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LOCOMOTOR COMPENSATION CREATES A MISMATCH BETWEEN LABORATORY AND FIELD ESTIMATES OF ESCAPE SPEED IN LIZARDS: A CAUTIONARY TALE FOR PERFORMANCE-TO-FITNESS STUDIES

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Abstract.—A key assumption in evolutionary studies of locomotor adaptation is that standard laboratory measures of performance accurately reflect what animals do under natural circumstances. One widely examined measure of performance is maximum sprint speed, which is believed to be important for eluding predators, capturing prey, and defending territories. Previous studies linking maximum sprint speed to fitness have focused on laboratory measurements, and we suggest that such analyses may be appropriate for some species and intraspecific classes, but not others. We provide evidence for a general inverse relationship between maximum laboratory sprint speed and the percentage of maximum capacity that animals use when escaping from a threat in the field (the model of locomotor compensation). Further, absolute values of field escape speed and maximum laboratory speed are not significantly related when comparing across a diverse group of *Anolis* and lacertid lizards. We show that this pattern of locomotor compensation holds both within (i.e., among intraspecific classes) and among lizard species (with some exceptions). We propose a simple method of plotting field escape speed (y-axis) versus maximum laboratory speed (x-axis) among species and/or intraspecific classes that allows researchers to determine whether their study organisms are good candidates for relating laboratory performance to fitness. We suggest that species that reside directly on, or near the ‘‘best fitness line’’ (field escape speed = maximum laboratory speed) are most likely to bear fruit for such studies.

Key words.—Evolution, fitness, lizards, performance, sprint speed.

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Over the past 20 years, field and laboratory biologists have extensively studied relationships among whole-organism performance capacities; morphology; and, to a lesser extent, fitness (Pough 1989; Bennett and Huey 1990; Jayne and Bennett 1990; Losos 1990; Arnold 1994; Wainwright 1994; Irschick and Garland 2001; Vanhooydonck and Van Damme 2001; Langerhans et al. 2004; Miles 2004). This classic paradigm posits that morphological variation should correlate with variation in an ecologically relevant performance capacity (e.g., maximum sprint speed), which, in turn, should correlate with variation in fitness within a population (Arnold 1983). Therefore, by directly linking morphology, performance, and fitness among individuals within animal populations, one can directly test the adaptive significance of morphological variation (Arnold 1983; Jayne and Bennett 1990; Watkins 1996; O’Steen et al. 2002; Miles 2004; Le Galliard et al. 2004). Many studies have correlated morphology to performance within and among species (for examples with squamate reptiles see Garland and Losos 1994; Aerts et al. 2000), but only a few studies have linked performance to fitness within animal species (Kingsolver et al. 2001), either in the field (Jayne and Bennett 1990; Huey et al. 1991; Miles 2004), or in a seminatural enclosure setting (Watkins 1996; O’Steen et al. 2002; Le Galliard et al. 2004).

The study of whole-organism performance capacity (e.g., locomotor endurance, maximum sprint speed) has been intensively examined within squamate reptiles, which have served as a valuable model system (Hertz et al. 1988; Pough 1989; Bennett and Huey 1990; Garland and Losos 1994; Aerts et al. 2000; Irschick and Garland 2001; Vanhooydonck et al. 2001). Maximum sprint speed has been a focus of such studies, as previous authors have argued that the ability of lizards and snakes to move at high speeds is critical for a variety of activities (e.g., escaping predators, capturing prey, etc.; Bennett and Huey 1990; Garland and Losos 1994; Van Damme and Van Dooren 1999; Aerts et al. 2000; Irschick and Garland 2001). Further, previous studies have shown that sprint speed in squamate reptiles is heritable (van Berkum and Tsuji 1987; Garland et al. 1990; Garland 1994), variable among individuals (Bennett and Huey 1990), and repeatable among individuals (Huey and Dunham 1987).

Although these studies have provided a valuable foundation, they nevertheless have focused (out of necessity) on maximum speed under standardized laboratory conditions. However, animals may not perform in nature to the same level as under standardized laboratory conditions (Irschick 2003). An important assumption of any study linking fitness to laboratory performance measures is that animals perform similarly in the field as in the laboratory (Irschick and Losos 1998; Irschick 2003). We propose that this assumption may be valid for some species and intraspecific classes but not others, and therefore, we suggest that studies linking laboratory performance to fitness may not be feasible for all species and/or intraspecific classes.

Specifically, we propose a general inverse relationship between laboratory maximum sprint speed and the percentage of effort (% maximum) that animals run when escaping from a threat in the field. We also provide evidence of a general mismatch between absolute values of field escape speeds and maximum laboratory speeds among widely divergent lizard species. We explain these trends in the context of ‘‘locomotor compensation,’’ in which intraspecific classes, and/or species with low intrinsic performance capacities, compensate in nature by moving at, or very close to, their maximal capacities

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(see discussions by Martin and Lopez 1995; Carrier 1996; Irschick and Losos 1998). Previous authors have suggested that such compensation might be expected in species and intraspecific classes that are poor performers, yet experience strong selective pressures (i.e., from predation), and hence must compensate behaviorally (Martin and Lopez 1995; Carrier 1996), although too few data are available to make broad generalizations. We aim to show the generality of locomotor compensation both within (among intraspecific classes) and among a variety of lizard species, and discuss the implications for studies linking performance to fitness. We also propose a simple method of plotting field escape speed (y-axis) versus maximum laboratory speed (x-axis) among species and/or intraspecific classes that allows researchers to determine whether their study organisms are good candidates for performance-to-fitness studies. We suggest that species that reside directly on, or near, the ''best fitness line'' (y = x; field escape speed = maximum laboratory speed) are the best candidates for relating laboratory speeds with fitness.

As supporting evidence, we first present new data from different sexes (males and females for all species; males, females, and subadults for *Podarcis muralis*) of four species of lacertid lizards (*Lacerta oxycephala*, *P. muralis*, *P. sicula*, *P. melisellensis*) that show a striking mismatch between field and laboratory estimates of escape sprinting speed. We show that when one measures maximum sprint speed in the laboratory, one detects highly significant differences both among intraspecific classes within species and among different species. By contrast, field escape speeds do not differ significantly either intra- or interspecifically. We then integrate previous analyses of field and laboratory escape speeds in other lizard species (Jayne and Ellis 1998; Irschick and Losos 1998; Irschick and Jayne 1999; Irschick 2000) to demonstrate the generality and potential exceptions to this trend.

MATERIALS AND METHODS

Species Studied

All field data were gathered between 17 May and 5 July 2004, during the peak of the activity season for European lacertid lizards. We studied four Lacertid lizard species at three sites: (1) an open field near the town of Marche in Southern Belgium (*Podarcis muralis*), (2) the relatively large island (56 km^2, 42.45°N, 16.53°E) of Lastovo in Croatia (*L. oxycephala* and *P. melisellensis*), and the nearby island of Pod Kopiste (*P. sicula*). *Podarcis muralis* inhabits open fields with scattered rocks and small flat pieces of concrete that act as retreats. In Lastovo, *P. melisellensis* typically occupies flat, sparsely vegetated fields and roadside areas, whereas *L. oxycephala* typically used vertical rock and dirt surfaces. Finally, *P. sicula* is a predominantly a ground-dwelling species on Pod Kopiste, which is a small (0.09 km^2) island about six kilometers off the coast of Lastovo. The habitat of Pod Kopiste consists of sparse grass interspersed with small piles of rocks and therefore is similar to the habitat of Lastovo and for the mainland Belgium site. We gathered field escape data for adult males and adult females for three species (*L. oxycephala*, *P. melisellensis*, and *P. sicula*), and adult males, adult females, and subadults for one species (*P. muralis*). Subadults were individuals that were born the previous reproductive season, but were clearly smaller than adults. Female and male lizards were large adults that were obviously sexually mature. Males were easily distinguished from females in all species by their enlarged heads. We excluded any females that were clearly gravid, as gravidity can affect locomotor behavior and escape speed in lacertid lizards (Bauwens and Thoen 1981).

Laboratory Measures of Maximum Speed

We gathered data on maximum speeds in the laboratory for the same intraspecific classes as examined in the field (e.g., males and females for *P. sicula*, *P. melisellensis*, and *L. oxycephala* and males, females, and subadults for *P. muralis*). We only collected samples for laboratory studies from the same populations in which field speeds were measured. To test for ontogenetic effects on laboratory maximum speeds within *P. muralis*, we measured the maximum sprint speeds of the same *P. muralis* ($N = 24$ individuals) at different stages of their ontogeny (one, three, five, and seven months old). *Podarcis muralis* juveniles (estimated at one month old) were first captured in August 2004, and maintained in 100 cm × 50 cm × 50 cm (l × w × h) terraria at the University of Antwerp, Belgium. Lizards were fed four to six small naturally captured insects (spiders, crickets, etc.) per week and provided with water ad libitum.

We used a standard 2-m long, horizontal, field-portable racetrack with infrared photocells positioned every 0.25 m (as in Irschick and Losos 1998; Vanhooydonck and Van Damme 2001) attached to an analog converter, and a laptop computer. A custom computer program automatically calculated the average speed for each 25-cm segment as the lizard ran the length of the racetrack. Each lizard was raced three times (by placing the lizard at the beginning of the racetrack and tapping its tail gently), and the fastest speed (fastest 25-cm average speed) was used as our estimate of maximum sprinting capacity for each individual. To ensure good traction during sprinting bouts, a flat, rough, wooden board was used as the trackway substrate. Lizards were either placed into buckets with heat lamps, or into incubators set to 35°C prior to trials. Each lizard for each species was heated to an internal body temperature of 35°C (±1°C), which was verified by insertion of a thermocouple into the cloaca of each lizard directly prior to sprinting. Only lizards that had internal body temperatures between 34 and 36°C were used. This temperature is close to the preferred body temperature of each species, and is the same as used in other studies of maximum speed in these species (Vanhooydonck and Van Damme 2001).

Field Measurements of Escape Speed

We walked around each habitat in each field site during normal activity hours (9 a.m. to 6 p.m.), and during good weather (i.e., warm, not rainy weather). We filmed field escape movements with a hand-held Redlake motion meter (Redlake Imaging, San Diego, CA) that recorded at a filming rate of 125 fps onto a tape recorder (hi-8 tapes). The same person, wearing similar clothing every day, approached lizards at an approximately constant speed of about 50 cm/sec until the lizard began to flee (as in Irschick and Losos 1998;

Irschick 2000). Following Irschick and Losos (1998), we measured the distances of all escape movements, and calculated average speeds for each movement by dividing the distance of each movement by the duration of each movement. Distances were recorded using a flexible tape measure (accurate to 1 mm). We also recorded the substrate type (dirt, rock, branch), and whether the movement was horizontal, upward, or downward. All escape movements were reviewed in the field to determine escape distances, and videotapes were later reviewed to determine the duration of all movements. After each escape, we attempted to capture each lizard to verify its sex (male, female) and age (adult, subadult). We avoided sampling the same area more than once to prevent repeated sampling of the same individuals.

Statistical Analyses

We first tested for both intra- (males, females only) and interspecific variation for maximum laboratory speeds. For this analysis, we conducted a two-way ANOVA using species ($N = 4$) and sex ($N = 2$, male, female) as fixed factors. We conducted this analysis both without accounting for body size differences, and also including logSVL as a covariate. We also conducted post-hoc tests to determine where the differences resided within the data structure for the above tests. To test for ontogenetic effects on sprint speed in *P. muralis*, we performed a repeated measures ANOVA on log-10 transformed speeds with age (one, three, five, and seven months) as the within-subjects factor. Because the sphericity assumption was not satisfied (Geisser-Greenhouse $\varepsilon = 0.81$), we multiplied the degrees of freedom with ε when evaluating the significance of age on speed.

We also conducted ANOVAs comparing species and sexes for two other measures of locomotor performance; (1) field escape speed (actual speeds used by lizards in nature), (2) percent maximum speed (field escape speed divided by laboratory speed, see Irschick 2000), and (3) field escape distances. Percent maximum speed provides an index of how close lizards sprint to their maximum capacity (Irschick 2000). Because we gathered laboratory and field escape speeds on different sets of individuals for each species, we divided each individual's field escape speed by the mean maximum sprint speed calculated for each intraspecific class (as in Irschick 2000). For the subadult *P. muralis*, we used the mean maximum laboratory sprint speed for five-month-old lizards, because these animals most closely correspond in size to the lizards observed in the field. We also investigated whether movement direction (up, down, or horizontal) affected field escape speeds across all individuals. Because the shaded ambient air temperatures were similar on each of the field sampling days (30–35°C), and maximum sprint speed shows a fairly broad plateau with temperature (Huey 1983), we did not statistically evaluate the potential effect of temperature on field escape speeds.

RESULTS

Figure 1 presents average values for laboratory speed, field speed, and percent maximum speed for age and sex classes (see Fig. 2 for mean values for different age classes of *P. muralis*) for each lacertid lizard species. In general, labora-

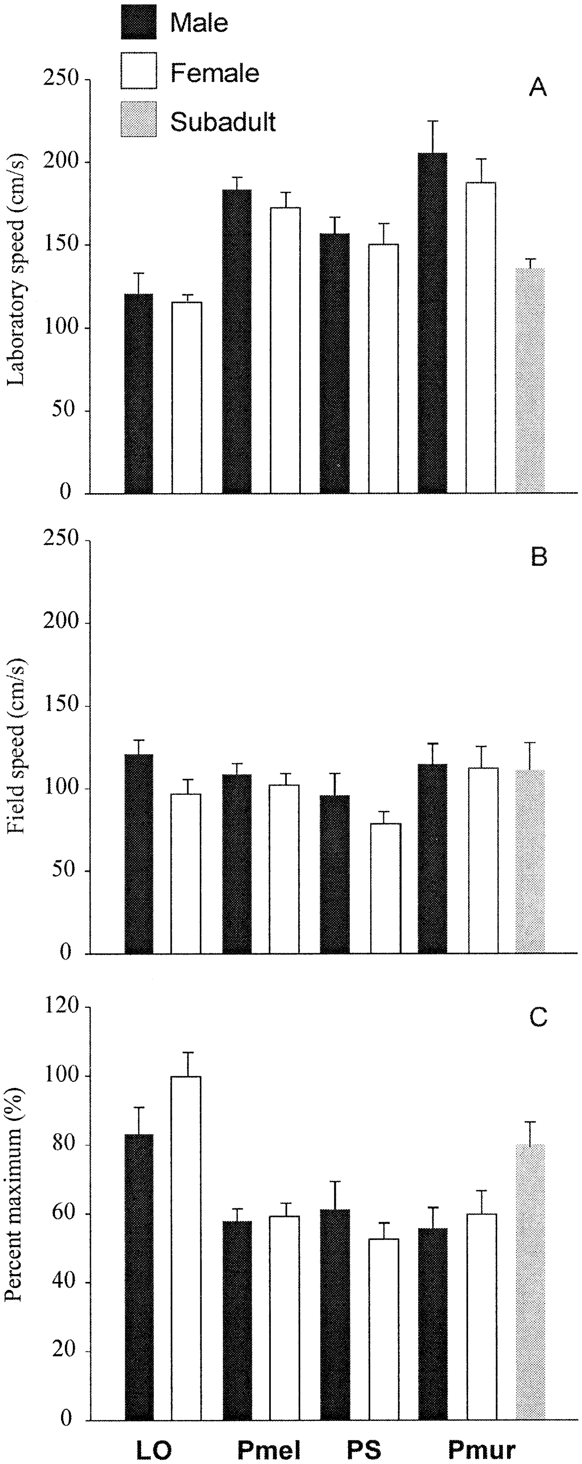

FIG. 1. Bar charts showing mean (+1 SE) values of (A) laboratory sprint speeds, (B) field escape speeds, and (C) relative (% max) escape speeds for various intraspecific classes of four lacertid lizard species. Sample sizes for the laboratory data are: *Lacerta oxycephala* (LO) males (10), females (7); *Podarcis melisellensis* (Pmel) males (32), females (17); *P. sicula* (PS) males (26), females (15); *P. muralis* (Pmur) males (10), females (9); *P. muralis* subadults (five months old, 24). Sample sizes for the field data are: *L. oxycephala* males (5), females (10); *P. melisellensis* males (15), females (7); *P. sicula* males (10), females (9); *P. muralis* males (11), females (11); *P. muralis* subadults (5).

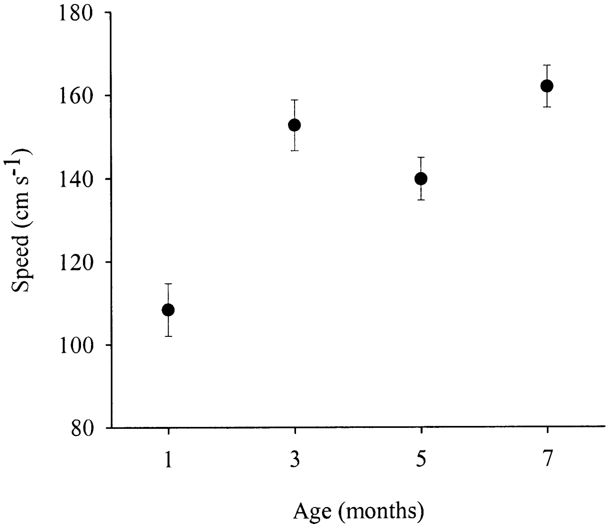

FIG. 2. A scatterplot showing mean (±1 SE) values for maximum sprint speed (cm/sec) for four different age groups (same individual lizards) within *Podarcis muralis*. Note the increase in speed with age (see text for statistics). Each mean value represents the same 24 individuals.

tory speeds were higher than field speeds, although *L. oxycephala* females had very similar values (Fig. 1). Percent maximum speeds varied dramatically inter- and intraspecifically, ranging from a low of 52.5% (*P. sicula* females) to a high of 99.9% (*L. oxycephala* females; Fig. 1).

Speed increased significantly with age within *P. muralis* ($F_{2.4,56} = 20.11$, $P < 0.001$, Fig. 2). Comparisons of consecutive levels of age revealed a highly significant increase between one month and three months ($F_{1,23} = 23.38$, $P < 0.0001$), no change between three and five months ($F_{1,23} = 2.72$, $P = 0.11$) and a significant increase between five and seven months ($F_{1,23} = 9.35$, $P = 0.006$). To check whether the differences in speed between age groups can be explained by differences in mass, we performed a similar analysis on residual speeds (residuals of log10 speed on log10 mass). The age-effect remained significant ($F_{2.5,58.6} = 5.52$, $P = 0.008$). Lizards at one month performed the poorest, even when correcting for their smaller size. That is, mass changes alone do not explain the effect of age on speed.

Laboratory speeds also differed highly significantly among species, and did not change with the inclusion of snout-vent length (SVL) as a covariate (Table 1, Fig. 1). By contrast, there were no significant sex or species × sex effects for laboratory speeds (Table 1). *Lacerta oxycephala* had significantly slower laboratory speeds compared to the other three species (post-hoc tests, $P < 0.001$, Fig. 1). Also, *L. oxycephala* had significantly higher values of percent maximum speed compared to the three other species (post-hoc tests, $P < 0.001$, Fig. 1, Table 1). However, there were no significant sex, or species × sex effects for any kind of performance variable (Table 1, Fig. 1).

Movement orientation did not significantly affect field escape speeds ($F_{2,76} = 0.33$, $P > 0.72$) for the four species, and hence, we pooled all escape movements. The four lacertid species showed no significant species or sex effects for field escape speeds (Fig. 1, Table 1), but the species differed significantly for escape distance, with *P. sicula* tending to move longer distances relative to the other three species (Fig. 3). However, all four species were generally similar in their escape distances being, on average, relatively short (i.e., <1 m, Fig. 3). Within *P. muralis*, the three intraspecific classes did not differ significantly in field escape speeds ($F_{2,43} = 0.04$, $P > 0.75$, Fig. 1), or in escape distances ($F_{2,43} = 0.07$, $P > 0.75$). Overall, in contrast to laboratory maximum speeds, there was no significant intra- or interspecific variation in field escape speeds for lacertid lizards.

DISCUSSION

Several results are apparent from our analyses: (1) The four lacertid lizard species examined differ significantly in laboratory estimates of maximum speed; specifically, *L. oxycephala* is substantially slower than the three *Podarcis* species (*P. muralis*, *P. melisellensis*, and *P. sicula*) in the laboratory, but field escape speeds were similar among all four species. (2) Maximum laboratory sprint speed increased significantly with size and age within *P. muralis*, but field escape speeds were similar for subadults and adult males. A final intriguing result was the lack of an effect of movement direction (e.g., up, down) on field speeds, which stands in contrast to other work (Jayne and Ellis 1998; Irschick and Jayne 1998). One possible factor may be the very small sizes of the lizards (<5 g), for which gravity effects are less relevant (Huey and Hertz 1982, 1984).

The reason for these above differences is that ''slower'' (in the laboratory) intraspecific classes (e.g., subadults) and species run close to their maximum sprint speeds in nature, whereas faster intraspecific classes (e.g., adult males) and species run far below their maximum sprinting capacities. Potentially useful labels for the two extremes observed in this study are ''slackers'' and ''overachievers.'' ''Slackers'' are species and intraspecific classes that possess high maximum sprinting capacities in the laboratory, yet sprint at low

TABLE 1. Results (*F*-values) from two-way ANOVAs on laboratory speed, field escape speed, percent maximum speed, and field distances comparing different species and different sexes (males and females) within each species.

Variable	Species	Sex	Species × sex
Laboratory speed (cm/sec), not size-adjusted	14.34***	0.70 ns	0.08 ns
Laboratory speed (cm/sec), size-adjusted	13.11***	0.47 ns	0.07 ns
Field escape speed (cm/sec)	2.36 ns	2.45 ns	0.44 ns
% max. speed (field speed/lab speed)	10.89***	1.19 ns	0.98 ns
Field distance (cm)	3.04*	0.75 ns	1.07 ns

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. ns, nonsignificant.

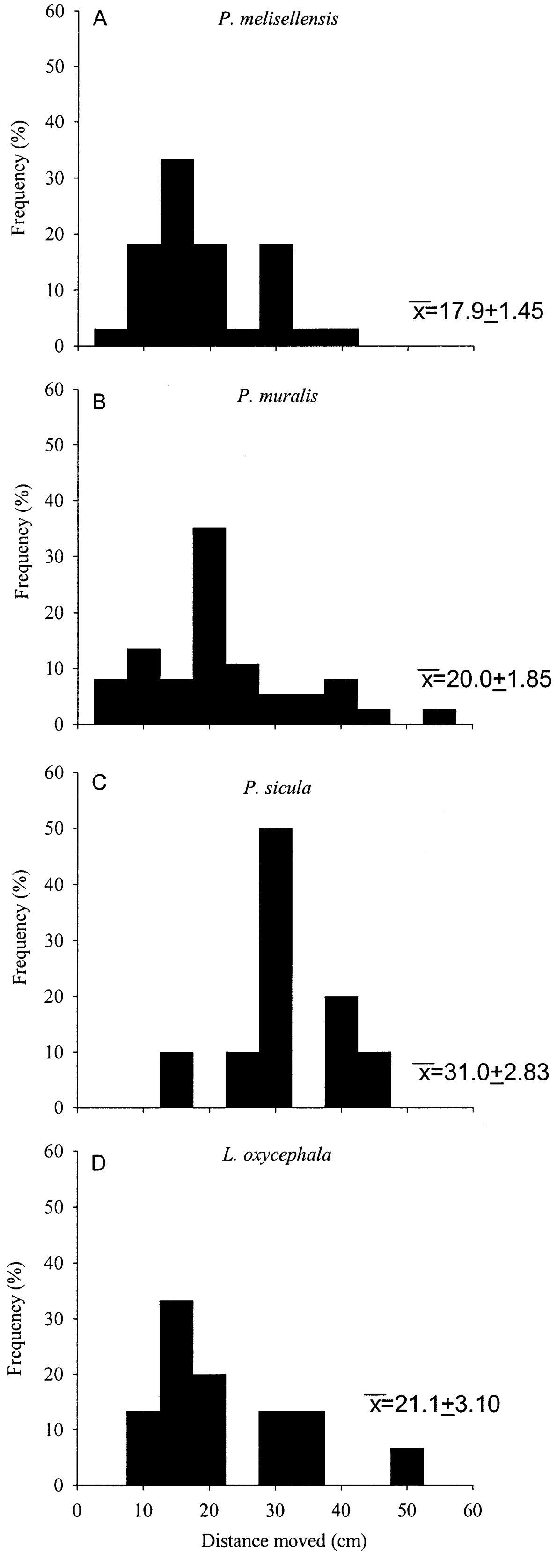

FIG. 3. Frequency histograms of escape distances for all four lacertid lizard species pooling all intraspecific classes (males and females for all species and males, females, and subadults for *Podarcis muralis*). Mean (±1 SE) values are shown in the figures.

capacities in nature. By contrast, ''overachievers'' are species and intraspecific classes that possess low maximum sprinting capacities in the laboratory, but sprint at high capacities in nature. Our results therefore provide a cautionary warning that standard measures of laboratory speed may not always be predictive of the speeds animals use in nature.

Examination of previously published field and laboratory estimates of speed in other lizard species shows that the pattern of locomotor compensation documented for lacertid lizards may be general, with some exceptions. Combined field and laboratory speed data are available for the four lacertid species examined here; seven species (adult males only) of arboreal *Anolis* lizards (Irschick and Losos 1998); males, females, and juveniles of the anole *A. lineatopus* (Irschick 2000); and two species (adult males only) of desert lizards (*Callisaurus draconoides* and *Uma scoparia*; Irschick and Jayne 1999). When field escape speed is plotted against laboratory maximum speed, two clusters of data appear (Fig. 4A); one cluster (18/20 points) composed of lacertid and *Anolis* lizards, for which percent maximum speed and maximum speed are strongly negatively related ($F_{1,17} = 24.9$, $P < 0.0025$), and another disparate cluster (2/20 points) of two desert lizard species.

Of course, because we are plotting both species means and different intraspecific classes within species, these datapoints are not statistically independent, and Figure 4A should be interpreted cautiously. However, the fact that the data for *Anolis* and lacertid lizards do not form separate ''clumps'' in space, but rather overlap, indicates that a phylogenetic effect (see Felsenstein 1985) is not responsible for this trend. Therefore, for two separate evolutionary radiations, there exists a clear pattern of locomotor compensation. We suggest that the unique ecological and behavioral characteristics of the two desert lizard species (*C. draconoides* and *U. scoparia*) could explain their distinct position. Whereas the lacertid and anole species in Figure 4 escape by running relatively short distances (i.e., <2–3 m), *C. draconoides* and *U. scoparia* will run up to 30 m to an escape retreat (Jayne and Ellis 1998; Irschick and Jayne 1999). Because these desert lizards increase in speed as they run long distances, field speeds will generally be higher than laboratory speeds due to the relatively short length of the racetracks (i.e., 2 m). In other words, laboratory racetracks provide good estimates of the underlying ''maximum'' speeds of most lacertids and anoles, but not of desert lizards that typically flee by running long distances (see also Bonine and Garland 1999).

Implications for Performance-to-Fitness Studies

What are the implications of the documented locomotor compensation for selection studies that attempt to link laboratory estimates of maximum speed to fitness? A mismatch between laboratory and field speeds is not necessarily problematic if the rank order of the two kinds of performance remain similar, even if one kind of performance is always lower than another (e.g., if field escape speeds were always a constant percentage of laboratory speeds). Inspection of Figure 4B shows this not to be the case when examining the combined data for *Anolis* and lacertid lizards ($F_{1,17} = 0.99$, $P > 0.25$), indicating that one cannot reliably predict field

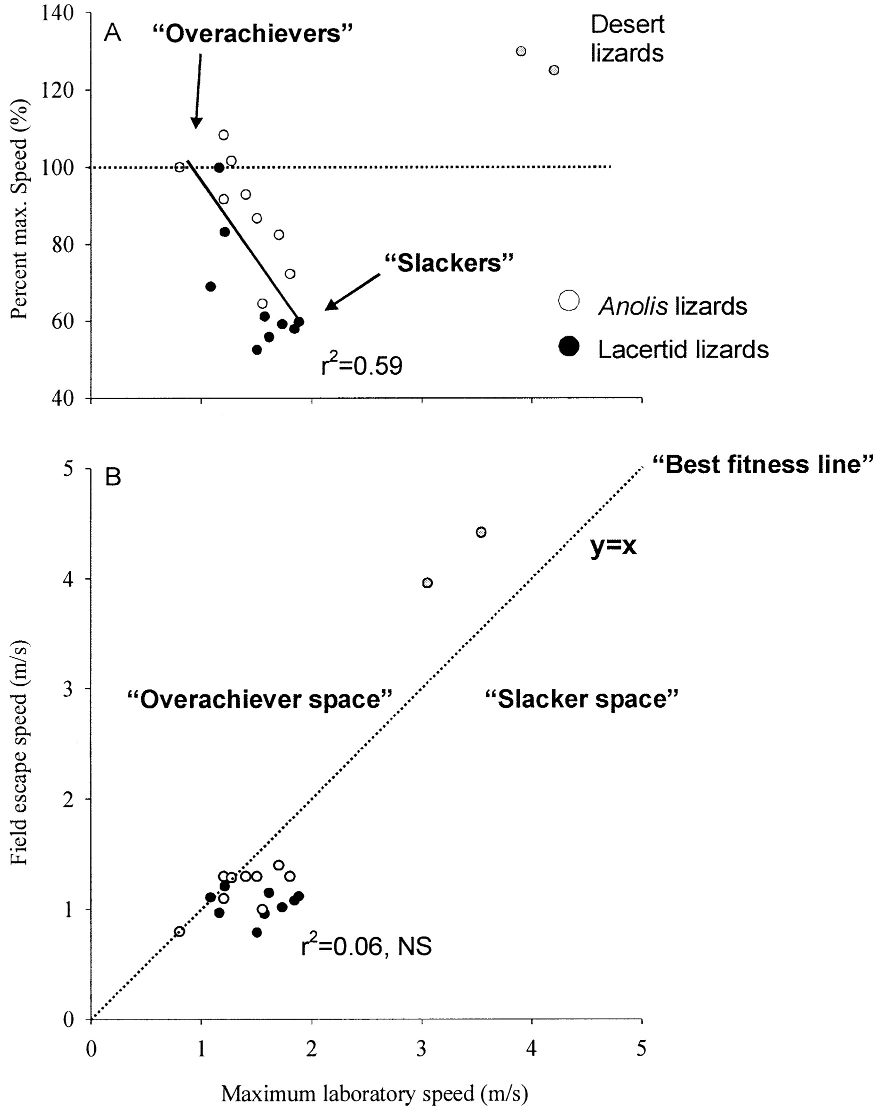

FIG. 4. (A) A plot of maximum laboratory speed (x-axis) versus percent maximum speed in the field (field escape speed/maximum laboratory speed, y-axis) for adult males of seven species of *Anolis* lizards, three intraspecific classes (adult male, adult females, and juveniles) of *A. lineatopus*, adult males and adult females of the four lacertid species examined in this study (including subadults of *Podarcis muralis*), and adult males of two desert lizard species (*Callisaurus draconoides* and *Uma scoparia*). Values of maximum speed are the averages of individuals within each species of their top sprint speeds in the laboratory (see Irschick and Losos 1999). The regression line is for all (*Anolis* and lacertid) species except the two desert lizard species (*C. draconoides* and *U. scoparia*). Values are means taken from the present study (lacertid lizards), Irschick and Losos (1998; adult males of *Anolis* lizards), Jayne and Ellis (1998; *U. scoparia*), Irschick and Jayne (1999; *C. draconoides*), and Irschick (2000; *A. lineatopus* males, females, and juveniles). (B) The same group of taxa as for panel A, but expressed as absolute values of laboratory maximum speed (x-axis) versus absolute values of field escape speed (y-axis), with a dotted line denoting y = x. Unlike panel A, these two variables are not statistically related for *Anolis* and lacertid lizards, indicating that at a macroevolutionary level, laboratory speeds are not predictive of field speeds. Species and intraspecific classes that fall directly on the y = x line (the ''best fitness line'') are the best candidates for studying relationships between laboratory performance and fitness. Species and intraspecific classes above the line are in the ''overachiever space,'' whereas species below the line are in the ''slacker space.''

escape speeds from laboratory speeds at a macroevolutionary level. Interestingly, this result stands in contrast to previous analyses that examined only adult males for different species of *Anolis* species, for which laboratory speeds are predictive of field escape speeds (Irschick and Losos 1998). Apparently, inclusion of intraspecific classes and more comparative data from other species increases the mismatch between laboratory maximum speeds and field escape speeds. Therefore, it is possible that researchers may detect different trends within different groups depending on whether one examines only one intraspecific class (e.g., adult males), or only one taxonomic group (e.g., one genus).

A potential critique of our approach is that we have not directly linked field escape speeds to fitness. We suggest that field escape speeds are more ecologically relevant for fitness studies because they describe the level of performance that animals use in their natural habitat (Wainwright 1994; Irschick and Garland 2001), with the caveat that humans are not natural predators of lizards (e.g., Leal and Rodriguez-Robles 1995). Of course, laboratory studies of maximum speed are valuable because they provide the top estimate of an animal's performance, which is accurate for some species and/or age classes (Fig. 4). Nevertheless, we argue that researchers should attempt to measure *both* field escape speeds and laboratory speeds for the same individuals. Indeed, examining field and laboratory speeds within the same individuals may reveal intriguing variation within a population; for example, even within a ''slacker'' species, one might find some individuals that move at 100% of maximum speed in the field, whereas other individuals may move at far less (e.g., 50%) of maximum speed in the field. We suggest that this variation may be a key target of natural selection, as opposed to only absolute values of speed (Van Damme and Van Dooren 1999).

Accordingly, our results may provide an explanation for why biologists have generally struggled to detect significant relationships between maximum laboratory speeds and fitness (Bennett and Huey 1990; Huey et al. 1991; Kingsolver et al. 2001), with some exceptions (e.g., Miles 2004). A key prediction stemming from our findings is that one should not expect to observe significant relationships between laboratory maximum speed and fitness in ''slackers'' (species and/or intraspecific classes), but might expect to find significant performance-fitness relationships within ''overachievers.'' We suggest that this prediction could be broadly applicable across many different animal taxa for which maximum speed is important for eluding predators (see Carrier 1996). Although data are scarce, they provide partial support for this prediction. We note that two field selection studies showing links between maximum laboratory speeds and fitness have documented the phenomenon primarily within younger individuals (*Thamnophis* snakes, Jayne and Bennett 1990; *Urosaurus* lizards, Miles 2004; although Jayne and Bennett [1990] found some support for a significant performance-to-fitness relationship within older snakes). A recent study (Le Gaillard et al. 2004) also revealed selection on maximum endurance capacity on juvenile lacertid lizards (*L. vivipara*). Indeed, the fact that juveniles are under constant threat from predators and conspecifics is consistent with both locomotor compensation and significant performance to fitness relationships (Werner and Gillam 1984; Jayne and Bennett 1990; Carrier 1996; Miles 2004). Thus, the species and/or age classes that sit directly on the $y = x$ line (field escape speed = maximum laboratory speed) in Figure 4B would seem the most logical candidates for relating laboratory maximum speeds to fitness. However, a study species that falls well into the ''slacker space'' (Fig. 4B) could provide negative results if one attempts to relate maximum laboratory speeds to fitness.

Behavioral Factors

Behavioral factors can play a key role in influencing relationships between morphology and performance (Lauder and Reilly 1996), and may also play a role for determining levels of performance used by animals (Losos et al. 2002). Indeed, the observed mismatch between field and laboratory estimates of maximum speed appears largely driven by motivation, which is apparently linked to intrinsic levels of performance (Fig. 4). In the laboratory, animals are forced to perform under extreme duress. For example, stress hormones in reptiles typically rise dramatically even several minutes after handling (Moore and Jessop 2003), and therefore, most animals are forced to perform under approximately the same level of high motivation (and hence achieve high performance). However, the assumption that animals will always sprint at similarly high levels of motivation in more natural circumstances appears plausible only for some species. We attempted to chase all lizards with zeal in nature, but it is apparent that ''overachieving'' species may perceive the same ''predator'' (in this case a human) as more of a threat compared to ''slacker'' species. Therefore, animals adjust their motivation according to the level of threat presented, and according to their own intrinsic capacities. Social factors, such as the willingness of adult males to depart far from a favored (and often greatly desired) perch may also be important (Stamps 1995).

Finally, our findings beg the question as to why ''slacker'' species or intraspecific classes run at such low levels of maximum sprinting capacity in nature. Currently, we can offer no compelling explanation, but one factor might be that ''slackers,'' already being fast, may not feel compelled to run at maximum capacity if they can effectively flee from a predator by running at less than maximum capacity. Hertz et al. (1988) pointed out that high performance capacities may only be necessary in rarely used circumstances for them to be maintained by selection. Hence, if a ''slacker'' individual encounters a dangerous and quick predator, then it is possible that the lizard will move maximally in that circumstance (for a discussion see Huey and Hertz 1982, 1984). Another factor may be energetics; recent work with desert iguanas (*Dipsosaurus dorsalis*) suggests some benefit for running submaximally (Hancock and Gleeson 2002; see also Weinstein 1995; Weinstein and Full 1998). Hancock and Gleeson (2002) found that the total metabolic cost of running (including recovery) is greater at higher intensities (speeds), which implies that running more slowly might be more economical per unit distance. Therefore, the submaximal field speeds of some lizard species may be influenced, in part, by energetic considerations.

In summary, our findings suggest that researchers should consider measuring both the maximum sprinting capacities, as well as the field escape speeds of their study species to ascertain the correct relationship between performance and fitness. We note that our findings for sprint speed may be broadly applicable across many different kinds of widely studied performance capacities (e.g., endurance, biting). Our findings also underscore the importance of behavior for understanding the evolution of performance capacity.

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