. ocellatus is unknown but appears to be similar to that of E. fasciatus in this regard (personal observation). Another potential use of the tail for C. ocellatus is sub-sand locomotion. However, observations by Gans (1986) and Arnold (1988) suggest that the tail is not particularly important for movement by fossorial species.

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Although E. fasciatus and C. ocellatus are members of the same subfamily, they are not closely related (Greer 1970). Thus, results of this study may simply reflect phylogenetic history rather than function. This is possible, but I believe that the differences exhibited by juvenile E. fasciatus and C. ocellatus reflect different selective pressures on tail function. Tail functions of lizards are a result of environmental selective forces and appear to be relatively independant of taxonomic relationships within families with both autotomic and non-autotomic species. For example, many Cnemidophorus (Teiidae) juveniles have bright blue tails that appear to function as do the blue tails of E. fasciatus (Scincidae). Likewise, rapid regeneration rates characterize species that use the tail for predator deflection (Vitt et al. 1977). For example, Gerrhonotus multicarinatus (Anguidae) relys on aggressive behavior (biting, jumping at) to deter predator attacks and consequently does not autotomize readily and has a relatively slow regeneration rate. On the other hand, Coleonyx variegatus (Gekkonidae) uses its tail for predator deflection and consequently does autotomize readily and has a relatively rapid regeneration rate.

DISCUSSION

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Appendix A. Tables

Table 1. Statistical summary of two way ANOVAs for both E. fasciatus and C. ocellatus. Significance levels are given as: * - significance at the 0.05 level, ** - significance at the 0.01 level, *** - significance at the 0.001 level, NS - not significant.[1]

Analysis	Eumeces Main effects Temp	Tail	Interaction	Chalcides Main effects Temp	Tail	Interaction
Scat production						
Sample 1&2[1]	*	NS	NS	*	NS	NS
Absorption efficiency						
Food intake	**	NS	NS	NS	NS	NS
Adm	NS	NS	NS	NS	NS	NS
Aam	NS	NS	NS	NS	NS	NS
Growth						
SVL	***	NS	NS	***	***	NS
BODY MASS	**	NS	NS	***	NS	*
TTL	NS	NS	NS	***	***	NS
TAIL MASS	NS	**	NS	***	***	NS
ΔTTL/ΔSVL	*	***	NS	***	***	**
ΔTDM/ΔBDM	NS	***	NS	NS	***	NS
Percent lipid						
Body	NS	NS	NS	NS	NS	NS
Percent H₂O						
Body	*	NS	NS	*	NS	NS
Tail	NS	***	NS	*	NS	NS
Temperature selection						
SBT	**	NS	NS	NS	NS	NS
Cloacal	**	NS	NS	NS	NS	NS

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[1] Results of the three-way ANOVA also indicated that scat production was greater during the first time period than the second.

Table 2. Summary of Means ± Standard Errors for all analyses for both E. fasciatus and C. ocellatus. Numbers in parentheses represent sample sizes.

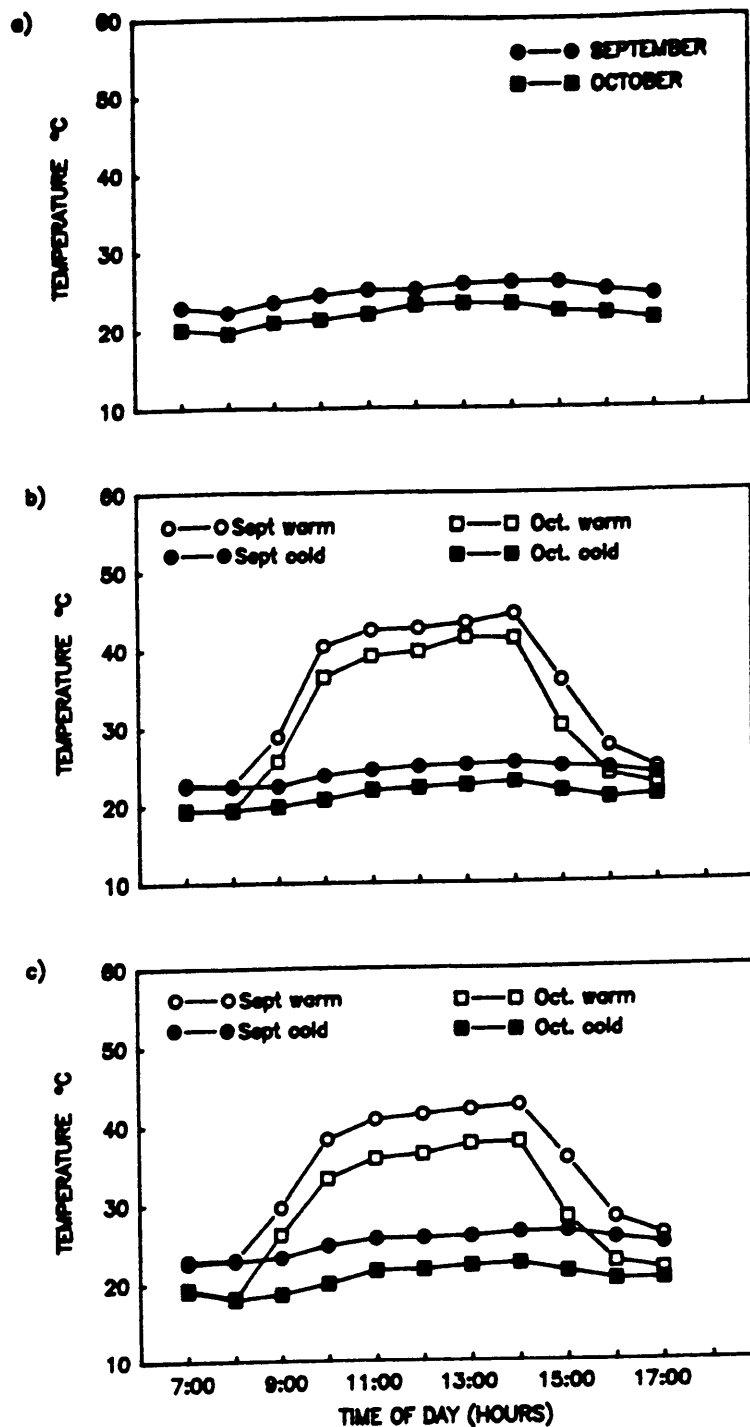| | E. fasciatus | | | | C. ocellatus | | | | |
| | Cold | | Warm | | Cold | | Warm | |
	Tail-removal	Tailed	Tail-removal	Tailed	Tail-removal	Tailed	Tail-removal	Tailed	Tailed
Scat production g/g									
Sample size	7.31±1.00 (17)	8.57±0.94 (16)	11.33±1.09 (20)	10.29±1.81 (14)	2.93±0.58 (18)	2.91±0.59 (21)	3.93±0.89 (23)	4.49±0.94 (20)	
Absorption Efficiency									
Food intake (mg/g)	328±11 (3)	310±14 (3)	399±13 (4)	374±20 (4)	289±48 (4)	252±57 (3)	305±44 (4)	289±105 (4)	
Am	83.7±1.2 (3)	83.8±1.3 (3)	82.8±1.1 (4)	79.8±0.8 (4)	71.0±5.7 (4)	71.5±7.1 (3)	71.2±5.3 (4)	69.7±5.7 (4)	
Ams	86.1±7.5 (3)	74.7±12.2 (4)	87.6±10.8 (4)	80.2±2.4 (4)	87.8±3.0 (4)	83.3±8.7 (3)	87.2±4.8 (4)	70.4±2.7 (4)	
Growth									
SVL mm/day	0.14±0.01 (6)	0.15±0.01 (6)	0.18±0.01 (10)	0.21±0.01 (9)	0.08±0.01 (11)	0.07±0.01 (11)	0.08±0.01 (12)	0.13±0.01 (10)	
BODY MASS mg/day	2.05±0.24 (6)	2.44±0.17 (6)	3.47±0.28 (10)	3.01±0.37 (9)	1.22±0.14 (11)	1.03±0.10 (11)	2.08±0.15 (12)	2.49±0.18 (10)	
TTL mm/day	0.39±0.03 (6)	0.31±0.02 (6)	0.41±0.02 (10)	0.37±0.05 (9)	0.12±0.01 (11)	0.07±0.02 (11)	0.22±0.01 (12)	0.73±0.03 (10)	
TAIL MASS mg/day	0.40±0.05 (6)	0.84±0.02 (6)	0.44±0.04 (10)	0.78±0.17 (9)	0.06±0.007 (11)	0.22±0.04 (11)	0.32±0.05 (12)	0.82±0.05 (10)	
Relative growth									
ΔTTL/ΔSVL	2.75±0.15 (6)	2.08±0.04 (6)	2.35±0.16 (10)	1.74±0.18 (9)	2.79±0.48 (11)	8.77±0.93 (11)	2.98±0.33 (12)	8.91±0.35 (10)	
ΔTDM/ΔBDM	0.14±0.01 (6)	0.37±0.02 (6)	0.13±0.01 (10)	0.25±0.01 (9)	0.06±0.025 (11)	0.20±0.034 (11)	0.152±0.022 (12)	0.210±0.018 (10)	
Lipid									
Body %	19.18±1.86 (9)	17.01±2.73 (8)	21.51±1.92 (10)	15.57±2.05 (9)	14.29±1.44 (11)	13.08±2.39 (12)	16.95±1.01 (12)	14.79±1.11 (10)	
H₂O									
Body %	73.47±0.94 (9)	77.11±0.94 (8)	74.30±1.04 (10)	77.50±0.85 (9)	73.25±0.44 (11)	78.14±0.08 (12)	73.07±0.58 (12)	74.30±0.54 (10)	
Tail %	80.65±1.90 (9)	85.45±1.14 (8)	87.02±1.78 (10)	81.98±1.90 (9)	72.18±1.13 (11)	73.05±0.78 (12)	72.48±0.65 (12)	69.57±0.74 (10)	
Temperature selection									
EBT °C	30.9±0.8 (9)	30.8±0.3 (8)	27.9±0.8 (9)	28.1±1.11 (9)	32.0±0.6 (9)	32.9±0.6 (9)	31.9±0.4 (10)	31.4±0.3 (9)	
Closest °C	31.2±0.7 (9)	30.1±0.7 (7)	27.5±0.7 (10)	28.1±1.1 (9)	31.9±0.8 (11)	32.3±0.7 (9)	31.7±0.4 (12)	32.1±0.3 (10)	

Appendix B. Figures

Fig. 1. Laboratory temperature conditions during September and October 1987. Each point is the mean of three days of each month: a) ambient lab temperature, b) cage substrate temperature directly below the heat lamps in Eumeces cages, c) cage substrate temperatures directly below heat lamps in Chalcides cages. September temperatures were consistently ~3°C higher than those in October.
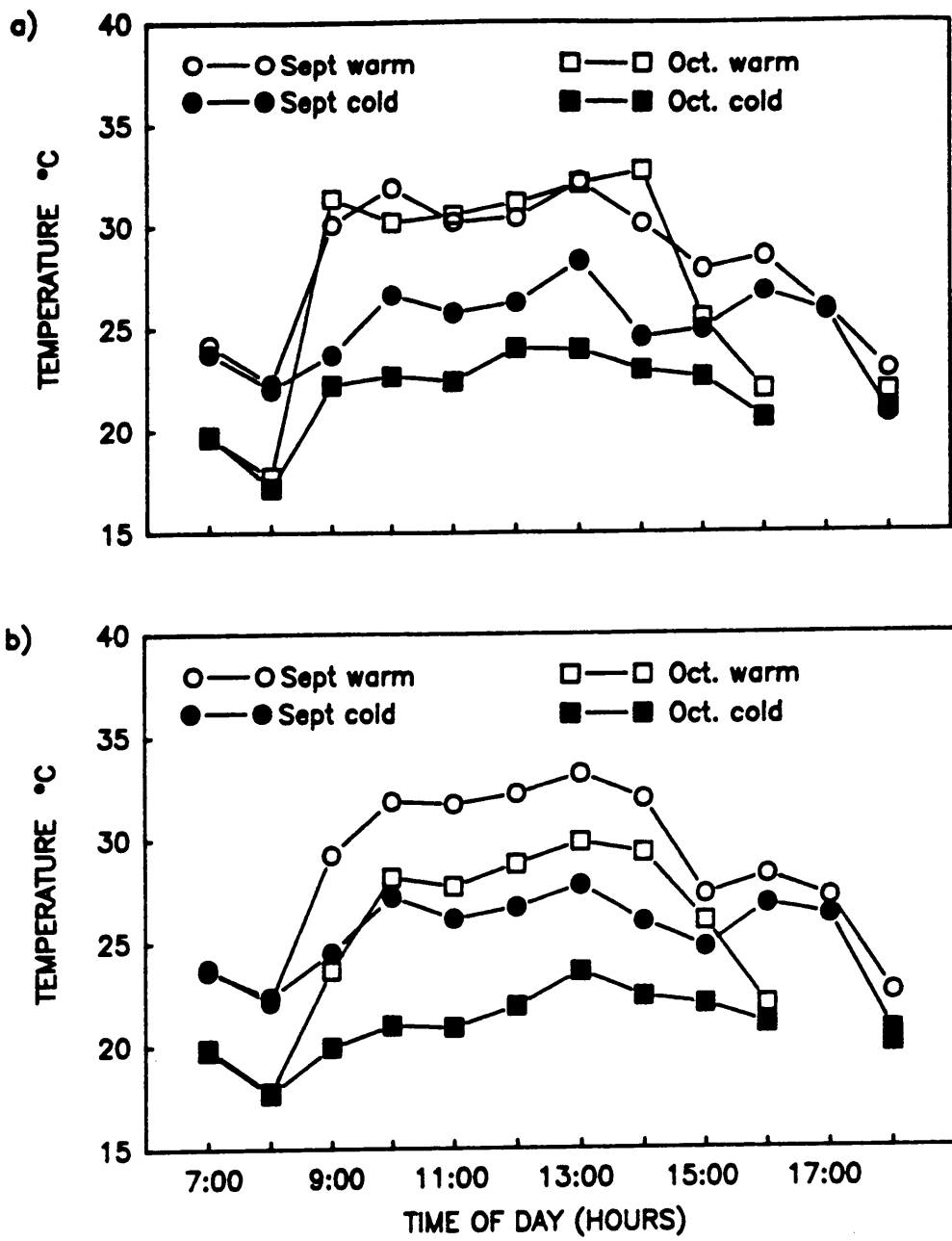
Fig. 2. Cloacal temperatures of lizards within warm and cold groups during September and October 1987. Data points represent the mean of three days within each month. a) mean cloacal temperatures of <u>Eumeces</u>. b) mean cloacal temperatures of <u>Chalcides</u>.
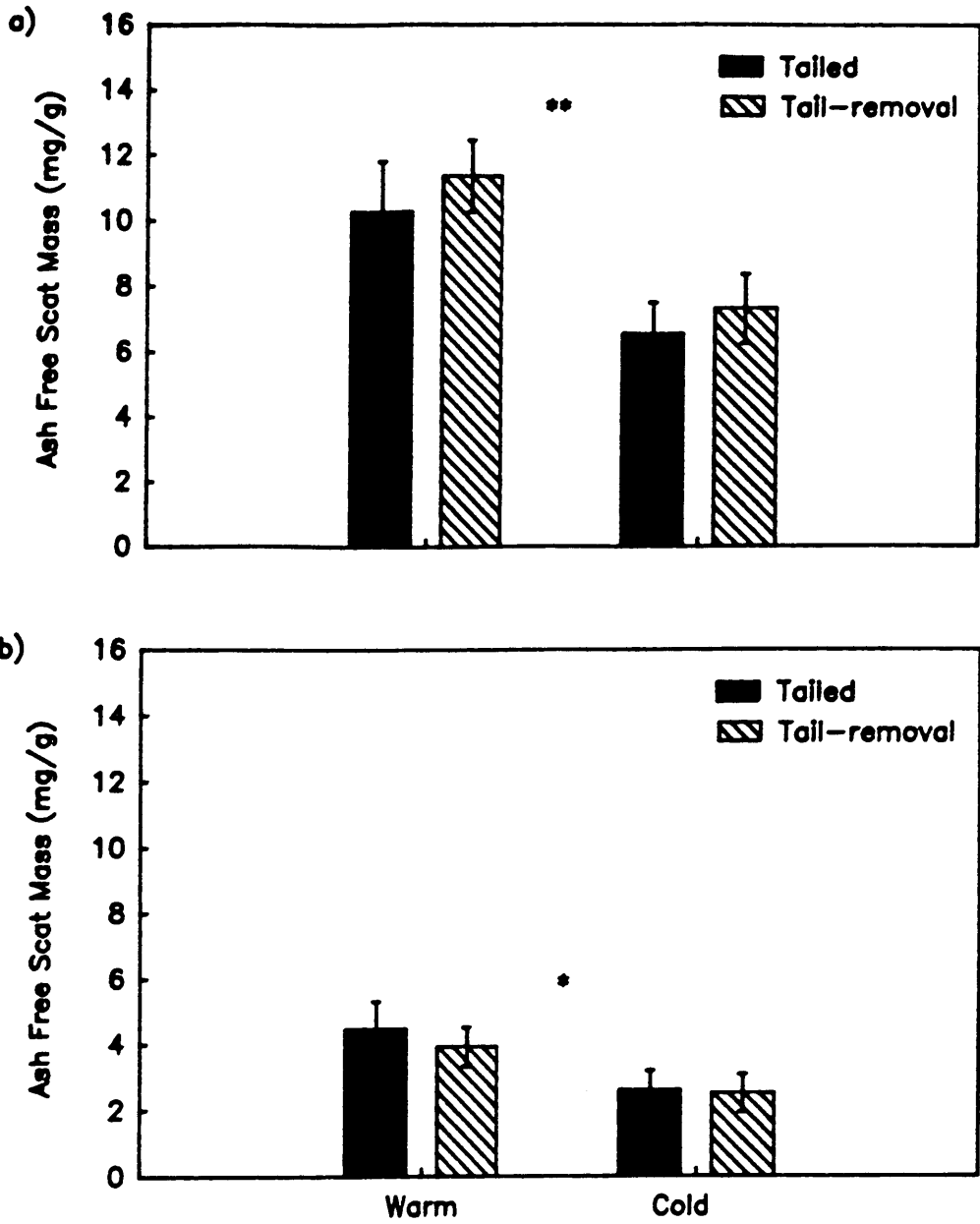
Fig. 3. Ash free scat mass mg/g (AFSMmg/g) for a) <u>Eumeces</u> b) for <u>Chalcides</u>. The cold groups had a significantly lower scat production than the warm controls for both species. * = P < 0.05 and ** = P < 0.01.
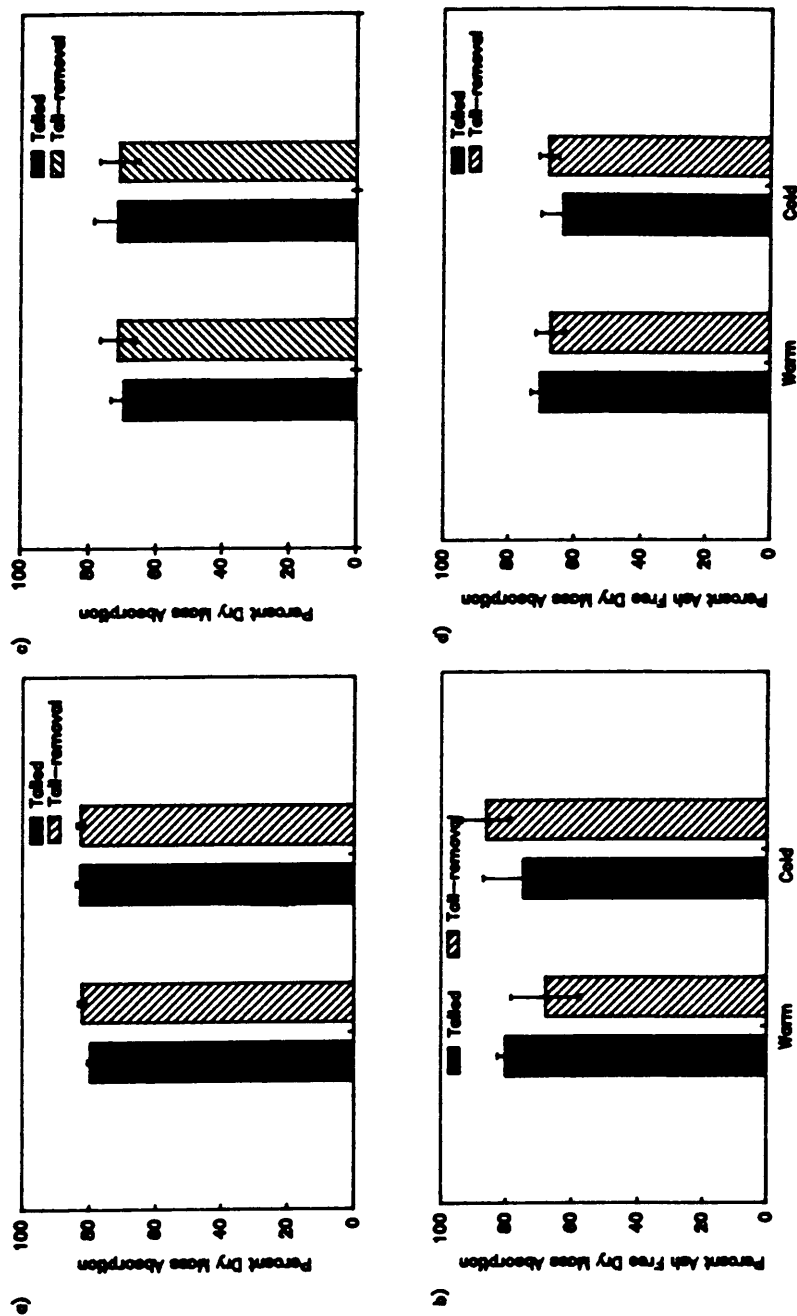
Fig. 4. Apparent absorption efficiencies for both species. a) Apparent dry mass absorption efficiency for E. fasciatus, b) Apparent ash free absorption efficiency for E. fasciatus, c) Apparent dry mass absorption efficiency for C. ocellatus, d) Apparent ash free absorption efficiency for C. ocellatus. There was no significant difference in treatments for either estimate of absorption efficiency.
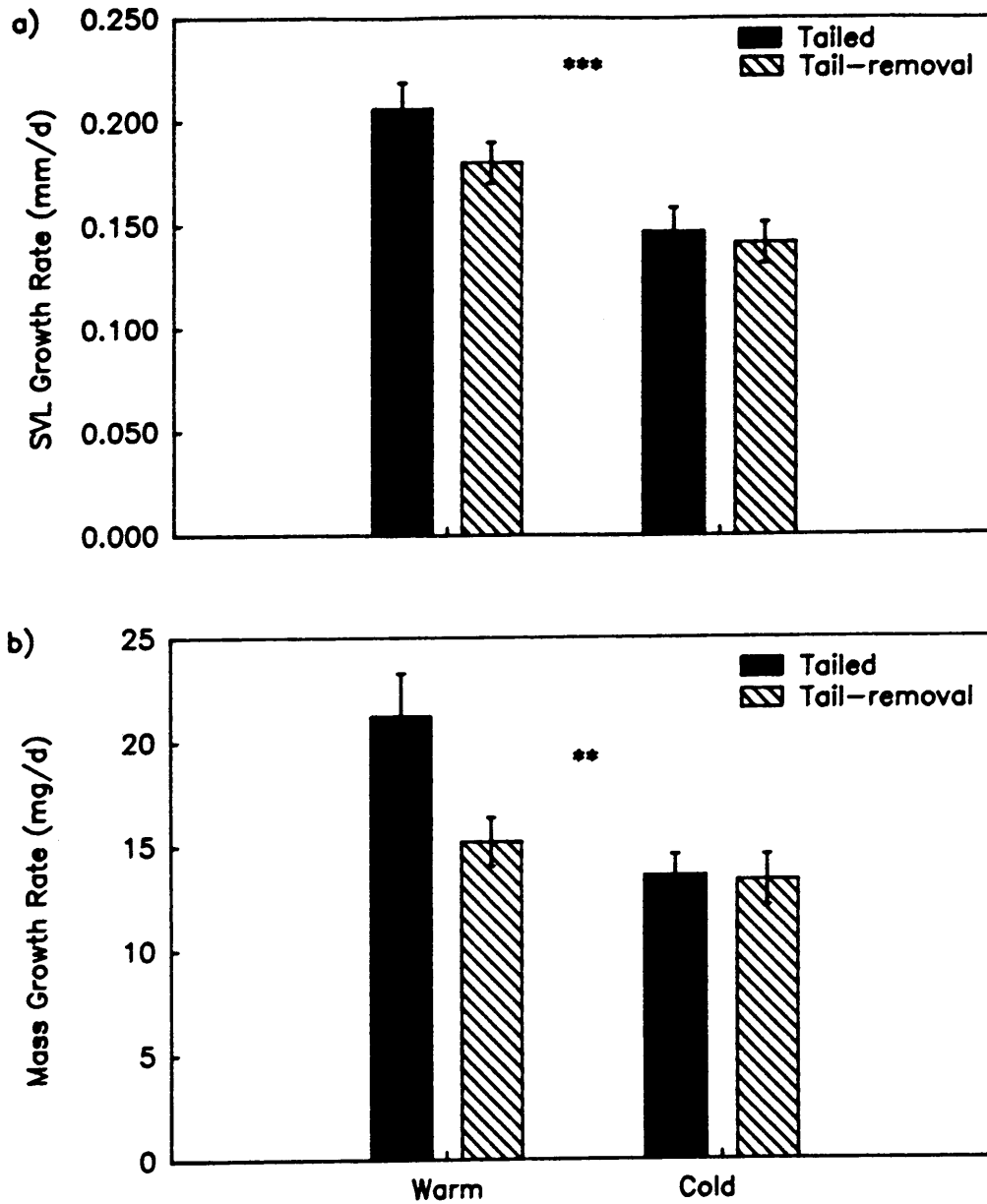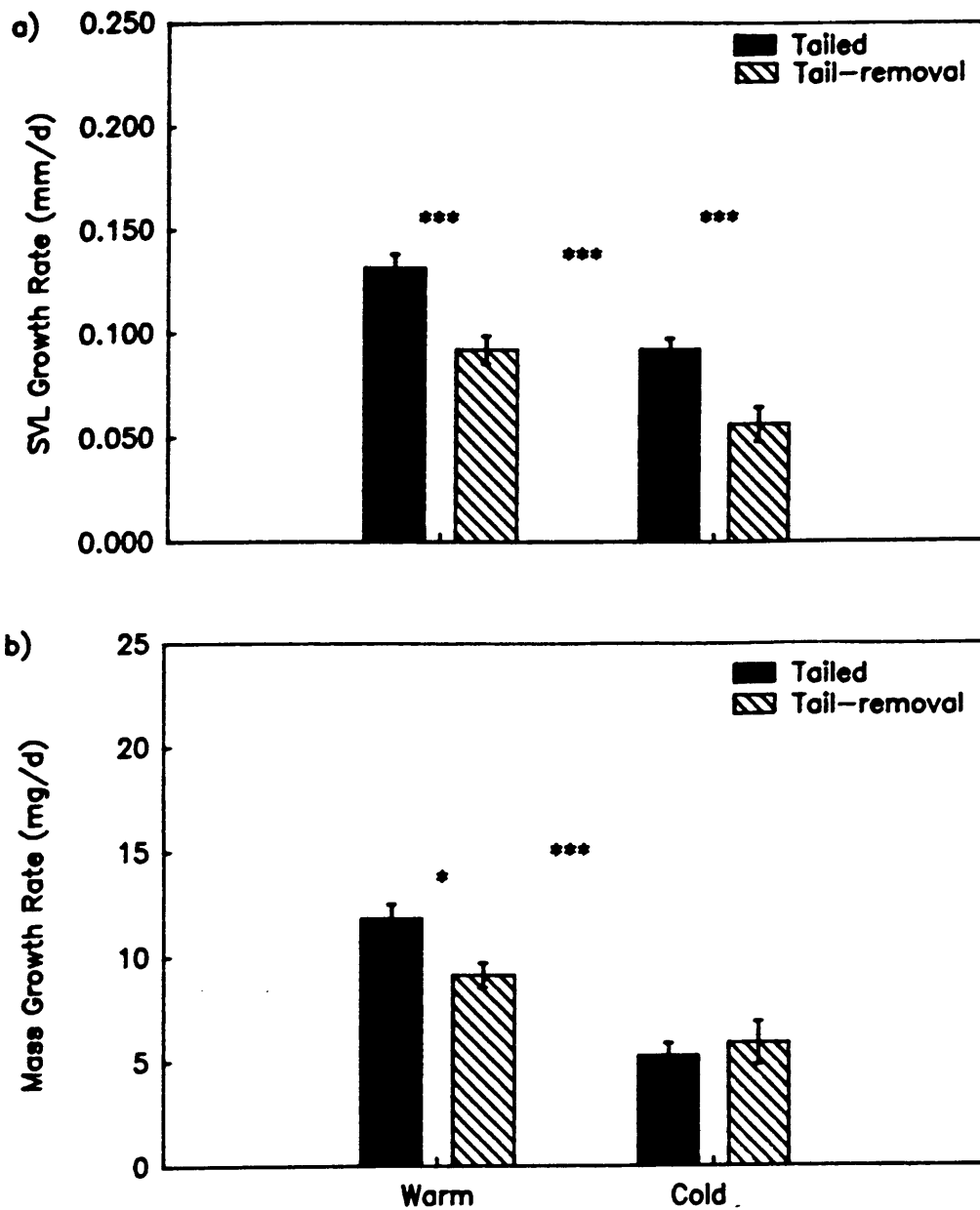
Fig. 5. Absolute body growth rates, both linear and mass for <u>Eumeces fasciatus</u>. a) Snout-vent length (SVL) growth rate in mm/day. b) Dry mass growth rate in mg/day. In all cases cold groups had significantly lower growth rates than did the warm controls. ** = P < 0.01 and *** = P < 0.001.
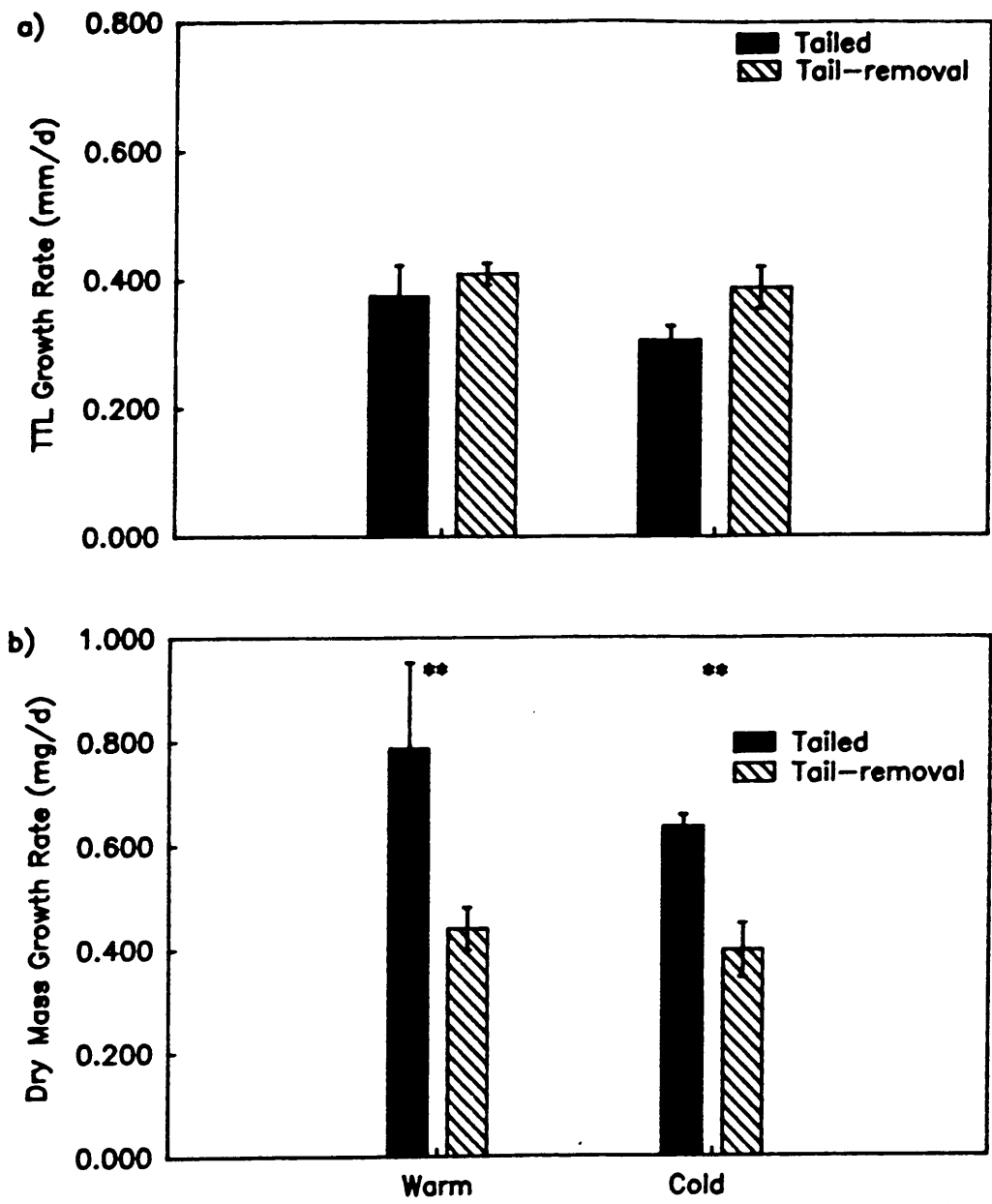
Fig. 6. Absolute tail growth rates, both linear and mass, for E. fasciatus. a) Total tail length (TTL) growth rate in mm/day. b) Dry mass growth rate in mg/day. Mass growth was affected by the tail manipulation treatment only. Tail-removal resulted in significantly lower tail mass growth than the tailed controls. ** = P < 0.01.

Fig. 7. Absolute body growth rates, both linear and mass, for C. ocellatus. a) Snout-vent length (SVL) growth rate in mm/day. b) Dry mass growth rate in mg/day. In all cases cold groups had significantly lower growth rates than did the warm controls. Linear growth was also significantly reduced by the tail-removal treatment. ***=P<0.001.
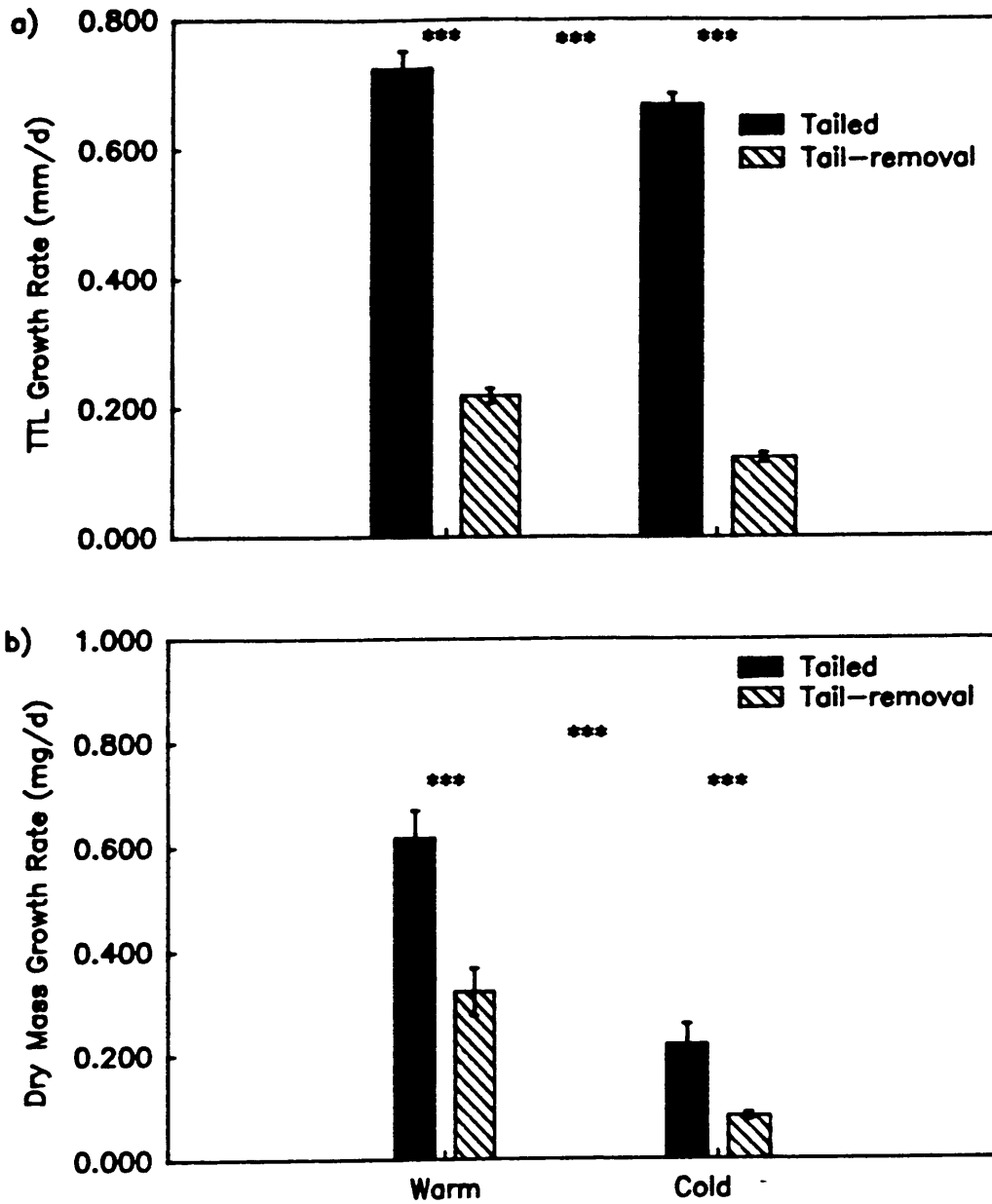
Fig. 8. Absolute tail growth rates, both linear and mass, for C. ocellatus. a) Total tail length (TTL) growth rate in mm/day. b) Dry mass growth rate in mg/day. In all cases growth was significantly reduced in the cold group and in the tail-removal group. *** = P < 0.001.
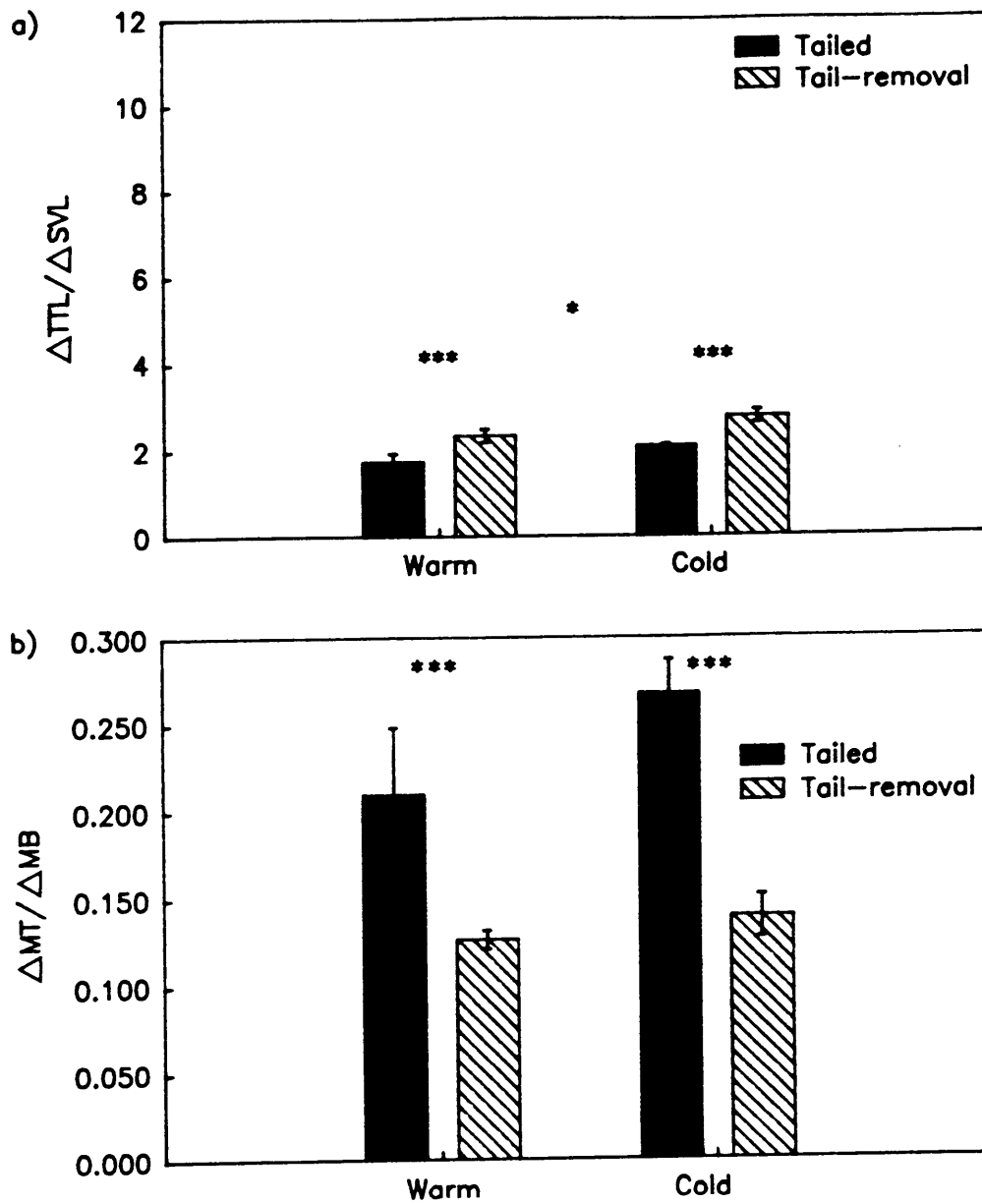
Fig. 9. Relative tail growth, both linear and mass, for E. fasciatus. a) Relative tail growth expressed as the ratio of linear tail growth to linear body growth. b) Relative tail mass growth expressed as the ratio of tail mass growth to body mass growth. $* = P < 0.05$ and $*** = P < 0.001$.
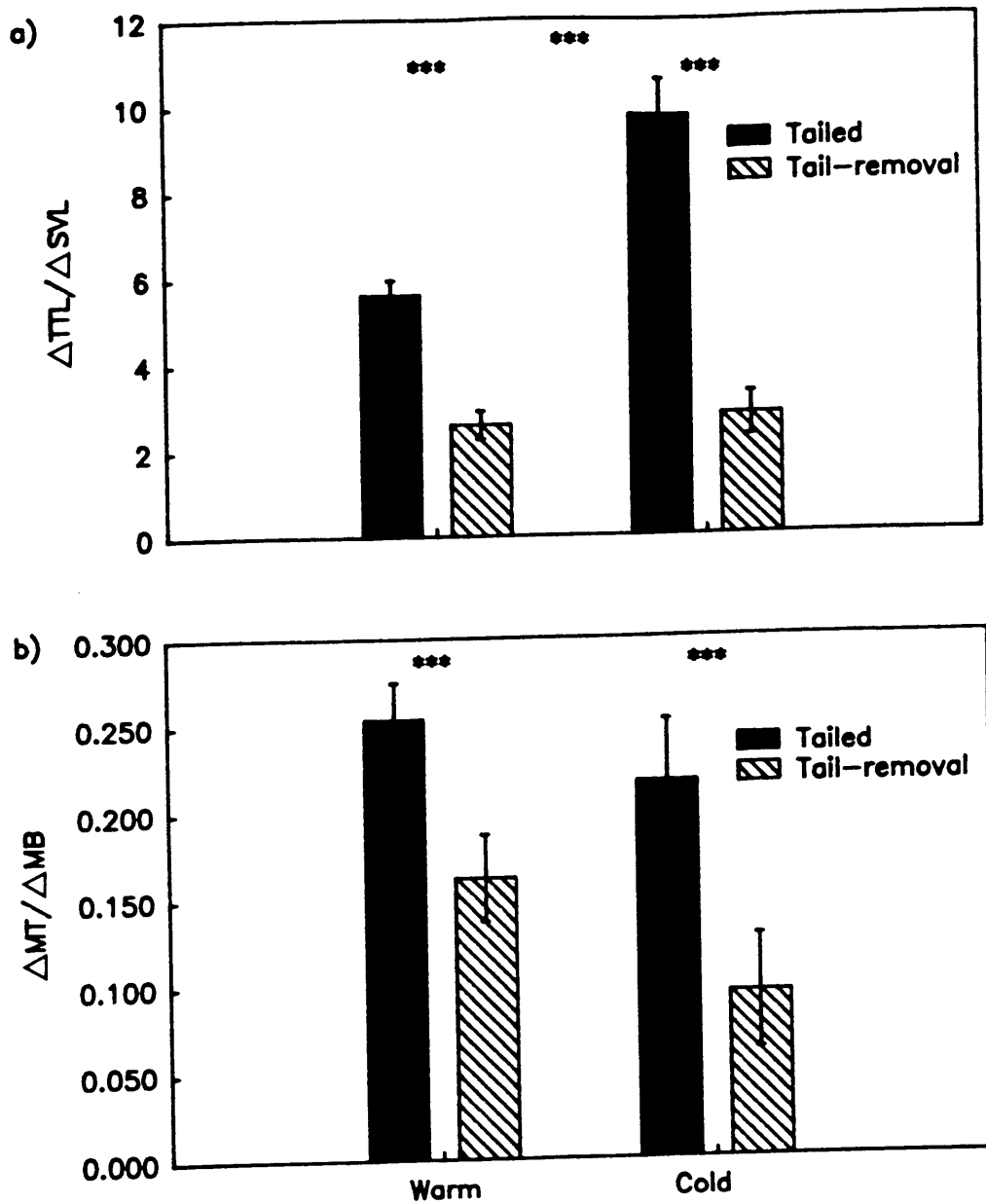
Fig. 10. Relative tail growth, both linear and mass, for <u>C. ocellatus</u>. a) Relative tail growth expressed as the ratio of linear tail growth to linear body growth. b) Relative tail mass growth expressed as the ratio of tail mass growth to body mass growth. ••• = P < 0.001.
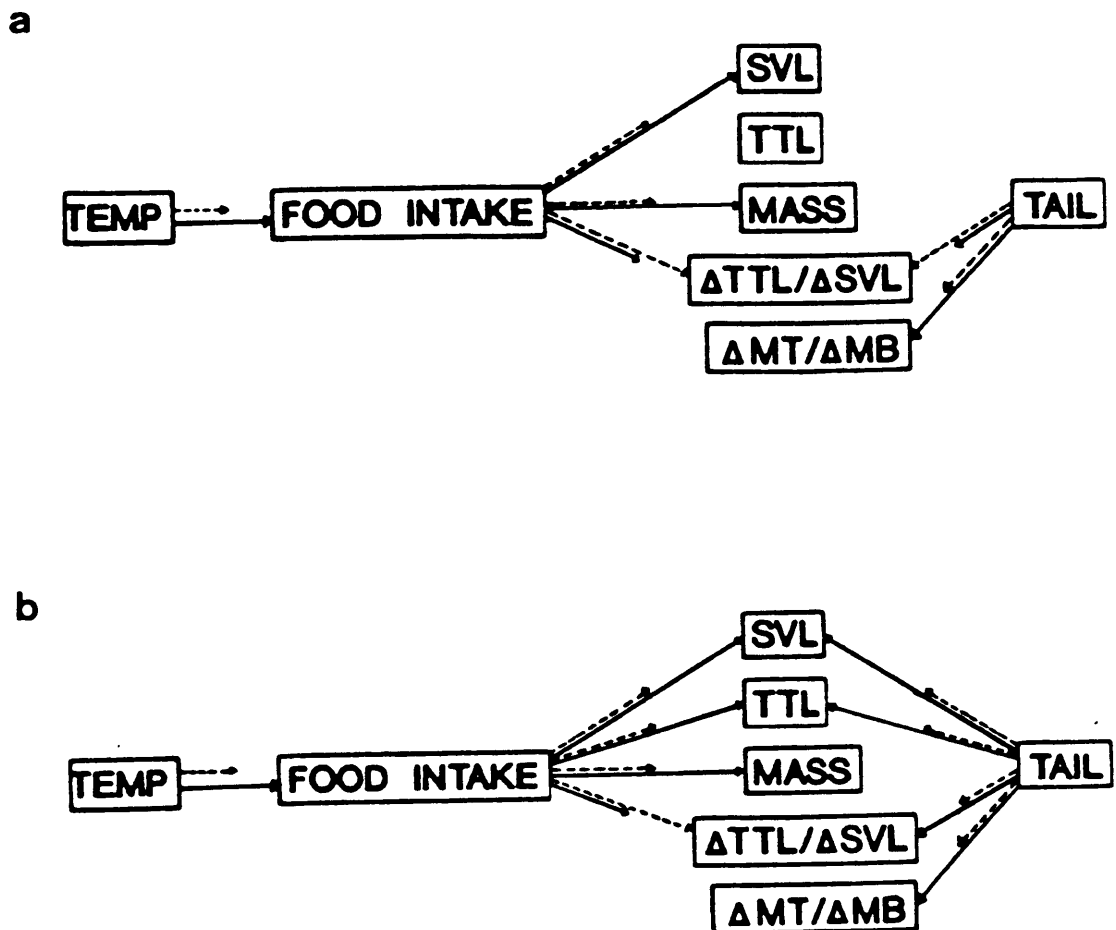
Fig. 11. Summary of the temperature and tail treatment affects. Only statistically significant factors are included. a) <u>Eumeces fasciatus</u> b) <u>Chalcides ocellatus</u>. The solid lines indicate warm groups on the left side and tailed groups on the right side. Dashed lines indicate cold groups on the left and tail- removal groups in the right. The relative length of the arrows shows the direction of the differences.

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