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RELATIONSHIP BETWEEN ESCAPE SPEED AND FLIGHT DISTANCE IN A WOLF SPIDER, *HOGNA CAROLINENSIS* (WALCKENAER 1805)

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ABSTRACT. The relationship between running speed and flight distance is an important one in terms of escape from predators, especially in species that may have multiple defensive strategies. In the wolf spider *Hogna carolinensis*, one important antipredator mechanism is flight. We examined the relationship between sprint speed and flight distance in wolf spiders by measuring sprint speed on a running track and, in a separate set of experiments with the same individual spiders, measured the distance at which they fled from an advancing model predator. Sprint speed was not significantly correlated with mass, size, or sex of the spiders. Sprint speed was positively correlated with flight distance. This correlation may be the result of a trade-off between two competing modes of antipredator mechanisms: escape and crypsis. In individuals with higher sprint speeds, escape may be the more advantageous option. Slower individuals may have a greater chance of surviving an encounter with a predator simply by remaining still and relying on crypsis.

Keywords: Antipredator strategy, risk, flee, sprint speed

Behavior patterns associated with predator escape and avoidance are important to individual survival. These result in strong selective pressure favoring individuals that successfully avoid or escape from predators. When an animal is approached by a potential predator, it must evaluate the level of predation risk, and utilize the appropriate antipredator mechanism to neutralize the risk. The distance from an approaching predator at which an animal chooses to flee has been referred to as ‘‘flight distance’’ (e.g. Fernández-Juricic et al. 2002), ‘‘flight initiation distance’’ (e.g. Bonenfant & Kramer 1996), ‘‘approach distance’’ (e.g. Martin & Lopez 1999), and ‘‘flush distance’’ (e.g. Fernández-Juricic et al. 2001). The latter two of these imply the perspective of the predator. Since we will be discussing the issue from the perspective of the prey, ‘‘flight distance’’ seems the most appropriate and concise terminology.

Ydenberg & Dill (1986) discussed in detail the economics of escape from predators. They suggested a cost-benefit model of flight distance, incorporating the costs and benefits of continuing a particular behavior (such as foraging) relative to the costs and benefits of fleeing. A concept critical to the predictions made by Ydenberg & Dill’s (1986) model is that ‘‘response’’ does not necessarily equal ‘‘detection,’’ in that it can often be difficult to assess whether or not the potential prey has detected a predator. In some cases, an individual may ignore an approaching predator until it becomes necessary to initiate flight. In other cases, certain ‘‘alert behaviors’’ may occur that precede a flight decision. The Ydenberg-Dill model generally predicts that individuals should delay flight until the costs associated with staying (e.g., increased predation risk) exceed the benefits associated with staying (e.g., time spent searching for food or mates).

Several studies have examined the relationship between flight distance and running ability. Rand (1964) found that body temperature affected the distance at which *Anolis* lizards fled from approaching predators, attributing differences in escape distances among individuals to lower body temperatures which reduced sprint speeds. Cooler individuals tended to flee at greater distances because lower body temperatures result in greater risk of capture. Heatwole (1968) suggested that crypsis might also play a role in flight distances. Cryptic species of *Anolis* may decrease their risk of capture by remaining motionless and fleeing at shorter distances than less cryptic species. Species that rely on crypsis may not flee from an approaching predator until detection by the predator is certain.

Schwarzkopf & Shine (1992) suggested that ‘‘vulnerability’’ (risk of capture) of prey should be evaluated in terms of the probability of being detected by a predator. They found that gravid female water skinks, *Eulamprus tympanum*, exhibited decreased running ability and shorter flight distances relative to nongravid females. They suggested that gravid females switched antipredator tactics from escape to crypsis because of the decrease in running speed. They interpreted these results as evidence that escape speed may not always be the most important element involved in determining when to flee. Formanowicz et al. (1990) investigated similar effects in the lizard *Scincella lateralis* with differences in sprint speed related to tail autotomy. Skinks with autotomized tails were found to exhibit slower running speeds and relatively shorter flight distances. They suggested that individuals that had lost their tails switched to a cryptic antipredator strategy to compensate for reduction in sprint speed.

In this study, we examined the relationship between running speed and flight distance in the wolf spider *Hogna carolinensis* (Walckenaer 1805). *Hogna carolinensis* is a large, burrowing wolf spider that is active on the surface of the ground from dusk until dawn and is distributed from southernmost Maine and Ontario throughout the southeastern U.S. and west to Baja California (Dondale & Redner 1990). Very little has been published concerning the life history of this species. Individuals of *Hogna carolinensis* construct a burrow with a turret of sticks and grass surrounding the mouth of the burrow. Or, in some cases, these spiders may inhabit a deserted rodent burrow (Shook 1978). The depth of the burrow likely varies between geographical regions and possibly with the substrate. In west Texas, where this study was conducted, I have found burrows as deep as 25 cm (pers. obs.). Likely predators include lizards, centipedes (pers. obs.), scorpions, coyotes, owls and various predacious insects (Shook 1978). If a burrow is near, individuals will retreat to a burrow when disturbed (Kuenzler 1958); however, if a burrow is not near, the animal will usually flee a meter or so, and then remain motionless (pers. obs.).

We examined the relationship between body size and running speed in male and female *H. carolinensis*, testing the hypothesis that larger individuals were faster. Since there is a sexual dimorphism in body size in this species, we also predicted that females and males should differ in running speed. Using the same spiders, we examined the distance at which they fled from an approaching model predator. We used the data collected on running speed and flight distance to test the following hypothesis based on Ydenberg & Dill’s (1986) model: faster individuals would be expected to flee at shorter distances from the predator.

METHODS

Hogna carolinensis (*n* = 77; 44 males, 33 females) used in this study were collected on 26 March and 11 April, 1997 at the Texas Nature Conservancy’s Independence Creek Preserve, approximately 37 km south of Sheffield, Terrell County, Texas, on the northeastern edge of the Chihuahuan desert. Voucher specimens have been deposited at the Denver Museum of Nature & Science. Most spiders were collected at night by using headlamps to produce eyeshine; a few were collected by turning rocks during the day. Spiders were not found to be active during the day. Females were often found near the mouth of a burrow, and sometimes removed from a burrow. In almost every case, females were found within a meter of the burrow. Males, however, were only occasionally found near a burrow but never in a burrow. Spiders were housed individually, in clear plastic containers (18.5 × 7.5 × 9 cm) with a sand substrate (approx. 1 cm deep). Each spider was fed one adult cricket/week, and water was available ad libitum. Temperatures in the housing and testing area ranged from 25–26 °C.

Escape Speed.—Spider escape speeds were measured on a wooden track 9 cm wide and 2 m long, with sheet-metal side walls approximately 21 cm high. All trials were conducted during daylight hours. A start box was separated from the track by a removable metal divider (21 × 9 cm). A spider was placed in the start box, allowed to acclimate for 15 minutes, the divider was raised, and the spider was prodded on the posterior end of the abdomen with a fiberglass rod until it ran. Using a stopwatch, we recorded the time that the spider crossed each 50 cm segment of track. Each spider was run twice with 24 hours between trials, after which time its mass was recorded. Spider cephalothorax lengths were measured at the end of the study with a caliper.

The fastest 50 cm speed (cm/s) for each spider was used for statistical analyses. T-tests were used to determine whether mass, cephalothorax length and speed differed between the sexes. Normality was evaluated using Shapiro-Wilk's W, and none of the groups violated this assumption at 0.05 level. Pearson correlation coefficients were used to examine relationships between speed and mass, speed and cephalothorax length, and mass and cephalothorax length.

Flight distances.—The distances at which spiders fled from an approaching model predator were recorded using a wooden runway apparatus 2.7 m long, and 28 cm wide with black plastic walls approximately 48 cm high. The spider chamber (32 × 28 × 51 cm) was located at one end of the runway, and separated from the runway by a glass divider. The walls of the spider chamber were sheet metal with two observation holes (0.5 cm diameter) that allowed the spider to be viewed with minimal disturbance. The floor of the spider chamber had a sand substrate 11 cm deep. To minimize vibratory cues, the runway and the spider chamber were separated from the counter top by 5.5 cm of foam rubber, and separated from each other by a space of 2 cm. A 15 cm tall green plastic lizard was used as a model predator (meant to represent a novel predator rather than a particular known predator) to elicit escape behavior. Each spider was placed in the spider chamber for 10 min. to acclimate. The model predator was concealed by a black plastic curtain at the end of the runway, opposite the spider chamber. After 10 min., the model predator was pulled toward the spider using a length of fishing line connected to a spool that was turned by a small motor at a speed of approximately 33.9 cm/s (mean = 1.4747 ± 0.0922 [seconds per 50 cm segment]). We ran a set of 10 test trials where we measured four 50 cm segments of track to test for consistency of speed of the model predator. Repeated-measures ANOVA (using trial as the repeated measure) showed no significant effect ($F_{9,27} = 0.4963$; $P = 0.8640$) indicating that the speed of the model predator from trial to trial was not significantly different. Another set of trials was run using only the motor without the model predator to rule out the possibility of cues from the sound and vibration of the motor. In these trials, none of the spiders responded to the activation of the motor ($n = 10$). The response of the spider to the approaching model predator was viewed through the observation holes in the wall of the spider chamber. Escape was operationally defined as a spider turning and running in the opposite direction from the model predator. When the spider exhibited an escape response, the motor was stopped and the distance was measured from the front end of the model to the original position of the spider. Spiders were run only once, unless no response occurred, in which case they were given a second trial. Flight distances were determined for thirty-eight of the individuals (19 males, 19 females) whose escape speeds had been measured.

Flight distances were transformed using the natural log to alleviate normality issues. Pearson correlation coefficients were calculated to examine the relationships between flight distance and spider size (mass & cephalothorax length) and sprint speed (as measured above). Discrepancies in sample size between tests resulted from specimen mortality and unresponsiveness of some individuals. All statistical tests were carried out using SPSS 11.0.2.

RESULTS

Escape Speed.—This species shows some degree of sexual size dimorphism (cephalothorax length: females, $n = 43$, mean ± SE = 12.92 ± 1.09 mm; males, $n = 33$, mean ± SE = 11.94 ± 0.74mm). Female *H. carolinensis* are significantly larger than males (mass, $t_{52} = 3.946$, $P < 0.001$ two-tailed; cephalothorax length, $t_{72.947} = 4.641$, $P < 0.001$ two-tailed [unequal variances]). Mass and cephalothorax length were significantly correlated (Pearson's $r = 0.470$, $P < 0.001$). However, when correlations were examined separately for the two sexes, this relationship only held true for the males ($r = 0.439$, $P = 0.017$, males; $r = 0.209$, $P = 0.326$ females). Although males and females differed in both measures of size, their sprint speeds were not significantly different ($t_{55} = 1.439$, $P = 0.156$, two-tailed). Neither mass nor cephalothorax

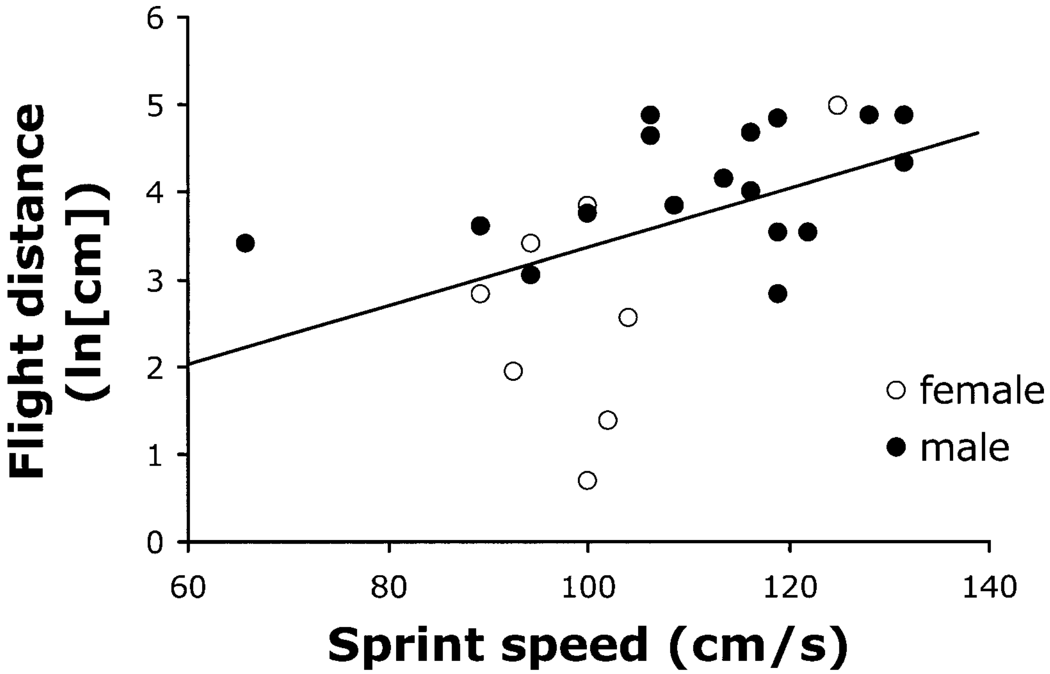

Figure 1.—Scatterplot of the natural log of flight distances and sprint speeds ($r^2 = 0.241$, $P = 0.013$).

length was significantly correlated with fastest sprint speed (Pearson's $r = -0.145$, $P = 0.296$, $n = 54$; $r = 0.077$, $P = 0.571$, $n = 56$, respectively).

Flight distance.—There was no significant correlation between spider size and log flight distance (mass, Pearson's $r = 0.024$, $P = 0.916$, $n = 22$; cephalothorax, $r = -0.314$, $P = 0.055$, $n = 38$). However, males tended to flee from the model predator at greater distances than females ($t_{37} = 2.663$, $P = 0.011$, *two-tailed*). Furthermore, there was a positive correlation between fastest sprint speed and log flight distance (Pearson's $r = 0.491$, $P = 0.013$, $n = 25$, see Figure 1).

DISCUSSION

The results of our study indicate that sprint speeds and flight distances of *H. carolinensis* are not affected by spider size. There were no significant differences in speed between males and females and no significant correlation between sprint speed and either measure of size (mass or cephalothorax length). Although size does not affect sprint speed or flight distance, sex appears to affect the decision to flee. Males fled from the model predator at greater distances than females.

Differences in flight distances for males and females may be the result of different cost-benefit relationships for males and females. Males and females may have very different lifestyles that require different considerations. Shook (1978) suggested that females might tend to stray farther from the burrow than males. If this is true, they may have a different escape strategy. For spiders associated with burrows, escape consists of only a short sprint to a burrow. However, for an individual that is not near its burrow, escape may involve a longer sprint, as well as an assessment of available shelter. To date, we have not been successful in getting this species to occupy burrows in the lab. Although females will occasionally inhabit a man-made burrow, none of our spiders have excavated their own burrows in the lab. In the field, males were rarely found near a burrow. It is possible that male *H. carolinensis* are not usually associated with a burrow and, therefore, are more reliant upon running to escape a predator. It would be interesting to determine whether flight distance is related to distance from the burrow in this species as has been shown in other organisms (squirrels, Dill & Houtman 1989; Cichlid fish, Dill 1990; woodchucks, Bonenfant & Kramer 1996; and skinks, Cooper 1997).

Sexual size dimorphism is common in spiders. Although not as exaggerated in wandering spiders as it is in web-builders, size dimorphism is still present. In wolf spiders, females may have longer cephalothoraxes, larger chelicerae, and larger abdomens than males (Walker & Rypstra 2001). The different body shape of males and females may result in different values for costs and benefits used in decision-making. The lack of a correlation between mass and cephalothorax length among females reflects the overall difference in body shape between males and females. The stouter build of the female in this species results in the size of the abdomen contributing more to overall mass than in males. Males have a smaller abdomen relative to cephalothorax length. As a result, males may possess lower energy stores, therefore placing a higher value on foraging. Females are generally considered to be more effective foragers than males, since they often consume more prey items (e.g. Walker & Rypstra 2001). It is, however, possible that males consume less due to their smaller size, but are more reliant on regularity of foraging success than females. In this case, a male that has not fed recently may be willing to risk predation in order to continue foraging. However, a male that has recently fed may flee when an approaching predator is farther away. It would be interesting to determine if feeding regime or the time since last feeding has an effect on flight distance and if that effect is different for males and females.

There was a positive correlation between sprint speed and flight distance. Spiders that were faster fled at greater distances from the approaching model predator while slower spiders waited until the model predator was closer before fleeing. This relationship between sprint speed and flight distance may seem counter-intuitive. The cost-benefit model of Ydenberg & Dill (1986) predicted that faster individuals should wait until the predator was closer before attempting to escape. When the predator is still relatively far away, the cost of flight (lost foraging time) would be higher than the risk of predation (risk of capture), resulting in an inverse relationship between maximum sprint speed and flight distance. According to the model, faster individuals are more likely to continue foraging, since the risk of capture for any given distance is less for a faster individual than for a slower individual.

In the present study, the individuals were not performing any specific task. We therefore need to consider what costs may be associated with flight and what benefits may be associated with staying. For spiders, the energy expended during escape can be costly (Prestwich 1988). Therefore, in cases where the risk of capture is low, it may not be worth the effort for the individual to attempt to escape. This cost might be higher for females, since they are larger than males and may have to expend more energy when running.

Another, perhaps more important cost of flight in some species involves cryptic antipredator mechanisms. In cryptic species, flight may actually increase the risk of capture (Heatwole 1968; Regalado 1998; Cuadrado et al. 2001). As a predator approaches a cryptic individual, the individual must decide whether it has been detected, making it necessary to flee. If, however, the individual flees before the predator has detected it, the individual may draw attention to itself and increase its risk of capture. The individual may also attract other potential predators. In this type of situation, the cost of flight is related to the probability of detection by the potential predator. This is a function of the perceptual fields of both the predator and prey species. If the predator has a larger perceptual field than the prey, the prey would benefit by fleeing while the potential predator is still relatively far away. When the predator has a smaller perceptual field than the prey, the prey would benefit by waiting to flee until the predator is closer, and the probability of detection is higher (Heatwole 1968; Martín & López 1999; Cuadrado et al. 2001).

The wolf spiders used in this study are a light mottled brown color and blend in readily with the desert substrate where they are likely to be encountered. We believe, therefore, that the results of this study can be explained upon the basis of crypsis. In faster individuals, it may be advantageous to flee at farther distances, since there is a higher probability that the individual will survive entirely on the basis of escape speed. In slower individuals with less chance of escaping solely on the basis of speed, individuals may rely on crypsis to escape detection. It may be advantageous for slower individuals to remain still, relying on crypsis for survival rather than fleeing and becoming more conspicuous to the predator.

Our results are similar to those obtained by Formanowicz et al. (1990) in ground skinks, *Scincella lateralis*. In individuals that had experienced tail loss 48 hours prior to testing, sprint speeds were significantly reduced, and individuals exhibited shorter flight distances. They interpreted the shorter flight distances in slower individuals to be the result of a behavioral compensation for tail loss. They suggested that autotomized individuals compensated for decreased speed by adopting a cryptic anti-predator strategy. This interpretation was based on information involving the relationship between flight distances and crypsis in lizards (Heatwole 1968; Bauwens & Theon 1981). Heatwole (1968) examined the relationship between flight distance and levels of crypsis in *Anolis* lizards. They found that cryptic species exhibited shorter flight distances than those that were less cryptic. Bauwens and Theon (1981) found similar results in gravid lizards, *Lacerta vivipara*. Gravid lizards compensated for decreased speed by adopting a cryptic anti-predator strategy.

In summary, maximum sprint speed was not significantly different for males and females, and maximum sprint speed was not significantly affected by the size of the individual. Furthermore, flight distance was not significantly related to size, but males tended to flee at a greater distance from a model predator. Sprint speed and flight distance were positively correlated. This positive correlation was considered to be the result of a trade-off between two alternative modes of predator avoidance: escape and crypsis.

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