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Effects of tail loss on the movement patterns of the lizard, *Psammodromus algirus*

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Summary

1. Many lizards use caudal autotomy as a defensive strategy. However, subsequent costs related to the alteration of locomotor abilities might decrease the fitness of individuals. In this paper, the movement patterns of spontaneously moving *Psammodromus algirus* lizards and their escape performance running at high speed were compared before and after tail loss. A control tailed group was also studied to assess the repeatability of locomotor patterns between trials.
2. Tail loss had a significant effect on spontaneous movement patterns. Tailless individuals moved at significantly slower speeds during bursts of locomotion, and distances moved within bursts were significantly reduced. The overall time spent pausing increased, and, as a result, overall speeds decreased to an even greater extent than burst speeds. However, mean durations of individual locomotor bursts and mean pause durations did not change significantly after tail loss.
3. Loss of the tail decreased mean stride length, although the positive relation between stride length and speed was retained.
4. Escape performance was also greatly affected; loss of the tail resulted in substantially reduced attained, maximal and overall escape speeds. These changes resulted in shorter escape distances (the time of the first pause after the initiation of the escape response) because the mean duration of escape responses did not change.
5. The relevance of these alterations for the ecology of this species, and how individuals may compensate for the costs of tail loss, favouring autotomy as an escape strategy, are discussed.

Key-words: Autotomy, escape performance, locomotion, speed

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Introduction

Autotomy of the tail is a defensive tactic used by numerous lizards to escape from predators when other strategies, such as fleeing or crypsis, have not been effective (Bellairs & Bryant 1985; Arnold 1988). Tail loss has the obvious benefit of survival, but subsequent costs associated with tail regeneration might decrease the fitness of individuals (review in Arnold 1988). Tailless lizards are more vulnerable to predation than tailed lizards (Congdon, Vitt & King 1974; Dial & Fitzpatrick 1984; Wilson 1992), but some lizards are able to compensate through behavioural changes such as adoption of a cryptic antipredator strategy (Formanowicz, Brodie & Bradley 1990), reduction of activity levels (Martín & Salvador 1995), microhabitat restrictions (Martín & Salvador 1992; Salvador, Martín & López 1995) or selection of shorter distances to refuges (Martín & Salvador 1993b). Energetic regeneration costs in tailless lizards may be met by increasing feeding rates (Dial & Fitzpatrick 1981) or by diversion of energy from other functions such as somatic growth (Ballinger & Tinkle 1979; but see Althoff & Thompson 1994) or reproductive effort (Dial & Fitzpatrick 1981; Martín & Salvador 1993a).

One of the more conspicuous costs of tail autotomy is the loss of agility and the alteration of locomotor abilities of tailless individuals (Snyder 1949; Ballinger 1973; Arnold 1984). In some lizard species tail removal causes a decrease in sprint speed (Pond 1978; Ballinger, Nietfeldt & Krupa 1979; Punzo 1982; Arnold 1984); however, in other species tail loss has no effect on speed (Huey *et al*. 1990; Hamley 1990) or can actually increase it (Daniels 1983; Brown, Taylor & Gist 1995). This has been related to the tail being, respectively, functionally ‘active’ or ‘passive’ for locomotion (Vitt, Congdon & Dickson

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1977). These studies examined the role of the tail in locomotion only when lizards ran to their maximal sprint speed. However, although sprint speed is believed to be a measure of whole-animal performance, lizards do not routinely use their maximal capacities for locomotion (Hertz, Huey & Garland 1988). The possible effects of tail loss on the spontaneous locomotor patterns of lizards remain almost unexplored.

Many lizard species move in a characteristically discontinuous way, alternating short periods of locomotor activity with short pauses (Avery *et al*. 1987a,b; Avery & Bond 1989). Alteration of these locomotor patterns may influence activities of such vital importance as foraging, patrolling of territories, searching for mates or antipredator behaviour. However, there are few data on the effect of tail loss on the 'normal' movement patterns (i.e. walking speed) of tailless lizards. The only data available show that, in the laboratory, tailless *Scincella lateralis* reduce the frequency of movements (Formanowicz *et al*. 1990), and, in the field, tailless males of *Psammodromus algirus* and *Lacerta monticola* decreased the distances moved per unit of time and reduced the size of their home range (Salvador *et al*. 1995; Martín & Salvador 1997). These reductions of movements were, however, considered mainly as an antipredator strategy of lizards increasing crypsis, while biomechanical constraints were not analysed.

In this paper we compare the locomotor patterns of *P. algirus* lizards before and after tail loss in the laboratory. This lizard has a long tail which is presumably used in locomotion and in climbing or travelling across flimsy vegetation (Arnold 1988). A long tail is also typical of species that rely on running for escape from predators (Vitt 1983; Martín & López 1995). Individuals of this species have a reasonably high probability of losing their tail at some time during their lifetime; in one study population more than half of the individuals had regenerated tails (Salvador *et al*. 1995). In the present work, we specifically examined the characteristics of locomotion of lizards moving spontaneously, and also the escape performance of lizards running at high speed. The experimental design allows determination of tail loss effects while controlling for the repeatability of the locomotor measures in a control group.

Materials and methods

EXPERIMENTAL ANIMALS

Eleven *P. algirus* (six males and five females) with complete tails were captured in an oak forest near Navacerrada (central Spain) and transported to the laboratory. To minimize effects of size on locomotor performance adult individuals with similar body (mean snout–vent length ± SE = 75·4 ± 1·0 mm, range 75–80 mm) and tail dimensions (mean ± SE = 147·7 ± 3·6 mm, range 130–165 mm), and with similar body mass (mean ± SE = 9·9 ± 0·5 g, range 8–12·5 g) were selected. Females used were nonreproductive throughout the experimental period. The lizards were kept in terraria with a natural photoperiod, and radiant heat was provided from tungsten bulbs during daylight hours. Additionally, a 'blacklight' fluorescent tube provided UV radiation. Lizards were given water *ad libitum*, and were fed three times per week with mealworms and crickets dusted with a multivitamin powder.

EXPERIMENTAL DESIGN

All 11 lizards were filmed (see below) individually with their tails intact. Analyses showed no differences between sexes in locomotor patterns, so males and females together were considered. Five individuals (experimental group) were then randomly selected and autotomy was induced by grasping the base of the tail with forceps ≈ 2 cm from the cloaca. Lizards released the tail voluntarily when allowed to escape. To avoid differences in stress related to manipulation, the six other individuals (control group) were manipulated in a similar way, but without allowing induction of autotomy (by releasing individuals before the tail autotomized). All individuals were again filmed 2 weeks after this manipulation. This was an interval long enough for wound healing but not long enough to allow tail regeneration. Lizards passed all the trials without apparent signs of stress and all individuals were alive at the end of the experiment. The tailless individuals regenerated a new tail after a few months.

Lizards were tested in a $2 \times 0{\cdot}5\ \mathrm{m}^2$ linear arena with a floor of a rough substratum of wood, which provided excellent traction. Both ends of the track were set up as the original terraria (light bulbs providing radiant heat, water *ad libitum* and refugia). Individuals were placed in the arena a day before trials for acclimatization, and were allowed to bask for at least 2 h before filming. The temperature of lizards had been measured on previous days, showing that they were able to attain a body temperature within the activity temperature range of the species (Carrascal & Díaz 1989) after 2 h of basking. Experiments were recorded on videotape (Hi-8 format, 25 frames s^{-1}) using a Sony CCD-V800E video-camera aligned perpendicularly over the centre of the arena. Lizards were filmed as they moved spontaneously along the racetrack. The experimenter was not present in the room during filming.

MOVEMENT PATTERNS

Seven movement sequences per individual were selected in each trial (overall duration of movements: mean ± SE = 2·85 ± 0·08 s) with linear trajectories (total distance moved: mean ± SE = 51·8 ± 1·2 cm). Previous analyses showed that a greater number of sequences offered no change in the results, and that a more lengthy observation of individuals did not result in differing patterns of movement and pauses. Tapes were analysed frame by frame to describe the movement patterns of lizards, with measurements based on calibrated distances measured (in mm) from the video monitor, using the tip of the snout as a position reference. The variables recorded were the distance moved and the duration of each burst of locomotion, and the duration of the short pauses between bursts (Avery *et al*. 1987a). With these data the burst speed could be calculated as the distance moved within an individual burst divided by the time taken. Thereafter, an average value of these four variables was calculated for each sequence. The overall speed was calculated as the distance moved in the entire sequence divided by the time taken, including pauses. The frequency of pauses and the proportion of time spent paused in the entire sequence of movement were also calculated.

STRIDE LENGTH AND CURVATURE OF THE BODY

The tapes were analysed frame by frame, and those frames in which all four limbs were in contact with the substrate were selected from the middle of locomotor sequences. These corresponded to the end of each cycle of limb movement. The angle of each limb with respect to the longitudinal axis of the body at the appropriate girdle was measured from the screen with a protractor. As different individual lizards differed in the length of their limbs, and thus in stride length, the angle through which each limb moved was calculated because it represented a standardized measure of the stride length. Average values for the forelimbs and for the hindlimbs were calculated from the angles of the appropriate right and left limbs. The burst speed of the lizard in that particular burst of locomotion was also recorded. Ten angles for the forelimbs and ten for the hindlimbs were calculated for different speeds of each individual lizard in each trial.

The angle of maximum curvature of the body was also measured. This was the angle between the line perpendicular to the pelvic girdle axis, and the line perpendicular to the thoracic girdle axis. An angle was calculated for each burst of locomotion analysed as the average of the angle to the right, and that to the left.

ESCAPE PERFORMANCE

Lizards were induced to flee at high speed to study their escape responses before and after the treatment (tail loss or control). Lizards were individually tested in the $2 \times 0{\cdot}5$ m^2 arena (see above), but all potential obstacles had been removed. Lizards were tapped on the tail with the hand to stimulate them to run. Experiments were recorded from above on videotape. Ten escape sequences were analysed from each individual in each condition and, thereafter, an average value from the ten sequences of each individual was calculated. The escape sequences were spaced sufficiently so that fatigue resulting from one run did not affect subsequent runs. For each sequence the distance between the initial position (lizard paused) of the lizard's snout and the final position in the first pause after fleeing (escape distance), and the time interval between the initial and final position (escape duration) were measured. From these data the overall escape speed (distance moved divided by the time taken), the initial attained speed (arbitrarily chosen as the speed attained in the first 80 ms, i.e. two frames) and the maximal speed (the greatest speed recorded within any two successive frames (80 ms) during the escape response) were measured.

STATISTICAL ANALYSES

To detect effects of tail loss on locomotor variables, for each individual an average value from all the sequences analysed of that individual before manipulation and one average value from the sequences analysed following manipulation were calculated. Differences of these average values within the control or the experimental group before and after the treatment were compared by two tailed Wilcoxon matched-pairs signed-ranks tests (Siegel 1956).

The relationship between limb angles or body curvature and speed were evaluated by Pearson's correlation. Regression lines were calculated by fitting to a multiplicative model ($Y = a^{bx}$), which gave a better fit than a linear model. Normality of the variables was examined previously using the Lilliefors test. Differences among trials within the control or the experimental group were tested with analyses of covariance (ANCOVA) with burst speed as covariate (Zar 1984; Jayne & Davis 1991; Ashley-Ross 1994).

Results

MOVEMENT PATTERNS

Although there was a great deal of variation among individuals, Wilcoxon matched-pairs signed-ranks tests show that individuals in the control group did not change their movement patterns among trials ($P > 0{\cdot}25$ for the seven variables). In contrast, in the experimental group there were significant effects of tail loss on movement patterns (Fig. 1). In summary, tailless individuals moved at significantly slower speeds during bursts of locomotion ($P = 0{\cdot}04$) and, as a consequence, distances moved were significantly shorter ($P = 0{\cdot}04$). Also, they increased the time spent in pauses ($P = 0{\cdot}04$) which led to lower overall speeds ($P = 0{\cdot}04$). Experimental lizards did not change the duration of single bursts of locomotion ($P = 0{\cdot}22$), nor did they change the average duration of single short pauses after tail loss ($P = 0{\cdot}17$).

The analysis of the data of each individual in the experimental group suggests that individuals were affected differentially by tail loss (Fig. 2). However,

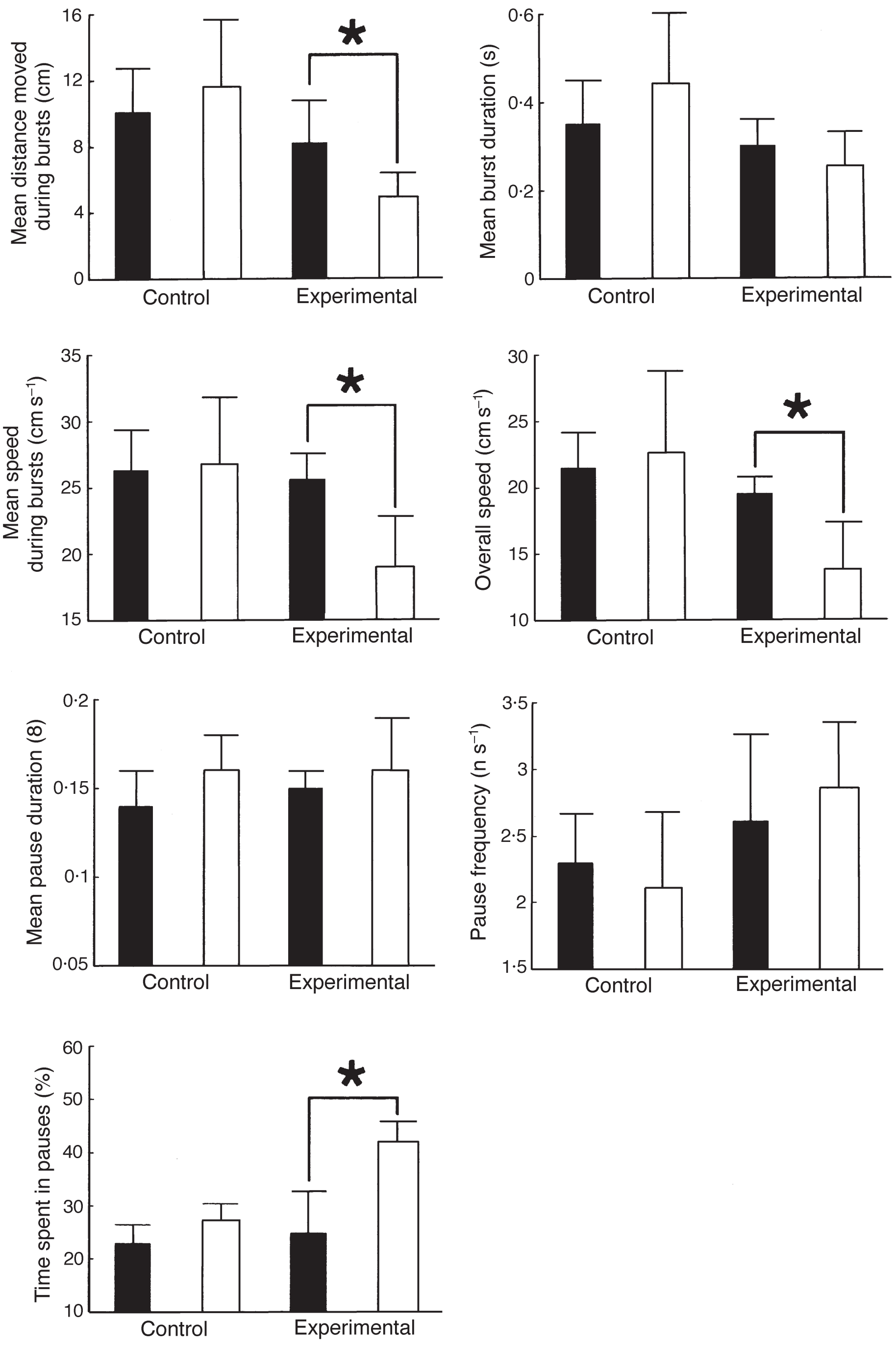

Fig. 1. Mean values (+ SD) for locomotor variables of *P. algirus* lizards walking spontaneously before (filled bars) and after (open bars) the treatment in the control ($N = 6$ individuals) and experimental groups ($N = 5$ individuals). An asterisk denotes a significant effect of the treatment ($P < 0{\cdot}05$) in a two tailed Wilcoxon matched-pairs signed-ranks test.

the variables affected by tail loss changed in the same direction in all individuals. For example, burst speed decreased in all individuals (Mann–Whitney *U*-tests for all the sequences of each individual compared before and after tail loss, $P < 0{\cdot}05$ in all cases), although the magnitude of change varied. Similar patterns were noted for the other variables affected by tail loss ($P < 0{\cdot}05$ in all cases) (Fig. 2). In contrast, in the control group, although there were differences among individuals, repeatability of the locomotor patterns of each individual between trials was high (Mann–Whitney *U*-tests, $P > 0{\cdot}30$ in all cases).

STRIDE LENGTH

The angle through which the limbs moved (i.e. stride length) was clearly related to burst speed in the premanipulative trial (multiplicative regressions on data for control and experimental groups pooled; forelimbs: $r = 0{\cdot}54$, $P < 0{\cdot}0001$; hindlimbs: $r = 0{\cdot}60$, $P < 0{\cdot}0001$; Fig. 3). Thus, lizards increased speed by increasing the stride length, and particularly by increasing stride length of the hindlimbs.

Tail loss affected the stride length of lizards. At any given speed, experimental individuals took shorter strides in the tailless condition than in the tailed, both with the forelimbs (ANCOVA: covariation with speed, $F = 10{\cdot}41$, $P < 0{\cdot}001$; tail effect, $F = 4{\cdot}62$, $P = 0{\cdot}03$; Fig. 4a) and with the hindlimbs (ANCOVA: covariation with speed, $F = 26{\cdot}23$, $P < 0{\cdot}001$; tail effect, $F = 75{\cdot}95$, $P < 0{\cdot}001$; Fig. 4b). In contrast, control individuals did not change the length of their stride between trials for either forelimbs (ANCOVA: covariation with speed, $F = 60{\cdot}02$, $P < 0{\cdot}001$; trial effect, $F = 0{\cdot}02$, $P = 0{\cdot}88$) or hindlimbs (ANCOVA: covariation with speed, $F = 64{\cdot}94$, $P < 0{\cdot}001$; trial effect, $F = 0{\cdot}52$, $P = 0{\cdot}51$).

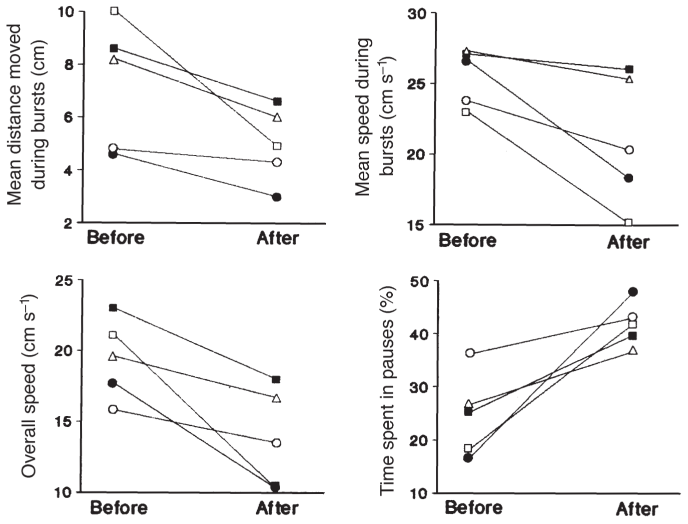

Fig. 2. Plot of individual average values of four locomotor variables that were significantly affected by tail loss. Mean values for each individual before and after tail loss are connected by lines.

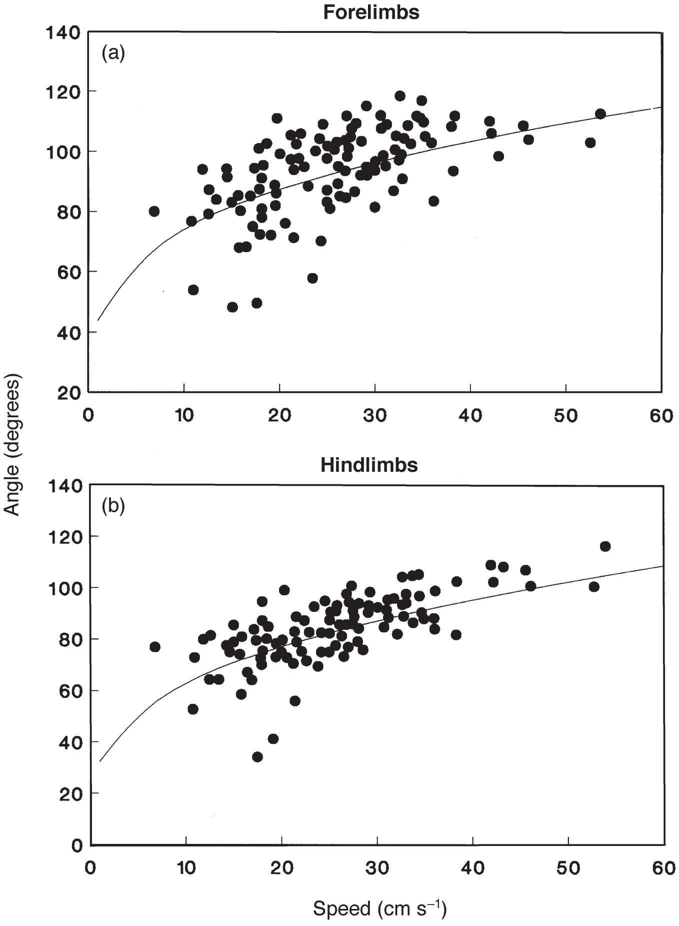

Fig. 3. Relationship between burst speed and the angle through which the forelimbs (a) or the hindlimbs (b) moved. Data pooled for control and experimental groups in the premanipulative trials.

CURVATURE OF THE BODY

The angle of the body axis at the moment of maximum curvature was not significantly related to burst speed in the premanipulative trials (data for control and experimental groups pooled; $r = -0{\cdot}14$, $P = 0{\cdot}11$; Fig. 5). Thus, lizards did not increase their speed by increasing the angle of the body axis but mainly by increasing stride length. The same lack of relationship was maintained between trials in the control group (ANCOVA: covariation with speed, $F = 1{\cdot}39$, $P = 0{\cdot}24$; trial effect, $F = 0{\cdot}46$, $P = 0{\cdot}54$), and also in the experimental group, in which tail loss did not affect the body axes' angle (ANCOVA: covariation with speed, $F = 1{\cdot}47$, $P = 0{\cdot}23$; tail effect, $F = 1{\cdot}91$, $P = 0{\cdot}26$).

ESCAPE PERFORMANCE

The effects of treatment on escape performance in both control and experimental groups, before and after tail loss, are summarized in Fig. 6. Although there was considerable variation among individuals, Wilcoxon matched-pairs signed-ranks tests show that individuals in the control group did not modify their escape performance between trials ($P > 0{\cdot}60$ for the five variables). In contrast, in the experimental group tail loss significantly affected four variables that characterize the lizards' escape response ($P < 0{\cdot}05$ in all cases; Fig. 6). Attained, maximal and overall speeds decreased substantially in tailless lizards. These reductions lead to shorter escape distances, because tailless lizards did not modify the duration of their escape response ($P = 0{\cdot}71$). Although individuals in the experimental group were not equally affected by tail loss, the direction of change of each variable was identical for all individuals (e.g. attained speed always decreased after tail loss) (Mann–Whitney *U*-tests for all the sequences of each individual compared before and after tail loss, $P < 0{\cdot}05$ in all cases), although the magnitude of change may vary. In contrast, in the control group, repeatability of escape performance between trials was high (Mann–Whitney *U*-tests, $P > 0{\cdot}40$ in all cases).

Discussion

LOCOMOTOR PATTERNS

The results show that tail loss affects spontaneous locomotion of *P. algirus*. Individuals seem to maintain constant patterns of locomotion, as the duration of the bursts of locomotion and the duration of the short pauses between bursts did not vary. The consistency of movement patterns among trials may be maintained by the central neurological mechanisms that regulate locomotory movements and short pauses between burst of locomotion (Avery *et al*. 1987a). Repeatability of locomotor performance of individuals appears general among reptiles (Avery *et al*. 1987a; Van Berkum *et al*. 1989; Huey *et al*. 1990).

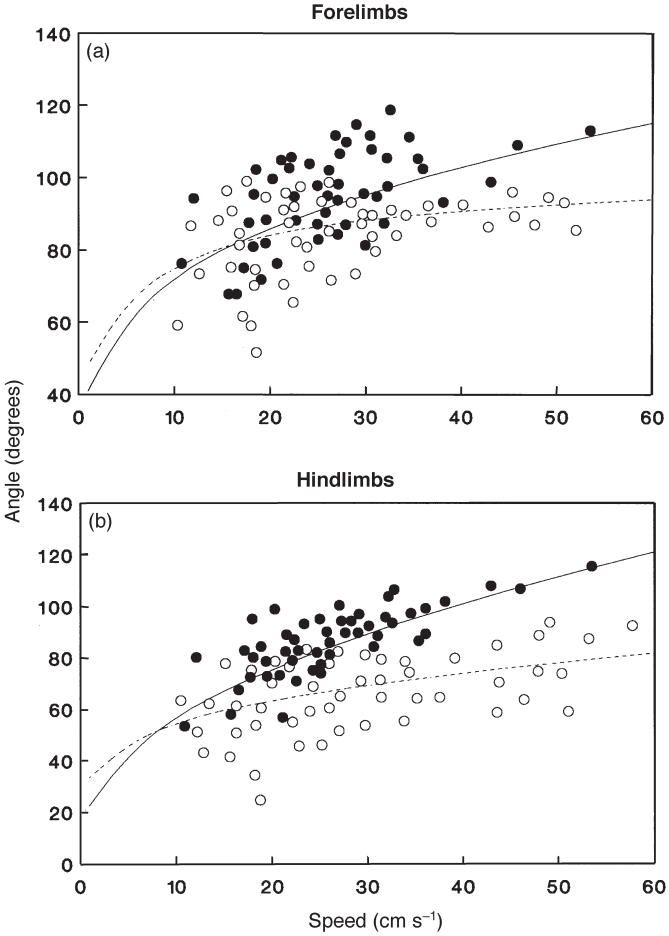

Fig. 4. Relationship between burst speed and the angle through which the forelimbs (a) or the hindlimbs (b) moved in the experimental group before (filled circles) and after (open circles) tail loss. Regression lines for a multiplicative model (see text) from data for tailed (continuous line) and tailless lizards (dashed line) are shown.

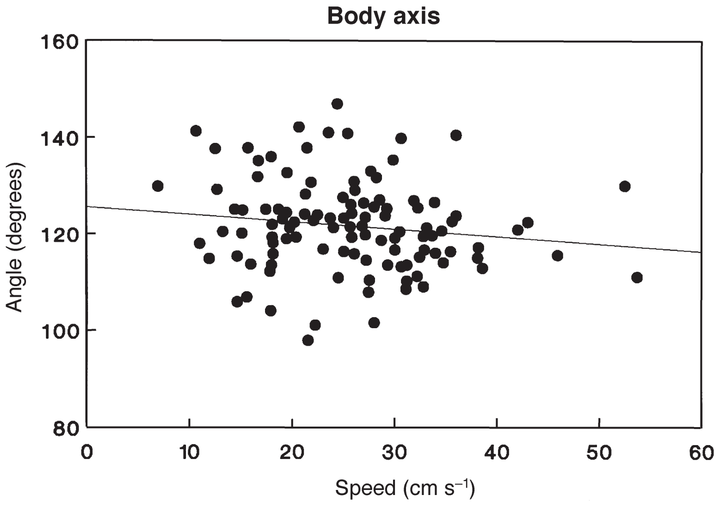

Fig. 5. Relationship between burst speed and the angle of maximum curvature of the body. Data pooled for control and experimental groups in the premanipulative trials.

Why tailless lizards decrease burst speed is not clear. Changes in stride length associated with tail loss (see below) may induce a reduction of burst speed. Also, the loss of equilibrium potentially caused by tail loss (Snyder 1954; Ballinger 1973; Daniels 1985) may force the lizards to walk slowly, and continuously to correct the small disequilibrium caused by the lack of tail in each step. Evidence for such disequilibrium is provided by the irregularity of trajectories of the central point of the pelvic girdle in lizards running at high speeds (J. Martín & R. A. Avery, unpublished observations).

The alteration of spontaneous locomotion may not only be a biomechanical constraint, because lizards were able to attain greater speeds when required to escape (e.g. in tailless lizards average walking burst speed was about 210 mm s^{-1} while overall speed in the escape sequences was nearly 810 mm s^{-1}). Lizards may, for example, reduce speed and increase the time spent paused as an antipredator strategy (Formanowicz *et al*. 1990; Salvador *et al*. 1995; Martin & Salvador 1997). Pauses have been explained as increasing the chance of visually perceiving prey or predators (Avery *et al*. 1987a; Avery 1991, 1993). Tailless lizards spent more time paused during locomotor sequences and thus may be more vigilant to potential predators.

Alteration of locomotor patterns may affect space use of lizards. Some tailless lizards restrict their microhabitat use to those where their morphological and locomotor traits are most suited (Martín & Salvador 1992). However, the use of safer microhabitats may also limit the access to some resources, such as food (Martín & Salvador 1993c), thermoregulatory opportunities (Martín & Salvador 1993b) or potential mates (Salvador *et al*. 1995; Martín & Salvador 1997).

STRIDE LENGTH

Psammodromus algirus have relatively long limbs, and can increase speed by increasing stride length. The *caudi-femoralis* musculature presumably helps the most efficient use of the hindlimb retractor muscles (Snyder 1954; Gatesy 1990; Russell & Bauer 1992). The result of contraction of these muscles is to produce a rapid retraction of the femur (Rewcastle 1983). Lateral bending of the trunk and tail may serve to increase the stride length of lizards (Ritter 1992). By adjusting the frequency of tail oscillation (via the tension in the caudal musculature), cursorial lizards can use the harmonic motion of the tail as an aid to femoral retraction (Hamley 1990). For any given speed, a lizard lacking a complete tail will have a higher frequency of tail oscillation and therefore of stride frequency. Thus, tail loss increases stride frequency and decreases stride

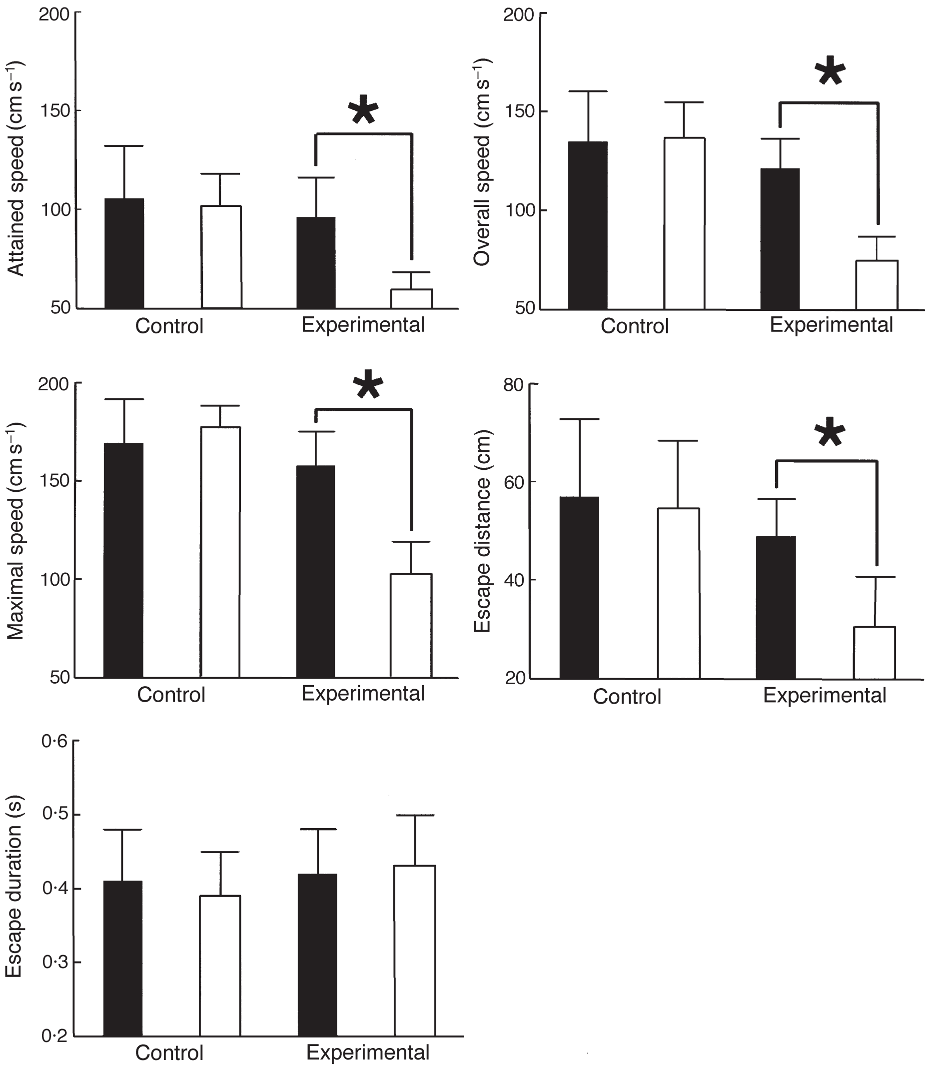

Fig. 6. Mean values (+ SD) of escape performance variables for *P. algirus* induced to flee at high speeds before (filled bars) and after (open bars) the treatment in the control ($N = 6$ individuals) and experimental groups ($N = 5$ individuals). An asterisk denotes a significant effect of the treatment ($P < 0·05$) in a two tailed Wilcoxon matched-pairs signed-ranks test.

length. Tailless lizards therefore increase stride frequency to attain greater speeds. As a consequence, sprint speed may be limited in tailless individuals because it would be mechanically and energetically impossible to attain higher stride frequencies.

The relative extents to which limb movements and spinal flexion contribute to forward movement varies from species to species (Avery *et al*. 1987a,b). Flexion of the spinal cord scarcely contributes to the attainment of higher speeds in *P. algirus*. Tail loss did not modify this pattern, although it might be expected that tailless lizards, to compensate for limited stride length, might decrease the angle of maximum curvature of the body axes (i.e. increase the flexion of the spinal cord) to attain higher speeds.

ESCAPE PERFORMANCE

The escape performance of *P. algirus* lizards was greatly affected by tail loss. A similar decrease in sprint speed was noted in other lizard species with ‘actively functional’ tails that contribute to activities such as locomotion or climbing (Pond 1978; Ballinger *et al*. 1979; Punzo 1982; Arnold 1984). Sprint speed in these species was reduced to about 40% of the normal value. In our experiment, overall escape speed of *P. algirus* was reduced by 36% after tail loss; attained speed and maximal escape speeds showed similar reductions. Thus, considering the effect of tail loss on running speed, *P. algirus* should be included in the group of lizards with ‘actively functional’ tails. The lack of an effect of tail loss on sprint speed in lizards such as *Sceloporus merriami* may reflect the relatively slender and short tail in this species (Huey *et al*. 1990). In contrast, speed of the gecko *Phyllodactylus marmoratus* (Daniels 1983) and the lizard *Podarcis muralis* (Brown *et al*. 1995) increased after autotomy. The tail seems to play no part in cursorial locomotion in these species; the tail appears to impede locomotion because of its mass and because of friction with the substrate. In these species, the increase in speed after tail loss may increase the ability for predator avoidance by running faster, once the possibility of autotomy as an escape strategy has been lost (Daniels 1983).

The results of our experiment show that, in addition to the decrease in overall and maximal sprint speed after tail loss, there is also a decrease in initial acceleration, as reflected by the attained speed at the beginning of the escape sequence. This may be important for avoiding immediate capture by a close predator (Congdon *et al*. 1974; Dial & Fitzpatrick 1984). This may also have especially interesting implications for how lizards move on inclined surfaces (Huey & Hertz 1984).

If tail loss results in predator escape, selection should favour autotomy because those individuals that shed their tails would have a higher probability of escape. However, in species with actively functional tails, tail loss would significantly decrease subsequent fitness. Selection in such instances should favour retention of the tail and promote the use of other escape strategies, because the cost associated with tail loss is great compared with the gains of autotomy (Vitt *et al*. 1977). Tail loss in *P. algirus* significantly decreases their ability to move, and, moreover, their ability to escape by running. However, autotomy is an escape strategy used frequently by this species, as shown in the field by the high number of individuals that have lost their tails at least once in their life (Salvador *et al*. 1995). Two different explanations could be considered. First, predation pressure on this species is very high in Mediterranean habitats (e.g. Martín & López 1990), so that tail loss would be advantageous for survival even if fitness subsequently decreases. Second, individuals may be able to compensate tail loss costs through modifications of their behaviour, adopting more cryptic and conservative strategies that enhance their survival during the regeneration period (Martín & Salvador 1992; Salvador *et al*. 1995). Therefore, to estimate which are the actual costs of autotomy for a lizard species, data from laboratory experiments as well as detailed field observations of behaviour of tailless individuals should be considered.

In summary, tail loss in *P. algirus* substantially modified movement patterns and escape performance. However, tailless lizards may be able to compensate behaviourally for the mechanical costs of locomotion, so that their fitness would decrease less than expected, favouring autotomy as an evolutionarily stable escape strategy in this species.

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