

When predators become prey: flight decisions in jumping spiders

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Current optimal escape theory focuses on economic distance-based models that predict that animals will flee at greater distances when risk of capture is greater. Although these models have been tested extensively on vertebrate prey animals using large approaching stimuli (e.g., humans), it has never been tested on an invertebrate generalist predator with a stimulus that is in the size range of potential prey. I presented adult jumping spiders, *Phidippus princeps*, with a small black model to test flight decisions when physically handicapped, under different levels of threat, and on surfaces that potentially hindered escape. Predator approach speed, running surface texture, and leg autotomy had no effect on flight decisions. I also measured running distance and speed under different levels of hunger and energy state to test how these variables affect the decision to flee or to turn and defend oneself against a predator. When prodded, larger spiders fled shorter distances before switching to a defensive posture, hungry spiders fled longer distances than sated spiders, and rested spiders ran faster than tired spiders. There is likely a trade-off between body size and energy stores when deciding to flee from a threat or turning to defend oneself. These findings 1) reflect differences in how predators and prey assess risk in their environment and the distances at which they treat an approaching object as threatening and 2) suggest that future studies should focus on how animals optimize escape decisions in ways other than traditional distance-based economic models (e.g., relying absolutely on crypsis). *Key words*: antipredator behavior, autotomy, escape, flight initiation distance, jumping spiders. [*Behav Ecol* 20:318–327 (2009)]

For the past 20 years, much research has been focused on the environmental, behavioral, and morphological factors that influence the decision of prey animals to flee from predators (Ydenberg and Dill 1986; Stankowich and Blumstein 2005). Ydenberg and Dill's (1986) influential model states that prey should not flee immediately on detecting an approaching predator but should monitor its approach and flee when the expected benefits of escaping are equal to the costs of escaping, thus making an economic decision regarding flight. This economic hypothesis predicts that flight initiation distance (FID: the distance between the predator and prey at which the prey flees) increases with risk of capture and decreases with increasing individual capability to escape.

That the decision to flee appears to be an economic one has been confirmed in a variety of vertebrate taxa (e.g., fish: Dill 1974, lizards: Cooper 2003a, 2003b, birds: Lord et al. 2001, and mammals: Stankowich and Coss 2006). However, tests of escape theory in invertebrate taxa are few (e.g., Hemmi 2005; Nelson and Formanowicz 2005; Cooper 2006). This bias may be due to the assumption by many that their small brain sizes might limit their ability to rapidly assess information and make economic decisions based on this new information, and their responses to predators are limited to innate flight responses immediately on detection of a threat. Additionally, most studies of flight decisions involve a prey animal fleeing from a "predator" that is much larger than itself (e.g., a human) and not a candidate for consumption by the prey animal. There are likely perceptual constraints on rapid recognition of heterospecific predators that are close in size to potential food items, and the costs of misidentification are greater: specifically, inappropriately running away from a large profitable food item or allowing a dangerous predator to ap-

proach too closely. Therefore, I tested escape behavior in an invertebrate generalist predator, the jumping spider, *Phidippus princeps*, which has highly acute binocular vision (i.e., the ability to detect fine detailed differences at long distances; Forster 1982a) and frequently preys on animals many times its size (Foelix 1996). I chose to test escape behavior by increasing risk in three ways: 1) by increasing the apparent risk of the predator by varying approach speed; 2) by manipulating the characteristics of the spiders that were likely to hinder their ability to escape; and 3) by manipulating the physical environment so that escape was likely to be more difficult. Each of these manipulations has been shown to influence escape behavior in other taxa.

Several physical factors influence locomotor performance in animals, and these factors have significant potential impacts on the ability to avoid predation and fitness in general. Reduced locomotor capacity has been shown in arthropods that carry offspring after birth (Moffett and Doell 1980; Shaffer and Formanowicz 1996), in reptiles at reduced temperatures (e.g., Martín and López 2000), and gravid reptiles (Bauwens and Thoen 1981; Cooper et al. 1990). Further, Colancecco et al. (2007) found that female wolf spiders (*Pardosa milvina*) carrying egg sacs were less effective at avoiding predation by other wolf spiders (*Hogna helluo*). The type of substrate on/in which an animal is located also affects their ability to run (Irschick and Losos 1999; Aerts et al. 2000; Vanhooydonck et al., 2006), and this may affect escape decisions (Stankowich and Coss 2007). Finally, leg autotomy in arthropods has been shown to reduce running speed and increase susceptibility to predation (Amaya et al. 2001; Apontes and Brown 2005; Bateman and Fleming 2006; Fleming and Bateman 2007; Stankowich T, unpublished data). However, lizards appear to be able to compensate for tail loss behaviorally during escape (Brown et al. 1995), and leg autotomy in spiders has little impact on foraging ability (Amaya et al. 2001; Brueseke et al. 2001), predator avoidance (Brueseke et al. 2001; but see Klawinski and Formanowicz 1994), and competitive ability

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(Johnson and Jakob 1999). Guffey (1999) suggested that spiders have a “spare leg” and can afford to lose one or more without paying significant costs in locomotion. Nevertheless, animals may suffer a reduced ability to locomote when they are handicapped physically or are on surfaces that make maneuvering and rapid running difficult, which can affect their decision to flee and selection of escape tactic.

Flight decisions are largely affected by the speed of the predator and the ability of the prey to escape (i.e., running speed, agility, and availability of refugia). For example, grasshoppers (*Dissosteira carolina*) show increased FID in response to a rapidly approaching human compared with a slowly approaching human (Cooper 2006). An individual’s maximum flight speed also has been shown to correlate positively with FID (measured separately) in wolf spiders, *Hogna carolinensis*, suggesting a trade-off between two competing antipredator defense tactics: escape and crypsis (Nelson and Formanowicz 2005); slower individuals may increase survival by being cryptic, whereas escape may be more advantageous for faster individuals. Escape strategies are condition dependent in some animals: gravid lizards and lizards with autotomized tails, both of which have reduced escape capabilities, switch to a more cryptic strategy and flee at shorter distances than nongravid lizards and lizards with intact tails, respectively (gravid: Bauwens and Thoen 1981; Schwarzkopf and Shine 1992; Braña 1993; autotomy: Burger and Gochfeld 1990; Smith, 1996; Kelt et al. 2002, but see Cooper 2003c). Similarly, escape strategy is likely condition dependent in skylarks (*Alauda arvensis*) attacked by predatory merlins (*Falco columbarius*), where birds in good condition are able to sing during attack and are more likely to escape by flying, whereas nonsingers seek refuge on the ground (Cresswell 1994). Hungry or otherwise physiologically stressed animals show reduced FIDs (Kenward 1978; Andrén 1982; Handeland et al. 1996; Scrimgeour et al. 1997), indicating reduced flight capability and a switch in tactics from escape to crypsis or defense. Early escape may be more advantageous for lighter, faster individuals in good physical condition with enough energy to sustain prolonged flight, whereas slower, heavier, injured individuals may do better by either 1) remaining still and relying on crypsis until it becomes absolutely necessary to flee or 2) defending itself against the approaching threat.

I aimed to test two main hypotheses: 1) that spiders economically assess approaching stimuli and base their decision of when to flee on the level of threat posed by the stimulus, the ease of escape in the current environment, and on their own physical state (Stankowich and Blumstein 2005) and 2) during escape behavior, spiders base their decision of whether to continue fleeing or turning to defend themselves on their own physical condition and energetic state. For the first hypothesis, I predicted that if spiders make economic flight decisions then:

- 1.1 they will perceive a more rapidly approaching stimulus as more threatening and flee at greater distances (Experiments 1 and 2).
- 1.2 they will flee at greater distances when on surfaces that slow down running speed and hinder escape performance (Experiment 1).
- 1.3 they will perceive greater amounts of risk and will flee at greater distances when they are physically handicapped (e.g., have lost a leg) (Experiment 2).

It is important to note that an alternative to hypothesis 1 that is not tested directly here is that spiders approached by stimuli in the size range for potential prey must wait for the object to approach very near before deciding if it is predator or prey, will not have time to assess risk economically, and will not take into account behavioral, environmental, or physiological factors

when deciding when to flee. For the second hypothesis (Experiment 3), I predicted that if the decision to continue fleeing or to defend oneself is based on energetic reserves and physical state, then:

- 2.1 larger individuals will abandon flight sooner.
- 2.2 hungry individuals will be lighter and will flee for longer distances and at greater speeds than recently fed individuals.
- 2.3 rested individuals will have more energy stores and flee for longer distances and at greater speeds than individuals that recently ran rapidly for an extended period.

MATERIALS AND METHODS

Study organisms and housing

Phidippus princeps is a generalist predator that feeds on a wide variety of other organisms in the wild and is found throughout Eastern North America. Its terrestrial predators are primarily praying mantids (Order Mantodea), other spiders, and much larger vertebrates (e.g., birds and small mammals). In general, Salticid spiders use their different sets of eyes for different purposes. The anterior-lateral (AL) eyes are used to obtain information about the angular velocity of the target (i.e., prey or predators), and these eyes have about 25° of binocular overlap immediately in front of the spider (Forster 1982a). All postdetection behavior (i.e., anything after alert and alignment to the target) is mediated by the anterior-median (AM) eyes (Land 1971), which only have ~2° of highly acute horizontal retinal subtension (n.b., the AM eyes can survey a horizontal angle of 70° as a result of retinal movement, thereby allowing them to assess immobile targets without moving their head: Forster 1982a, 1982b). A spider can detect movement up to a range of 75 cm away (Forster 1977); as it gets closer, it quickly categorizes targets as prey, conspecifics, or predators based on size, distance, and speed using its AM eyes (Forster 1982b). This ability to detect movement at long distances is a function of changes in angular speed (the ratio of distance to the approacher vs. approacher speed), and when angular speed is very small, it may be masked by environmental motion noise (Peters et al. 2008). Therefore, spiders likely can detect very slight movements at long distances when environmental noise is low, as it was in Experiments 1 and 2 (see below).

Adult and penultimate (developmental stage just before adult) *P. princeps* were collected from fields and bridges in Western Massachusetts, USA. *Phidippus princeps* forage on flat surfaces (e.g., rocks, bridges, fences, and stone walls) and in more complex habitat (e.g., stems and leaves in fields). The experimental runways described below are meant to mimic the former habitat, and the extension of these results to flight decisions on stems and leaves is tenuous. Spiders were maintained at 25 °C, on a 15:9 h light:dark cycle, on a diet of crickets (*Achaeta domestica*), and provided ad libitum water in cotton-stoppered test tubes. Spiders were housed individually in plastic cages (31.5 × 23.5 × 10 cm high) with screened lids, plastic plants, a short opaque tube for refuge, and a painted green dowel to lessen the effects of captivity (Carducci and Jakob 2000). I conducted all experiments in the winter and spring of 2007 on spiders collected as penultimate or adults in the fall of 2006. Therefore, all spiders had a chance for exposure to natural predators before collection. All spiders were mature at the time of testing. Spider mass (mg) at maturity was measured using an OHAUS GT210 digital balance.

Experiment 1: effects of predator speed and surface texture on flight decisions

An enclosed runway was constructed out of foam board to test spiders with an approaching simulated predator. The runway

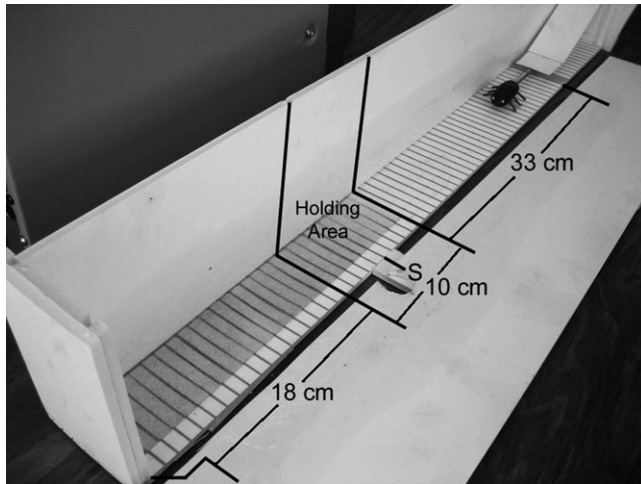


Figure 1
Photograph of the experimental runway for Experiments 1 and 2 with one sidewall removed. Predator model is shown at the right near its concealed starting position. Image shows a piece of sandpaper in place used in the rough texture trials of Experiment 1.

(Figure 1) was 75 cm long \times 4 cm wide \times 12 cm tall with an open ceiling to allow for videotaping from above. Lines were drawn horizontally across the runway at 1 cm intervals, and the floor of the runway was covered with a sheet of transparent plastic contact paper to allow for cleaning and to provide a smooth surface. The simulated predator (five exemplars) was an oblong black rounded piece of clay (~ 5 cm \times 2 cm) with six legs (short toothpicks; the width of the predator with the body and legs spanned nearly the entire 4 cm width of the runway so the spiders could not run around it) and two yellow eyes and was affixed to the end of a long steel rod and concealed under an index card at one end of the runway. Twenty-two centimeters from the other end of the runway, a hole was cut in the base of one wall (denoted by "S" in Figure 1) to allow for the introduction of a spider through an open-ended 20 cc syringe. Spiders were given ≥ 5 min inside the syringe to calm down from the cage-removal process, then slowly "injected" into the runway. Typically after injection, spiders explored the area slowly, then sat motionless until the trial began. Subjects were confined to a 10 cm long section of the runway ("Holding Area" in Figure 1) by removable transparent acetate walls (not shown in Figure 1) and a thin layer of petroleum jelly on the floor of the runway between the spider and the concealed predator; all walls of the runway also had a thin layer of petroleum jelly from the floor up to ~ 3 cm high to prevent subjects from crawling onto the walls and out of the runway.

Spiders were allowed to acclimate in the holding area of the arena for 2 min; the transparent walls were then removed gently so as not to disturb the spider. The concealed predator model was then advanced down the runway by pushing the steel rod from outside the runway. The predator became visible to the spider at a distance of 33 cm (Figure 1) from the forward wall of the formerly enclosed area, 38 cm from the syringe opening and 61 cm from the end of the runway. The model was advanced at a rate of 1 cm/s (the approximate approach speed of a praying mantis) or 3 cm/s down the runway and stopped when it was 6 cm from the end of the runway. Although the minimum difference in angular speed that an animal can detect is unclear, the visual system in jumping spiders is better than most all other invertebrates (Foelix 1996; Land and Nilsson 2002), and their visual system is highly sensitive to movement of small prey items in their environment up to 75 cm away (Forster 1977, 1982b, 1985;

Bednarski J, Jakob E, unpublished data). Following Dill (1974), at a distance of 38 cm (the initial distance between the model and the syringe), the model had a loom rate of $0.16^\circ \text{ s}^{-1}$ at the slow speed and $0.47^\circ \text{ s}^{-1}$ at the fast speed; at 10 cm away, this increases to $2.18^\circ \text{ s}^{-1}$ at the slow speed and $6.59^\circ \text{ s}^{-1}$ at the fast speed.

The running surface for the spiders was also varied (flat and smooth vs. rough and potentially difficult to traverse) in order to see if surface texture affects flight decisions: *Phidippus* spp. have been found living in cracks in large concrete walls and foraging on the rough surface (Stankowich T, personal observation). Strips of 60-grit sandpaper were cut to fit the end of the runway (28 cm \times 6 cm; the entire holding area and escape region of the runway were covered so that the spider could acclimate to the surface before approach) and lightly spray painted with white primer to match the rest of the runway (sandpaper is in place in Figure 1).

All trials were recorded using a Panasonic PV-GS300 miniDV video recorder. Fourteen spiders were subjected to all four combinations of speed and texture in random order with 2 days between trials to minimize habituation and learning, and the predator model exemplar used in each trial was assigned at random. The surface of the runway was cleaned with 91% isopropyl alcohol to disrupt and remove chemical cues left by spiders, and a clean, fresh sheet of sandpaper was used for every "rough" trial. From recordings, the following variables were scored for every trial: alert distance (distance between spider and model when the spider oriented to the model; if the spider was already oriented in the direction of the model when the approach began, the initial distance was recorded as the alert distance), response type (e.g., fleeing directly away, allowing the model to reach the spider then running with the model, allowing the model to pass overhead without moving, or running under the model in the opposite direction), FID (flight was defined as movement toward or away from the model), assessment time (elapsed time between alert and flight), and backup distance (distance the spider walked backward away from the model before turning and fleeing in a forward direction). If subjects let the model pass overhead or ran with the model, they were assigned an FID of 0.

After all trials were conducted, the maximum running speeds of the subjects were measured. The runway walls were narrowed to 4.5 cm wide, and spiders were introduced at one end of the runway. The experimenter lightly prodded the abdomen of the spiders with a wooden dowel to encourage them to run down the runway and back again (i.e., 120 cm). Spiders were gently prodded only when they stopped and never pushed. Running trials were video recorded from above, and the fastest speed (cm/s) over a distance of 5 cm was recorded as that subject's "maximum running speed" ($\text{Speed}_{\text{max}}$). Female *P. princeps* are larger than males (Edwards 2004), and sex and body mass are highly correlated; therefore, when available, body mass was used instead of sex to satisfy noncollinearity assumptions of parametric tests.

FID was subjected to a logarithmic transformation ($\log_{10}[\text{FID} + 1]$) to satisfy normality assumptions, and alert distance was categorized as "near" (< 10 cm) or "far" (> 10 cm) due to its bimodality. Spearman rank correlations were calculated to test for relationships between Alert Distance and FID, Response Type and FID, and Response Type and Alert Distance. A repeated measures multivariate analysis of covariance (MANCOVA) was used to test for within-subjects effects of approach speed and surface texture on FID, Response Type, Backup Distance, and Assessment Time (four levels each), between-subjects effects of sex, and $\text{Speed}_{\text{max}}$ as a covariate. Multivariate effects are described in the results as "overall flight response" because it is a composite measure of several dependent measures of flight response. Planned pairwise

comparisons were conducted on hunger and energy state for both average running speed and distance traveled before rearing. Data are presented as mean \pm SE. Significance was reached at $\alpha = 0.05$, and all statistical tests were conducted in SPSS 10.0. Due to miscalculation errors in SPSS software (Levine and Hullett 2002), all effect sizes, reported as η^2 , for significant factors in analyses of variance, were calculated by hand according to Cohen (1973).

Experiment 2: effects of limb autotomy on flight decisions

To test if the loss of one or more appendages affects the way spiders decide when to flee from an approaching predator, I selected 12 adult *P. princeps* at random to undergo autotomy. The act of leg autotomy is voluntary in field populations of spiders, and adults commonly lose legs naturally during struggles with predators and conspecifics. When a leg is removed, some body fluid is lost, but if the spider can manipulate the wound with its mouthparts, minimal fluid is lost. Autotomy is a common experimental procedure in spider research and is not considered unethical (e.g., Johnson and Jakob 1999). Subjects were anesthetized with CO₂ gas for 15 s or until they failed to respond to touch. I then grasped the body with a pair forceps and pulled off one limb from each side of the body with another pair of forceps. The first pair of anterior legs was never removed, and a balanced design of the possible limb combinations was constructed so that each of the six possible limb-pair combinations were represented two times in the group (i.e., two subjects had the second left and third right limbs removed, two subjects had the third left and fourth right limbs removed, etc.). After limb removal, subjects were returned to their cages and typically regained consciousness within 2–3 min, allowing them to seal the wounds with their mouthparts; no spiders died during or within 1 week after the procedure. Twelve different adults were selected as control subjects; control subjects were anesthetized identically and handled briefly with forceps before being returned to their cages. Five days after the surgeries, each individual was tested in predator model approaches. The same runway and approach procedure were used from Experiment 1, and each subject received one fast approach trial (3 cm/s) and one slow approach trial (1 cm/s), with 2 days in between trials and the order of trial types randomized. All trials were videotaped from above and scored in an identical manner to Experiment 1. Due to time constraints and spider mortality, separate trials to measure maximum running speed were not conducted. Statistical analyses were identical to Experiment 1. Spearman correlations were used to test relationships between FID, Alert Distance, Assessment Time, Backup Distance, and Response Type. Repeated measures MANCOVA was used to test for within-subjects effects of approach speed, between-subjects effects of autotomy, and the covariate body mass.

Experiment 3: effects of hunger and energy on the decision to fight or flee

During tests for maximum running speed described in Experiment 1, spiders appeared to run variable distances before stopping, turning around, and raising their forelegs in a threatening manner toward the wooden dowel. There appeared to be consistent variation in this distance between individuals. Spiders have low endurance levels during rapid movement due to a low number of mitochondria in cells (Linzen and Gallowitz 1975), with circulatory failure playing a lesser role. Therefore, recent long bouts of exercise may have more of an effect on performance than energy stores due to hunger level. To determine the role of physiological state (rested vs. tired, hungry vs. sated) on the decision to flee

from a threat or attempt to defend oneself physically, I constructed a long runway (219 cm long \times 2 cm wide \times 15 cm tall) similar to the one used in Experiments 1 and 2. The lines were drawn on the floor 1 cm apart and covered with transparent contact paper to allow for cleaning in between trials. The long base and walls were constructed out of foam board and the end walls out of wood. A small hole was drilled into the base of one end wall to allow for a syringe to introduce spiders into the runway. A thin layer of petroleum jelly was applied to the base of all walls to prevent spiders from climbing up the walls. Hunger level was varied by testing each spider 1) when it had been fed 2–3 days prior (sated) and 2) when it had been starved (i.e., all live crickets were removed from the cage) for at least 7 days (hungry). Energy state was varied by testing each spider 1) after it had been quietly resting in the dark syringe for 5 min (rested) and 2) after it had been released on an open tabletop and chased around with a white index card for 1 min (tired; n.b., the tired spiders were then placed in the syringe and introduced into the runway without a resting phase). Nineteen adult *P. princeps* were tested in all four combinations of treatments (i.e., hungry–tired, hungry–rested, sated–tired, and sated–rested) in a random order, and treatments on the same individual occurred at least 2 days apart. The spider was introduced into the runway via the syringe, and a stopwatch was started. A wooden dowel (1 cm diameter) with a small green piece of cardboard (1.5 cm wide \times 4 cm long) affixed to the tip was used to gently prod the abdomen of the spider to encourage it to run down the runway, and it was prodded every time it stopped running. This size of cardboard was used so that the spider would not perceive itself to be far outmatched in size. When the spider ceased running in response to the dowel and turned and reared up (i.e., raised its first pair of forelegs up in a defensive/aggressive ‘V’ formation), the test was ended. I recorded the total distance each subject ran and the elapsed time; average running speed was calculated by dividing total distance by elapsed time. Some spiders ran all the way to the end of the runway and never reared up; they were assigned the maximum distance of 219 cm. Repeated measures MANCOVA was used to test for within-subjects effects of hunger and energy state and the covariate body mass. Planned pairwise comparisons were conducted on hunger and energy state for both average running speed and distance traveled before rearing.

Table 1
Response type versus response distance and trial type in Experiment 1

	Response type		
	Fled directly away	Ran under/past model	Ran alongside model
Alert distance	30.1 \pm 2.1	33.6 \pm 4.2	21.2 \pm 8.7
Flight initiation distance	5.3 \pm 2.1	1.5 \pm 0.5	0 \pm 0
Fast and smooth	10	1	3
Slow and smooth	11	3	0
Fast and rough	9	4	1
Slow and rough	12	1	1

Behavioral Responses measured in cm and reported as Mean \pm Std. Error. Note: If a spider initiated flight when the stimulus reached it and ran alongside the model, the FID is necessarily 0. Some individuals fled before the model reached them, but then the model caught up and they ran alongside the model as well. Frequencies for response types for each trial type are reported in the bottom half of the table.

Table 2
Repeated measures MANCOVA for Experiment 1

	Multivariate effects				Flight initiation distance				Assessment time			Backup distance			Response type		
	<i>F</i>	df	<i>P</i>	η^2	<i>F</i>	df	<i>P</i>	η^2	<i>F</i>	<i>P</i>	η^2	<i>F</i>	<i>P</i>	η^2	<i>F</i>	<i>P</i>	η^2
Within subjects																	
Test type	1.011	12,96	0.445	0.112	0.908	3,33	0.448	0.076	0.090	0.965	0.008	2.272	0.098	0.171	2.437	0.082	0.181
Test \times speed _{max}	1.014	12,96	0.442	0.113	0.839	3,33	0.482	0.071	0.177	0.911	0.016	2.151	0.113	0.164	2.541	0.073	0.188
Test \times sex	0.724	12,96	0.724	0.083	0.416	3,33	0.743	0.036	0.282	0.838	0.025	0.763	0.523	0.065	1.486	0.236	0.119
Between subjects																	
Speed _{max}	2.402	4,8	0.136	0.546	3.349	1,11	0.094	0.233	0.738	0.409	0.063	0.131	0.725	0.012	0.212	0.654	0.019
Sex	3.247	4,8	0.072	0.621	5.988	1,11	0.032	0.352	0.797	0.391	0.068	0.042	0.841	0.004	0.936	0.354	0.078

Results of Repeated Measures MANCOVA testing the within-subjects effects of Approach Speed and Surface Texture (Test Type with four levels: Fast–Smooth, Fast–Rough, Slow–Smooth, and Slow–Rough) and between-subjects effect of Sex, with Maximum Running Speed as a covariate. Effect sizes are reported in the form of η^2 . Note that the degrees of freedom reported for FID are the same for Assessment Time, Backup Distance, and Responses Time for all factors.

RESULTS

Experiment 1: effects of predator speed and surface texture on flight decisions

Fourteen spiders were exposed to all four types of trials: fast approach/smooth surface, slow approach/smooth surface, fast approach/rough surface, and slow approach/rough surface. Spiders responded to the model in three ways: running directly away from the model, waiting until the model arrived and running alongside the model, and running past/underneath the model in the opposite direction. Body mass did not affect Speed_{max} ($r = 0.309$, $N = 14$, $P = 0.282$). Alert distance was positively correlated with FID ($N = 56$, Spearman's $\rho = 0.275$, $P = 0.040$) where spiders that detected the model at a longer distance fled at a longer distance. There was also a significant relationship between response type and FID (Table 1, $N = 56$, $\rho = -0.472$, $P < 0.001$): Spiders that fled directly away from the model did so at longer distances than spiders that ran directly under the model and those that ran with the model. There was no effect of alert distance on response type (Table 1, $N = 56$, $\rho = -0.029$, $P = 0.834$).

Results of the Repeated Measures MANCOVA for Experiment 1 are reported in Table 2. There were no general (multivariate) effects on flight responses (i.e., the combination of all four measures of flight) of test type (i.e., the four levels of approach speed and surface texture), or Speed_{max}, and the interaction between test type and Speed_{max} was not statistically significant. Maximum speed (11.1 ± 0.6 cm/s) did not explain a significant amount of the variance of any measurement of flight response. Sex had no effect on any measure of flight response except FID, where females (4.8 ± 0.9 cm) fled at greater distances than males (1.8 ± 0.5 cm). There was no significant effect of test type (Table 2, Figure 2) on FID, Assessment Time, Backup Distance, or Response Type (Table 1), and the interaction between test type and Speed_{max} was not significant for FID, Assessment Time, Backup Distance, or Response Type. Planned pairwise comparisons showed no differences between factor levels in FID, Backup Distance, or Response Type (all $P > 0.05$).

Experiment 2: effects of limb autotomy on flight decisions

Twelve intact spiders and 12 autotomized spiders were each run in two types of model approaches: one fast approach and one slow approach. Despite the fact that autotomized spiders ran more awkwardly than intact spiders (personal observation) and *Phidippus audax* autotomized in the exact same way have reduced maximum escape speeds (Stankowich T,

unpublished data), the actual escape speeds of *P. princeps* here did not differ reliably (Intact: 6.8 ± 0.7 cm/s, Autotomized: 5.6 ± 0.9 cm/s; Mann–Whitney $U_{10,7} = 23.000$, $P = 0.239$). However, spiders may not have escaped at their maximum speed if the model was not consistently prodding them to move (i.e., most spiders fled on their own before the model reached them, unlike in the maximum running speed trials where the stimulus was consistently prodding them to run quickly), and maximum running speeds from Experiment 1 were greater than escape speeds in Experiment 2 (Experiment 1: 8.5 ± 0.6 cm/s, Experiment 2: 6.3 ± 0.5 cm/s; $U_{14,17} = 18.000$, $P < 0.001$); therefore, intact spiders probably were able to outperform autotomized spiders if pressed to do so. Spiders that fled at greater distances were more likely to flee directly away from the model (Table 3, $N = 48$, $\rho = -0.736$, $P < 0.001$). There was no effect of alert distance on FID ($N = 48$, $\rho = -0.057$, $P = 0.701$) or response type (Table 3, $N = 48$, $\rho = 0.004$, $P = 0.977$).

There were no effects of body mass or leg state on flight responses (Table 4, Figure 3), but approach speed did affect overall response ($P = 0.028$, $\eta^2 = 0.437$). There were no effects of the interaction between approach speed and body mass or leg state on overall flight response. Neither body mass nor leg state had any main effects on any singular response

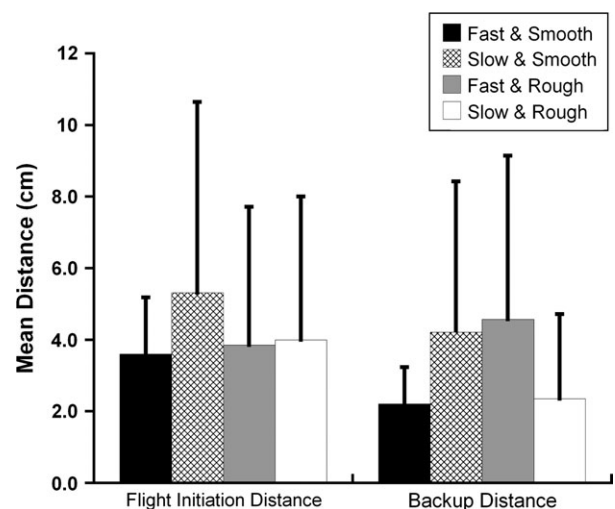


Figure 2
 The effect of model approach speed and surface texture on mean (\pm SE) FID and backup distance. $N = 14$ for all bars.

Table 3
Response type versus response distance and trial type in Experiment 2

	Response type		
	Fled directly away	Ran under/past model	Ran alongside model
Alert distance	30.3 ± 2.2	31.8 ± 4.0	19.6 ± 7.2
Flight initiation distance	6.6 ± 1.2	1.2 ± 0.8	0 ± 0
Fast and intact	7	2	3
Fast and autotomized	6	3	3
Slow and intact	9	2	1
Slow and autotomized	6	6	0

Behavioral Responses measured in cm and reported as Mean ± Std. Error. Note: If a spider initiated flight when the stimulus reached it and ran alongside the model, the FID is necessarily 0. Some individuals fled before the model reached them, but then the model caught up and they ran alongside the model as well. Frequencies for response types for each trial type are reported in the bottom half of the table.

variable (Figure 3). Approach speed had a reliable effect on Backup Distance (Table 4), but there were no other significant main effects of approach speed on individual flight responses (Figure 3). Therefore, the multivariate effect of approach speed on overall flight responses was driven predominantly by marginal and nonsignificant effects on Backup Distance and Assessment Time, respectively (n.b., the relationship between approach speed and Assessment Time is an artifact of the fact that spiders necessarily have less time to assess the approaching object during fast approaches). The interactions of approach speed with body mass or leg state were not statistically significant for any response variable.

Experiment 3: effects of hunger and energy on the decision to flee or fight

Nineteen spiders were run down the runway under all four conditions: hungry/rested, hungry/tired, sated/rested, and sated/tired; and distances traveled and average speeds were recorded. Body mass had a significant effect on overall escape response (Table 5, $P = 0.012$, $\eta^2 = 0.427$) where larger spiders ran shorter distances before turning in defense. There were no general effects on flight response of treatment type or the

interaction between treatment type and body mass. There were no individual effects of treatment type or the interaction between treatment and body mass on either distance traveled or average flight speed. Body mass had a strong effect on distance traveled (Figure 4; $P = 0.001$, $\eta^2 = 0.427$) where smaller spiders traveled longer distances, but there was no effect on average flight speed ($P = 0.300$). In the planned pairwise comparisons, there was no reliable effect of tiredness on distance traveled for either hungry or sated spiders ($P > 0.05$). Although there was no effect of hunger level on distance traveled in tired spiders (Figure 5a), there was a trend for rested spiders to run farther when hungry than when sated ($P = 0.071$). Rested spiders ran faster than tired spiders, irrespective of hunger level (Figure 5b; hungry: $P = 0.001$; sated: $P = 0.017$). Hungry spiders ran faster than sated spiders when they were rested ($P = 0.026$), but there was no such effect for tired spiders ($P = 0.725$).

DISCUSSION

The experimentally manipulated factors of surface texture, predator approach speed, and leg autotomy had very little effect on flight decisions in jumping spiders. FID, assessment time, and response type were all unaffected by these factors, and only minor effects were found on backup distance. Spiders backed up greater distances in response to a rapidly approaching predator. FIDs were greater when spiders became alert at greater distances, and spiders that fled directly away from the model were more likely to initiate their flight at greater distances than spiders that ran under the model or alongside the model. Although the lack of significant effects in Experiments 1 and 2 is due, in part, to a high degree of variability in the data (e.g., large standard error measurements in FID), much of this can be attributed to individual variation in behavior and escape strategy, and the low effect sizes for all factors and metrics (Tables 2 and 4) suggest that even with greater sample sizes and reduced variation, the effects would remain nonsignificant. In Experiment 3, larger spiders traveled shorter distances when prodded, and spiders that were rested ran faster than tired spiders. These results suggest that although the decision of when to flee from an approaching predator is unaffected by the predator’s speed, the substrate, or the physical state of the spider, the ability or decision to continue running during escape or turning to defend against predation is affected by the physical condition of the spider (i.e., mass, hunger level, and energy state).

As predicted by escape theory (Ydenberg and Dill 1986), numerous studies have shown (reviewed in Stankowich and

Table 4
Repeated measures MANCOVA for Experiment 2

	Multivariate effects				FID				Assessment time			Backup distance			Response type		
	F	df	P	η^2	F	df	P	η^2	F	P	η^2	F	P	η^2	F	P	η^2
Within subjects																	
Speed	3.490	4,18	0.028	0.437	0.517	1,21	0.480	0.024	3.624	0.071	0.147	4.366	0.049	0.172	0.312	0.582	0.015
Speed × mass	1.723	4,18	0.189	0.277	0.112	1,21	0.741	0.005	0.694	0.414	0.032	4.026	0.058	0.161	0.188	0.669	0.009
Speed × legs	0.858	4,18	0.508	0.160	1.421	1,21	0.247	0.063	0.175	0.680	0.008	0.0142	0.710	0.007	0.615	0.442	0.028
Between subjects																	
Mass	0.491	4,18	0.742	0.098	0.001	1,21	0.979	0.000	0.131	0.721	0.006	0.075	0.787	0.004	0.776	0.388	0.036
Legs	0.533	4,18	0.713	0.106	0.510	1,21	0.483	0.024	0.012	0.912	0.001	0.063	0.804	0.003	0.299	0.590	0.014

Results of Repeated Measures MANCOVA testing the within-subjects effects of Approach Speed (“Speed” with two levels: fast and slow) and between-subjects effects of Leg State (“Legs” with two levels: intact and autotomized) with Body Mass as a covariate. Effect sizes are reported in the form of η^2 . Note that the degrees of freedom reported for FID are the same for Assessment Time, Backup Distance, and Responses Time for all factors.

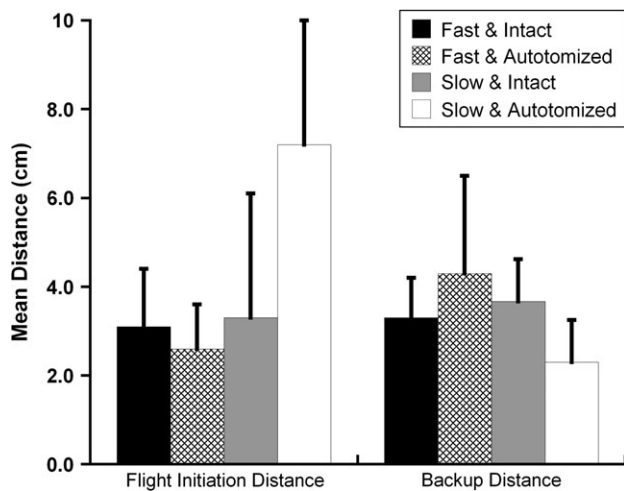


Figure 3
The effect of model approach speed and leg autotomy on mean (\pm SE) FID and backup distance. $N = 12$ for all bars.

Blumstein 2005) that prey should flee at greater distances when they are on surfaces that are difficult to maneuver on, when they are physically disabled, or when they are approached at a higher rate of speed. However, this study found no such effects on any measure of flight behavior except the distance spiders walked backward before turning and running forward. There are a few possible explanations for this unanticipated finding. First, the experiments may have been biologically unrealistic: If most antipredator decisions involve ducking behind a leaf or dropping to the ground, then turning and running in the opposite direction may have been an artificial choice for this species. Although this is a plausible explanation, jumping spiders often live on flat surfaces (e.g., concrete walls; Stankowich T, personal observation), and the spiders were housed in plastic containers with flat walls and ran on the walls regularly when being removed from their cages. Therefore, these individuals should not have found the situation of having to flee on a flat surface to be particularly unfamiliar.

Second, the treatment levels may not have been sufficiently different enough to warrant changing flight decisions. Although there was no difference in escape speeds between intact and autotomized spiders, spiders did not escape at their maximum running speed, and others have found that wolf spiders show reduced running speeds when their legs are autotomized (Amaya et al. 2001; Apontes and Brown 2005). It is possible that leg autotomy would have had

a greater effect on flight decisions at faster approach speeds that would require them to run at maximum speeds. The rough surface texture may not have been disruptive enough to hinder normal movement, and a rocky or narrow surface might have led to changes in flight decisions. Finally, the faster approach speed was three times greater than the slower speed, and there is good reason to believe that the spiders could detect the difference in approach speed (see Methods for rationale).

Third, spiders may adopt a strictly cryptic strategy on initial detection of a predator, followed by flight when it is apparent that they have been detected by the predator. Indeed, the first response to large looming objects (e.g., human hand) and real predators (e.g., a praying mantid model) is to orient to the threat and freeze (Stankowich T, personal observation), and freezing to remain cryptic is a common line of defense in many animals, especially when opportunity costs are low (e.g., time lost to hunting; Ruxton et al. 2004). However, if this were the case, we still might expect approach speed to affect FID because the speed of approach is a strong indicator of threat level posed by the predator. Additionally, the “backing up” behavior of the spiders would not be predicted by crypsis because backing up reveals its presence and position to the predator at close range while still vulnerable to attack, and cryptic animals typically take flight in a sudden burst of speed to potentially surprise the predator. Nevertheless, this explanation cannot be rejected because remaining motionless until the predator approaches to a close distance before making a last ditch effort to flee is in agreement with the results here.

Finally, the way in which animals optimize their escape decisions might primarily depend on the interaction between trophic level and distance at which predator recognition occurs. Jumping spiders are generalist, stalking predators that prey on animals larger than themselves. Nearly all investigations of flight decisions and escape behavior have been conducted on animals that are regularly vulnerable to predators (Stankowich and Blumstein 2005). In these studies, animals typically have time to detect a predator and flee before being captured, and rarely do these species prey on other organisms larger than themselves. It is unknown if economic flight decision algorithms (Ydenberg and Dill 1986; Broom and Ruxton 2005; Cooper and Frederick 2007) are useful for predators. For a generalist predator approached by an object in the size range of potential prey, it may be beneficial to allow it to approach more closely to allow more time to acquire information on whether it is prey, a conspecific, or a predator. Objects larger than a certain size are not classified as potential prey, and spiders may flee from large objects at much greater distances (e.g., see predator size studies in fish: Dill 1974; Hurley and Hartline 1974; Karplus and Tuvia 1979; Helfman and Winkelman 1997), potentially conforming to the

Table 5
Repeated measures MANCOVA for Experiment 3

	Multivariate effects				Distance traveled				Average running speed		
	<i>F</i>	df	<i>P</i>	η^2	<i>F</i>	df	<i>P</i>	η^2	<i>F</i>	<i>P</i>	η^2
Within subjects											
Test type	0.557	6,12	0.756	0.218	0.154	3,51	0.927	0.009	0.681	0.568	0.039
Test \times mass	0.798	6,12	0.589	0.285	0.264	3,51	0.851	0.015	1.286	0.289	0.070
Between subjects											
Mass	5.961	2,16	0.012	0.427	12.650	1,21	0.002	0.427	1.143	0.300	0.063

Results of Repeated Measures MANCOVA testing the within-subjects effects of Hunger Level and Energy State (Test Type with four levels: Hungry–Tired, Hungry–Rested, Sated–Tired, and Sated–Rested) and between-subjects effects of the covariate Body Mass. Effect sizes are reported in the form of η^2 . Note that the degrees of freedom reported for Distance Traveled are the same for Average Running Speed for all factors.

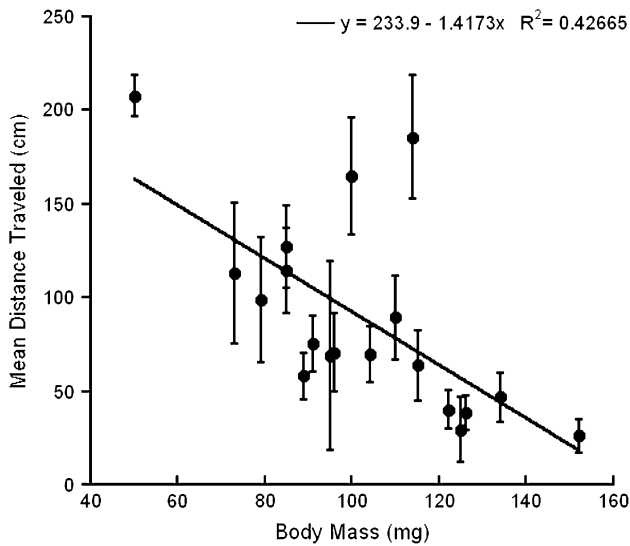


Figure 4 The relationship between individual body mass (mg) and mean (\pm SE) distance traveled (cm) for each spider through the four treatments of Experiment 3. The negative relationship is statistically significant ($P = 0.001$). $N = 19$ for all bars.

predictions of escape theory (e.g., Nelson and Formanowicz 2005; Cooper 2006). Predator recognition must occur before risk assessment can begin (Endler 1986; Lima and Dill 1990), and discrimination between potential predators and potential prey may take longer or may need to occur at relatively shorter distances for generalist predators than for vulnerable prey or even specialist predators. Additionally, predators may wait until a smaller stimulus approaches more closely because the costs of unnecessary flight are greater (missing an opportunity for a valuable prey item) than for larger stimuli or for nonpredators. Therefore, generalist predators like jumping spiders may not optimize escape behavior in the same way as other prey animals (i.e., taking flight at a distance economically based on costs of fleeing and remaining); instead, the optimal escape strategy may be to attempt to be cryptic until the approaching threat comes very close or initiates an attack before moving, allowing more time for discrimination between threatening and nonthreatening stimuli.

Spiders likely have two different strategies for responding to attacking predators: rapidly flee or defend oneself using strength and venomous bites, and making an incorrect strategic decision could mean the difference between life and death. Heavier spiders ran shorter distances, and hungry and rested spiders ran farther and faster than other spiders, suggesting that hungry and rested spiders are slightly lighter (by virtue of not having food in their body), faster, and have more energy available for immediate running speed. There are two potential, nonmutually exclusive explanations for this result. First, having just fed likely weighs spiders down temporarily, or their bodies are spending extra energy digesting food, making it difficult to quickly flee long distances from a pursuing threat. However, mass had no effect on flight speed. Second, larger, heavier spiders may have reduced endurance but may also have more short-term mechanical and biting strength and be better able to defend themselves against a pursuing predator. They may make the decision to fight sooner because after using a threshold amount of energy stores during flight, it pays to turn and use their larger size to their advantage against the threat. The decision to flee

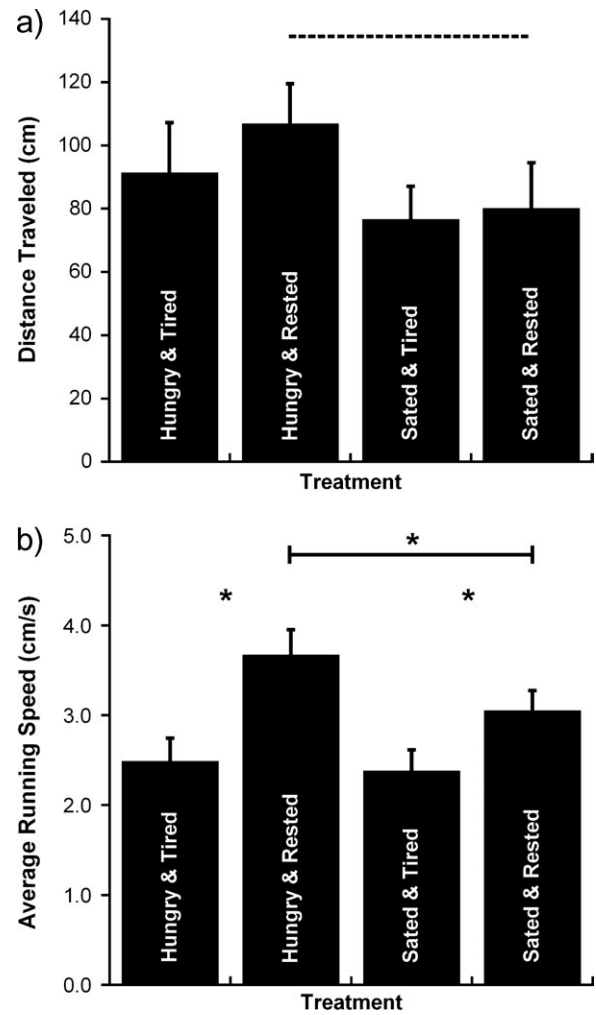


Figure 5 The effect of different levels of hunger and energy state (Experiment 3) on (a) distance traveled and (b) average running speed. Asterisks and solid lines indicate statistically significant pairwise relationships ($P < 0.05$) and dashed lines indicate nearly significant pairwise relationships ($0.10 > P > 0.05$). $N = 19$ for all bars.

or fight is likely based on energetic trade-offs between the two activities where body size acts to lower the threshold for turning to fight.

In summary, traditional economical based models of flight initiation failed to predict the flight responses of jumping spiders to an approaching object. Surface texture, leg autotomy, and predator approach speed had no effect on flight decisions; this suggests that either spiders rely heavily on crypsis to avoid predation, or generalist predators do not use typical risk assessment algorithms when confronted by an approaching prey-sized animal because it takes longer to discriminate between potential predators and prey. Future experiments should test these responses on larger objects that are outside the size range of prey items to determine if escape theory accurately predicts flight responses and to test how angular size influences flight decisions. The decision to flee versus turning to defend oneself against a predator likely reflects a dichotomy in defense strategies where lighter, hungry, and rested spiders choose to flee longer distances before giving up rather than relying on fighting ability, whereas heavier, sated, and tired spiders may do better by defending themselves with mechanical force and venomous bites and choose not to waste energy carrying their heavier bodies for long distances.

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