Hindlimb Asymmetry Reduces Escape Performance in the Lizard
Psammodromus algirus

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ABSTRACT

Locomotor performance of lizards and its relationship to the ecology and morphology of the forms concerned has been well studied recently. Asymmetry of limbs might make the body unstable and make performance less effective. However, their effects on terrestrial locomotion remain almost unexplored. In this article, the escape performance of the lizard Psammomus algirus running at high speed was related to hindlimb morphology and fluctuating asymmetry levels. Femur length was significantly shorter than crus length. However, absolute fluctuating asymmetry in femur length was significantly larger than in crus length. Asymmetry was not related to body or limb size, thus larger individuals or those with longer limbs did not have significantly greater fluctuating asymmetry. Neither body size nor the length of the limbs (femur or crus) were significantly related to any of the variables describing escape performance. However, escape performance was affected by femur-length fluctuating asymmetry, which resulted in significantly reduced overall escape speeds. In contrast, asymmetry in crus length did not affect escape performance. We discuss the possible basis of these alterations of locomotion, the relevance of reduced performance for the ecology of this species, and how individuals may compensate for the costs of asymmetry.

Introduction

Locomotor abilities of animals are a fundamental factor in determining the result of a predator-prey encounter (Webb 1986). In lizards, the most usual escape response is rapid locomotion away from the predator. Escape will be successful if the prey has greater speed and stamina than the predator or if it is able to flee to a refuge where the predator cannot follow it. Sprint speed is often used as a measure of whole-animal performance (Hertz et al. 1988; Bonine and Garland 1999). For this reason, the factors that affect the sprint speed of lizards (e.g., Van Berkum et al. 1989; Huey et al. 1990; Garland and Losos 1994) and the use of running speed in escape behavior (Greene 1988; Bulova 1994) have received considerable attention. In particular, locomotor performance of lizards and its relationship to the ecology and morphology of the forms concerned has been well studied recently (review in Garland and Losos 1994).

Fluctuating asymmetries (FAs) are random deviations from perfect symmetry that arise because of the inability of individuals to undergo identical development of bilaterally symmetrical traits on both sides of the body (Van Valen 1962). Asymmetry might make the body unstable and performance less effective. Thus, a negative correlation between asymmetry levels and locomotor performance may be expected. However, the effect of asymmetry of locomotor structures on performance has been examined almost exclusively in the flight of birds (e.g., Thomas 1993; Swaddle 1997; review in Möller and Swaddle 1997), whereas their effects on terrestrial locomotion have scarcely been studied at all (Manning and Ockenden 1994). Particularly in lizards, the effects of limb asymmetry on a trait with important fitness consequences, such as sprint speed, remain unexplored. This is, however, important because low asymmetry is predicted to occur for functional reasons if asymmetry reduces biomechanical performance (Möller and Swaddle 1997). Thus, there might be strong selection against the most asymmetrical individuals.

In this article, we analyzed in the laboratory the escape performance of the lizard Psammomus algirus running at high speed. This lizard relies on running to escape from predators (Martin and López 1995, 1996), has relatively long limbs (Arnold 1998), and increases speed by increasing stride length and frequency of hindlimb strides (Martin and Avery 1998). We took morphological measurements of the hindlimbs and analyzed the relationship between asymmetry and escape speed. We hypothesized that higher asymmetry levels in the hindlimbs would have negative consequences on locomotor performance, which would be reflected, for the most part, in a decrease in sprint speed during escape sequences, when lizards use their maximal capacities for locomotion.

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Material and Methods

Experimental Animals and Morphological Measurements

Twenty-nine male Psammodromus algirus with complete tails were captured in an oak forest near Cercedilla (central Spain) and transported to the laboratory. The lizards were kept in outdoor terraria with natural temperature and photoperiod for 15 d before testing to allow acclimation to laboratory conditions. Lizards were given water ad lib. and were fed three times per week with mealworms and crickets dusted with a multi-vitamin powder. All lizards were healthy during the trials and were returned to their exact capture site at the end of the experiments. From each individual, we measured the snout-to-vent length (SVL: mean ± SE = 79.0 ± 0.8 mm, range 71–86 mm), tail length (146.5 ± 5.5 mm, range 100–194 mm), body mass (10.1 ± 0.4 g, range 6–14.5 g), and length of the femur and crus of the left and right hindlimbs (see below).

Digital calipers were used to make morphological measurements (to the nearest 0.1 mm) at the end of the trials. Lizards were previously cold anesthetized in a refrigerator to facilitate handling when we took the measurements. We did not intend to measure the actual lengths of the bones in the limbs. Thus, we used the words “femur” and “crus” to refer to the distinct parts of the limb in live animals that included these bones. Femur length was measured as the greatest distance from the most anterior point of insertion of the hindlimb in the body to the knee, and crus length was measured as the greatest distance from the knee to the sole of the foot (i.e., the plantar surface of the tarsals and metatarsals). Measurements were repeated by the same person three times in nonsequential order on each side and were shown to be highly repeatable, and the measurement error was small relative to FA (two-way mixed model ANOVAs; femur: interaction, $F = 34.37$, $df = 28,116$, $P < 0.001$; crus: interaction, $F = 2.06$, $df = 28,116$, $P = 0.004$; see Swaddle et al. 1994 for details of ANOVA analysis). The absolute value of asymmetry was calculated as the unsigned right-minus-left length of the femur or the crus (the average value of the three measures of each limb), and this exhibits the properties of FA, that is, a normal distribution (Filliben correlation coefficients, i.e., correlation of raw data with predicted normal probability scores [Aitken et al. 1989]; femur: $t = 0.90$, $n = 29$, $P < 0.0001$; crus: $t = 0.87$, $n = 29$, $P < 0.0001$) around a mean of 0 (one sample t-tests; femur: $t = 0.90$, $df = 28$, $P = 0.33$; crus: $t = 1.12$, $df = 28$, $P = 0.27$).

Escape Performance

We tested lizards individually in a 2 × 0.5-m² linear arena with a sand substrate from the study area that provided excellent traction. Individuals were allowed to bask for at least 2 h before filming. We measured the temperature of lizards in previous experiments (Martín and Avery 1998) and showed that after 2 h of basking lizards were able to attain a body temperature within the activity and preferred temperature range of the species for maximal sprint performance (30.9°–34.7°C; see Carrascal and Díaz 1989; Bawens et al. 1995). To study escape responses, we induced lizards to flee at high speed by tapping them on the tail with a brush. Experiments were recorded on videotape (Hi-8 format, 25 frames s⁻¹) with a video camera aligned perpendicularly over the center of the arena. We analyzed five escape sequences from each individual and then calculated an average value from the five sequences of each individual. Previous analyses showed that a greater number of sequences offered no change in the results. Escape sequences were spaced at least 1 h apart so that fatigue resulting from one run did not affect subsequent runs. Lizards passed all the trials without apparent signs of stress, and all individuals were alive at the end of the experiment and were released at their capture sites.

Tapes were analyzed frame-by-frame to describe the movement patterns of lizards; measurements were based on calibrated distances (mm) measured from the video monitor with the tip of the snout as a position reference (Martín and Avery 1998). For each sequence, we measured 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). From these data, we calculated the overall escape speed (distance moved divided by the time taken).

Statistical Analyses

We removed the influence of body size on femur and crus length by regressing each against SVL (all variables were ln transformed). Then, we retained the residuals and computed FA statistics. To detect effects of limb asymmetry on locomotor variables, we calculated for each individual an average value of each variable of escape performance from all the sequences analyzed. We also made parallel analyses on the single fastest of the five sequences, which should indicate the maximal performance abilities of lizards. Because average speed estimates might be submaximal if there was variation in speed within individuals, we also noted the maximum scores that each individual reached in any of the five sequences analyzed. We removed the influence of body size on locomotor variables by regressing each against SVL (both ln transformed) and used the absolute values of the residuals in posterior analyses. We used nonparametric rank Spearman correlations (Siegel and Castellan 1988) to analyze the relationships between asymmetry and escape-performance residuals because of the particular half-normal distribution of unsigned absolute asymmetry data (see Swaddle et al. 1994).
Results

Patterns of Fluctuating Asymmetry

Average femur length ($\bar{X} \pm SE = 8.7 \pm 0.1$ mm) was significantly shorter than crus length ($13.6 \pm 0.2$ mm; Wilcoxon matched-pairs signed-ranks test: $Z = 5.20, P < 0.0001$). The two parts of the hindlimb exhibited different levels of FA: absolute FA in femur length ($1.2 \pm 0.2$ mm; maximum FA = 3.3 mm) was significantly larger than absolute FA in crus length ($0.5 \pm 0.1$ mm; maximum FA = 0.9 mm; Wilcoxon matched-pairs signed-ranks test: $Z = 3.34, P < 0.001$). Individual FA in femur length was not significantly related to body size (SVL: $r_s = 0.05, P = 0.81$; body mass: $r_s = -0.10, P = 0.58$) nor mean femur length ($r_s = -0.12, P = 0.54$), and neither FA in crus length was significantly related to body size (SVL: $r_s = -0.04, P = 0.84$; body mass: $r_s = -0.08, P = 0.69$) or mean crus length ($r_s = -0.05, P = 0.80$). In a subsequent analysis, we analyzed the relationship between limb length and FA by using the residuals from the regression equation of ln femur or crus length on ln SVL. This analysis yielded similar results; neither FA in femur- or crus-length residuals were related to any body-size measurement ($P > 0.50$ in all cases). Thus, larger individuals or those with longer limbs did not have significantly greater FA.

Escape Performance

Neither body size (SVL or body weight) nor limb length (femur or crus length) was significantly related to any of the variables describing escape performance ($P > 0.20$ in all cases). However, FA in femur length (corrected for body-size differences) was significantly and negatively related to overall escape speed ($r_s = -0.41, P = 0.03$; Fig. 1a). This reduction in speed probably caused the more asymmetrical individuals to have shorter escape distances ($r_s = -0.32, P = 0.09$) because asymmetry did not modify the duration of the escape response ($r_s = 0.12, P = 0.51$). In contrast, FA in crus length was not significantly related to overall escape speed ($r_s = -0.04, P = 0.83$; Fig. 1b). Similarly, when we consider only the maximum scores of each individual in the five sequences analyzed, FA in femur length significantly affected the highest overall speed ($r_s = -0.43, P = 0.02$), whereas FA in crus length did not ($r_s = -0.05, P = 0.79$).

Discussion

Our results indicate that asymmetry in the hindlimbs of *Psammodromus algirus* decreases the ability of the lizards to escape by running. Although our average measures of speed were similar to those reported in previous studies of this lizard (Bauwens et al. 1995), the results also showed that more asymmetrical individuals suffer a reduction in overall escape speed (about 21% decline in average speed between the extremes of FA) and maximum sprint speed (about 30% decline). This impairment is likely to be of general ecological importance during an encounter with a predator and to directly affect individual survival. In fact, some studies have suggested that sprinting ability can affect survival within populations of reptiles (Christian and Tracy 1981; Jayne and Bennett 1990).

*Psammodromus algirus* have relatively long limbs and can increase speed by increasing stride length (Martin and Avery 1998). Within the same species, biomechanical models predict a positive relationship between limb length and sprint speed, which has been found in some species of lizards but not in others (e.g., Bonine and Garland 1999; review in Garland and...
Losos 1994). We have not found a relationship between hindlimb length and speed in *P. aligus*. However, our results point out that one of the sources of variation in sprint speed between individuals is asymmetry of the limbs. The concrete biomechanical causes of the lower sprint speed of lizards with asymmetrical femurs remain to be analyzed in detail. However, the *caudifemoralis* musculature presumably promotes the most effective use of the hindlimb retractor muscles (Snyder 1954; Gatesy 1990; Russell and Bauer 1992), and the result of contraction of these muscles is a rapid retraction of the femur (Newcastle 1983; Arnold 1998). Femoral retraction may be the major speed effector over a moderate range of ecologically relevant speeds (Reilly and Delancey 1997; but see Irshick and Jayne [1999a, 1999b] for hindlimb kinematics at high speed). Thus, it is likely that differences in length between the right and the left femur (i.e., higher FA) affected the effectiveness of these muscles and, consequently, sprint speed. Also, the loss of equilibrium potentially caused by asymmetric limbs may force the lizards to run slowly and to continuously correct the small disequilibrium caused by the difference in length of the limbs in each step. Nevertheless, because asymmetry may be a good indicator of the quality of an individual, we cannot exclude the possibility that reduced performance is not directly related to asymmetry of the limbs; instead, it may reflect a generally poor phenotypic condition. Thus, in the lizard *Sceloporus virgatus*, cold incubation temperatures induced significant developmental instability, and although these individuals showed high levels of FA in scale-count characters not related to limbs, they also exhibited poorer quality phenotypes for other traits, such as running speed and escape performance (Qualls and Andrews 1999).

In contrast, we did not find a relationship between crural length asymmetry and sprint speed. One possible explanation is that the crural may have a low contribution to the attainment of sprint speed (but see Irshick and Jayne 1999a for the opposite finding), such that crural-length asymmetry might be unimportant. However, an alternative and more likely explanation is that the different effects result from FA in femur length being substantially larger than FA in crus length. Therefore, with low FA levels, the effects on speed may be very small or undetected. This raises the question of why the crural length is more symmetric than the femur length. The degree of asymmetry of a morphological character may be related to its functional importance. In general, traits that are functionally important exhibit small levels of FA, whereas traits that are less functionally important exhibit relatively larger asymmetries (Møller and Hoglund 1991; Gummer and Brigham 1995). Because the distal elements of the limbs are the most important for running (Irshick and Jayne 1999a), the effects of higher levels of FA in crus length may be functionally more important than the effects of higher levels of FA in femur length. Thus, a strong selection of individuals with more symmetrical crus lengths could be expected (Møller and Swaddle 1997), which in evolutionary time might have been conducted to low levels of FA in crus length. Alternatively, the high levels of FA in femur length could be explained because morphological characters that have been subject to intense directional selection in selection experiments exhibit elevated levels of fluctuating asymmetry (e.g., Leamy and Atchley 1985).

Because repeatability of locomotor performance of individuals appears to be general among reptiles (Huey and Dunham 1987; Van Berkum et al. 1989; Huey et al. 1990), it is very likely that asymmetry of the limbs affected speed in all the escape sequences of an individual. Thus, a negative relationship between asymmetry and fitness would be expected (see review in Møller 1997) as a result of the differences in the effectivity of escape performance to avoid predators. However, in the lizard *Uta stansburiana*, there was no natural selection on FA in meiotic traits (Fox 1975). Individuals with high FA may be able to compensate through modifications of their behavior and locomotor patterns, adopting more cryptic and conservative strategies that enhance their survival, similar to those used by locomotor-impaired, tailless individuals (Salvador et al. 1995; Martin and Avery 1998), parasitized individuals (Clobert et al. 2000), or individuals with a full stomach (Martin 1996). Also, asymmetrical individuals might have a greater approach distance as do some lizards at low body temperatures (Rand 1964; Bulova 1994; Smith 1997) that are also more vulnerable to predation due to their lower escape performance. This would reflect behavioral decision making to allow for enough time to reach a refuge, taking into account the limitation of lower fleeing speeds. Therefore, to estimate what the actual costs of limb asymmetry in terms of predation risk are, data from laboratory experiments and detailed field observations of behavior should be considered.

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Literature Cited


Thomas A.L.R. 1993. The aerodynamic cost of asymmetry

