Absolute versus per unit body length speed of prey as an estimator of vulnerability to predation

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To study whether absolute (m/s) or relative (body lengths/s) speed should be used to compare the vulnerability of differently sized animals, we developed a simple computer simulation. Human ‘predators’ were asked to ‘catch’ (mouse-click) prey of different sizes, moving at different speeds across a computer screen. Using the simulation, a prey’s chances of escaping predation depended on its speed (faster prey were more difficult to catch than slower prey of the same body size), but also on its size (larger prey were easier to catch than smaller prey at the same speed). Catching time, the time needed to catch a prey, also depended on both prey speed and prey size. Relative prey speed (body lengths/s or body surface/s) was a better predictor of catching time than was absolute prey speed (m/s). Our experiment demonstrates that, in contrast to earlier assertions, per unit body length speed of prey may be more ‘ecologically relevant’ than absolute speed.

With the recent emphasis on direct measurement of whole-animal performance in physiological ecology and functional morphology, the measurement of maximal locomotor speed has become a popular occupation. This seems warranted for a number of reasons. Many animals run, crawl, swim or fly at high speeds to escape from predators, to catch prey or during intraspecific interactions. Although the exact relationship between speed capacity and survival or reproductive success has seldom been tested empirically (Hertz et al. 1988; see also Formanowicz et al. 1990), locomotor speed is usually considered an ‘ecologically relevant’ trait (Huey & Stevenson 1979). Speed can be measured with relative ease in laboratory set-ups (e.g. Huey et al. 1984), and the screening of many individuals is feasible (e.g. Sorci et al. 1995). In many species, individual measures of maximal locomotor speed seem repeatable over time (e.g. Huey et al. 1990). In addition, in the majority of cases studied, the variation in speed capacity between individuals has a genetic basis, making the trait interesting for evolutionary studies (e.g. Tsuji et al. 1989; Sorci et al. 1995).

Although Hill’s model of geometric similarity predicts that locomotor speed should be independent of body size (Hill 1950), more realistic scaling models (elastic similarity, constant stress similarity, McMahon 1984) predict that large animals should run, swim and fly faster than small animals (review in Garland 1983). The majority of empirical studies seem to corroborate the latter prediction (e.g. Zug 1972, 1978; Heglund et al. 1974; Webb 1978; Garland 1982, 1983; Garland et al. 1988; Tsuji et al. 1989; Jayne & Bennett 1990; Garland & Losos 1994; Zani & Claussen 1994; Brown & Taylor 1995).

The dependence of locomotor speed on size poses a problem when animals of different size are compared. Suppose, for instance, that individuals from population A on average sprint faster than individuals from population B. It may then seem reasonable to assume that the second population is more vulnerable to predation than the first. Perhaps one would even like to argue that the sprinting capacity in population A results from selection, caused, for example, by higher predation levels. But suppose that the two populations also differ in mean body size, and that animals from population A are larger than those of population B. How do we compare the velocities of both populations now? Do we correct for the size differences, by expressing velocity on a per unit body length basis (or by comparing size-corrected residual speeds)? Or do we ignore the size difference and just compare absolute speeds? The literature holds examples of both options, but the majority of authors do not argue why they preferred to use either relative or absolute speed.

For example, Elliot et al. (1977) used absolute speeds in a model to predict the outcome of interactions between
lions, *Panthera leo*, and various prey animals; in their model of prey-predator interactions in a zooplankton community, Gerritsen & Strickler (1977) reduced both predators and prey to points, thereby ignoring the implications of body size; and Jayne & Bennett (1990), in their study of crawling speed in the garter snake, *Thamnophis sirtalis fitchi*, judged absolute speed ecologically more relevant than a size-corrected value, ‘because absolute speeds will better predict the outcome of escaping the predator’. Garland (1994) agreed: ‘absolute performance [rather than speed relative to body size] would seem to be the behaviourally and ecologically relevant measure of performance. In my opinion, a potential predator or prey organism does not “care” about a lizard’s relative sprint speed, only how fast it can move in absolute terms!’. But later he also admitted: ‘In fact, however, we have essentially no empirical evidence on this point’. Nevertheless, Jayne & Bennett (1990) acknowledged the potential importance of body size by including it as a covariate in their analyses.

It seems intuitively logical that for a predator of a given size, a small prey moving at 1 m/s would be more difficult to catch than a larger prey moving at the same speed. If this were true, then vulnerability to predation may correlate better with relative speed than with absolute speed, and the body size-corrected speed would be the most ‘ecologically relevant’.

In this paper, we describe the results of a predation simulation experiment that was designed to test the hypothesis that relative speed (body lengths/s or body surface/s) rather than absolute speed (m/s) is relevant for vulnerability to predation. The experiment was designed to simulate an aerial predator hunting for terrestrial prey.

**METHODS**

Twenty-one biology students (of both sexes, aged between 22 and 36 years, and all experienced mouse users) were asked to ‘catch’ 200 prey items that moved across the screen of a PC. ‘Prey’ consisted of red squares of different size that emerged at a random place and then moved at a constant speed across the screen. Only one square was visible at a time. The squares moved in straight lines. When they reached the boundaries of the screen, they ‘bounced’ back at an angle of 45°. Clicking the left button of a mouse simulated a predation attempt; if the cursor was on the square at the time the button was clicked, then the attempt was successful. If the button was clicked while the cursor was outside the red square, then the predation attempt was considered unsuccessful. After each click (successful or not), the prey would disappear and the next one would show up within 1 s. Prey items came in five size classes (300 × 300, 400 × 400, 500 × 500, 600 × 600 and 700 × 700 twips; a twip is a screen-independent measure of distance used by Visual Basic programmers; 500 twips was about 1 cm on the screen used) and moved at five different speeds (20, 40, 80, 100 and 120 twips/s). The size and speed of each prey item was determined by chance, but on average each student saw eight examples of each speed and size combination. All students were exposed to at least one example of each of the speed–size combinations. The subjects were asked to ‘catch’ as many prey items as possible, in the shortest possible time, so there was pressure on both accuracy and speed. Individual scores were calculated as \( \Sigma (h/t_i) \), where \( h_i \) is 0 if prey item \( i \) was missed and 1 if it was caught, and \( t_i \) is the time needed to catch item \( i \) (\( i \) goes from 1 to 200, prey of different speed/size classes were considered to yield equal points). A bottle of whiskey was promised to the best predator to increase motivation. No maximal time limit was set. None of the students was aware of the purpose of the trials.

The simulation program was written in Visual Basic and run on an 8084 PC with a 14-inch monitor (1024 × 768 pixels). For each predation attempt, the program wrote a record to an Access database, containing a number identifying the subject, the speed and size of the prey item, the time that elapsed between the appearance of the prey and the predation attempt (hereafter referred to as ‘catching time’), and whether the attack was successful.

We estimated the effects of prey speed and size on predation success and catching time for mixed models with (1) random effects of test person, and (2) fixed effects of speed and size, using the maximum likelihood method (Littell et al. 1996). We also estimated parameters of so-called random coefficient models (Littell et al. 1996). The basic structure of these models builds on the analysis of covariance, but, next to a random effect of test person, the regression coefficients for the covariates are also assumed to be a random sample from a population of possible coefficients. Catching time was equated directly to a linear combination of independent variables (only successful attempts were considered). Because predation success is a binomially distributed variable, we used the GLIMMIX macro with a logit link function to test for effects of predator, size and speed (Littell et al. 1996). Satterthwaite’s formula was used to approximate the degrees of freedom in each test for a fixed effect. We compared nested models using likelihood ratio tests, and models with an equal number of estimated parameters with Akaike’s information criterion (Sakamoto et al. 1986). The speed and size variables were transformed to a logarithmic scale; this was not done when we compared absolute and relative expressions for speed.

As noted in the Introduction, empirical studies suggest that in the majority of animals, locomotor speed is positively associated with size. The program used here generated random combinations of speed and size, so some prey were big and slow, and some small and fast. Such combinations are unlikely to occur in nature and their inclusion in the analyses may jeopardize the conclusions. Therefore, we reran the analyses on a selection of prey items, leaving out such unrealistic combinations of speed and size. We assumed a linear relation between prey size and prey speed and then calculated residuals for all prey–speed combinations. All combinations for which the residuals were above the average of all residuals were eliminated. The following combinations were thus removed from the original data set: prey of length 300 twips that ran at 80, 100 or 120 twips/s (too fast for their small size); prey of length 400 twips that ran at 100 or
RESULTS

In the complete data set (all combinations of size and speed), the chances of a ‘prey’ escaping predation depended on the predator (random effect of test person: $\chi^2_{1} = 151.21, P < 0.0001$), on its speed ($t_{4196} = -23.60, P < 0.0001$) and on its size ($t_{4192} = 360.94, P < 0.0001$). The random slopes for speed and size per test person were not significant, indicating that the effects of speed and size on predation success were very similar for all test persons. Figure 1 shows that predation success depended on both prey speed and prey size; large, slow prey were easy to catch while fast, small prey had the best chance of escaping. In the model, the regression coefficients ± SE were 2.25 ± 0.14 for size and −3.21 ± 0.14 for speed on the logit scale, confirming that the chances of a prey getting caught was related to its length and inversely related to its speed. Because we transformed speed and size to a logarithmic scale, the parameter estimates on the logit scale correspond to the exponents of the effects of speed and size in a model with multiplicative fixed effects. The negative parameter estimate for size suggests that a relative measure of speed is likely to be a better explanatory variable than an absolute measure of speed. To compare absolute speed and relative speed as predictors of predation success, we fitted mixed models with speed expressed in absolute terms, in body lengths/s and in body surface/s. For each of the three models, we calculated Akaike’s information criterion (AIC; Akaike 1973; Bozdogan 1987). The model with speed in body lengths/s had the smallest AIC (4783.01), followed by the model with speed in body surface/s (4978.84). The model with speed in absolute terms had the highest AIC (5120.90). The large differences between the respective criteria suggest substantial differences in goodness of fit between the models (Sakamoto et al. 1986).

Very similar results were obtained for the restricted data set containing only realistic speed–size combinations. Both fixed effects (speed and size) and the random effect of test person remained highly significant (speed: $t_{2273} = -9.69, P < 0.0001$; size: $t_{2274} = 7.03, P < 0.0001$; test person: $\chi^2_{1} = 91.3, P < 0.0001$). From a comparison of models with speed expressed in the three alternative terms (see above), the model with speed in body lengths/s again emerged as the best.

120 twips/s (too fast); prey of length 500 twips that ran at 20 (too slow) or at 120 twips/s (too fast); prey of length 600 twips that ran at 20 or 40 twips/s (too slow); and prey of length 700 twips that ran at 80 twips/s or less (too slow).

Comparison of the AIC for models with speed expressed in absolute terms (AIC=3265), in body lengths/s (AIC=3183) and in body surface/s (AIC=3174), revealed that the latter best predicted the variation in catching time. Thus, in this set-up, a speed measure that took the size of the prey into account was a better predictor of catching time as the dependent variable. Only successful predatory attempts were considered. For the complete data set (i.e. all speed–size combinations), the effects of prey speed ($t_{160} = 4.32, P < 0.001$) and prey size ($t_{2084} = -10.80, P < 0.001$) on catching time were both highly significant. Catching time also varied between predators (random effect of test person: $\chi^2_{1} = 285.88, P < 0.0001$), although the effects of prey speed and prey size tended to be similar in all test persons (random slopes not significant). Figure 2 shows that more time was needed to catch a small, fast prey than a large, slow one.

We performed similar analyses with catching time as the dependent variable. Only successful predatory attempts were considered. For the complete data set (i.e. all speed–size combinations), the effects of prey speed ($t_{160} = 4.32, P < 0.001$) and prey size ($t_{2084} = -10.80, P < 0.001$) on catching time were both highly significant. Catching time also varied between predators (random effect of test person: $\chi^2_{1} = 285.88, P < 0.0001$), although the effects of prey speed and prey size tended to be similar in all test persons (random slopes not significant). Figure 2 shows that more time was needed to catch a small, fast prey than a large, slow one.
predictor of catching time than a speed measure that did not.

For the data set with realistic prey–speed combinations, differences between predators contributed significantly to the variation in catching time (random effect of test person: $\chi^2 = 134.20, P < 0.0001$). The effect of prey size was also significant ($t_{1209} = -5.63, P < 0.0001$), but, surprisingly, this was not the case for prey speed ($P > 0.05$). Comparing the AIC of models with speed (expressed in the three alternative ways) as the sole fixed effect suggests that speed expressed in body surface/s best explains the variation in catching time.

**DISCUSSION**

Our simple experiment seems to confirm the intuitive feeling that the catchability of a moving prey depends on its body size. Within the constraints of our simulation, speed corrected for body size seems a better predictor of the vulnerability to predation than absolute speed. This finding opposes the views of Jayne & Bennett (1990) and Garland (1994), who promoted absolute running speed as the ecologically most relevant measure.

The finding that relative speed, rather than absolute speed, predicts the outcome of a predatory event, may have consequences for our understanding of scaling issues in predation ecology. The majority of empirical studies (see references in Introduction) seem to confirm McMahon’s prediction that speed should increase with increasing body size, at least up to a certain point (Garland 1983). If absolute speed were the decisive factor determining the outcome of predatory events, we should expect strong selection for larger body sizes in smaller species. There is little evidence that such a pressure exists. Garland (1983) regressed maximal running speeds of 107 species of mammals against their body mass and came up with an ‘optimal’ body size for running ability of approximately 119 kg. The majority of today’s mammal species, however, have smaller body masses. Usually, high reproductive capacities or special antipredatory adaptations are invoked to explain why small species still exist (in spite of their poor running abilities). Our results suggest another explanation, namely that because of their smaller target area, small animals are as likely to evade predation as the faster large animals.

In many species, young animals are considered more vulnerable to predation because they are handicapped by small size and, hence, low speed (review in Carrier 1996). With this line of reasoning, rapid postnatal growth is considered adaptive, because it reduces the duration of the most hazardous period of life. However, our results indicate that by growing larger, young animals also become easier targets. The benefit of fast growth (increased velocity) must thus be weighed against this cost. Similarly, it has been suggested that animals not yet fully grown need special morphological (e.g. longer relative limb lengths) or behavioural (e.g. more secretive life styles) properties that help compensate for their low absolute speed of locomotion (Carrier 1996). This assertion may need reconsideration in the light of our findings.

Our simulation is unrealistic for a number of reasons. (1) The simulation involved predators that were not really hunting for food and that have probably never done so in their entire life. Real predators might have reacted in different ways. It is not clear, however, why inexperience or differences in motivation should result in size-dependent predatory skills. (2) The predatory community was the same for all size classes of prey. This may not be realistic; usually an allometric relation exists between predator size and prey size (review in Emerson et al. 1994). However, studies using locomotor speed as an approximation for survival seldom state which predators prey on the study species, or whether differently sized individuals are preyed upon by different predators. (3) In our simulation, the act of predation consisted merely of minute movements of the right wrist, the thumb and the little finger, and an occasional depression of the index finger. Real predation will usually involve the coordination of many more body parts. It is unclear whether this could affect the outcome of the experiment. (4) Prey movements in our simulation were highly predictable: prey moved at constant speed and, unless they hit the boundaries of the screen, in one direction. In nature, most prey will run at variable speeds and their path will contain angles, especially when predation is imminent (Bulova 1994). Indeed, this is another way in which body size may become important in predicting the outcome of predator–prey interactions. Maneuuvrability may be as important as speed capacity for escaping prey (Howland 1974), and has been shown to be size dependent (Webb 1976; Witter et al. 1994). If small prey are more manoeuvrable than large prey, then the simulations presented here may have underestimated the importance of relative speed on the probability of being caught. We plan to extend the simulation program to include these kinds of effects. (5) In our simulation, both speed and size classes of the prey items were assigned arbitrarily. The predator/prey size ratio is probably much larger than for most real situations. It could be argued that predators with the size of our test persons may not be adapted to catch prey items of a few cm. We do not know whether our results can be extrapolated to situations with prey of real dimensions, running at real velocities. Cursor size, too, may have implications for the outcome of the experiment. The area of overlap between prey and predator could be likened to the size of a raptor’s foot on a lizard’s body or the area of a newspaper used to swat a fly. (6) The simulation was also artificial because the prey was two-dimensional and moved in a two-dimensional space. While designing the set-up, we had a picture in mind of an aerial predator hunting for terrestrial prey (e.g. birds preying on lizards or snakes; Jayne & Bennett 1990; Garland 1994). Different rules may apply in a real, three-dimensional world. (7) Unlike in the real world, only one attempt was allowed per prey. (8) The prey was running in barren surroundings, with no cover in which to hide. Red on a white background also stands out. This may be too much of an approximation in many situations (e.g. with dense vegetation). We intend to expand the program so that prey items with different kinds and degrees of camouflage can be hunted. This would allow us to test,
for instance, the hypothesis that fast, striped animals and
cryptic, blotched animals are more difficult to catch than
fast, blotched and cryptic, striped ones (Jackson et al.
1976; Brodie 1992; Brodie et al. 1995).
In spite of the shortcomings of our simulation, we
believe that at least in some situations, the relationship
between sprint speed and catchability of prey animals
will be size dependent. This result is an additional
example of the ecological significance of body size
(LaBarbera 1989). It also adds to the notion that the
relation between speed performance (as measured in
laboratory conditions) and vulnerability, survival and
fitness in the field remains poorly understood and
requires further empirical evidence (Bauwens & Thoen

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