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Importance of hunger and prey type on predatory behavior stages in *Corythalia albicincta* (Araneae: Salticidae)

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Abstract. Predators often adopt strategies to capture prey that reflect both the characteristics of the prey and their own hunger level. In generalist spiders of the family Salticidae, predatory behavior typically consists of four phases: orientation towards the prey, pursuit, crouching, and jumping to capture. In this study, we conducted laboratory experiments in order to determine whether predatory strategies change according to prey type and hunger level in *Corythalia albicincta* (F. O. Pickard-Cambridge 1901). We used adult specimens of both sexes to evaluate variation in capture jump distance, time spent on each predatory stage and attack efficiency, in terms of prey capture. Jump distance was greater with prey that can more readily escape (crickets and flies), compared to fly larvae. The duration of both latency and orientation was greater in larval trials than in the cricket and fly trials. *Corythalia albicincta* spent less time in a crouching position with flies and the total duration of the predation process was shorter with flies than with crickets or larvae. Numbers of failures, defined as the number of failed attacks before a spider captures a prey item in the test, was higher in spiders that had been starved for one day compared to those that had been starved for 7 and 15 days. Predatory strategies were modified according to movement patterns and prey speed, while hunger level affected predation efficiency.

Keywords: Capture efficiency, foraging behavior, prey capture failure, spider behavior, starvation

Predators that forage widely actively search for their prey (Huey & Pianka 1981). Once prey is detected, the searching stage ends and hunting behavior begins (Forster 1977). The predator must then adopt a capture strategy that is appropriate for the characteristics of a given prey item (Forster 1977). When the available prey items present different characteristics, such as size (Gardner 1965) and/or ability to escape (Forster 1977; Bartos 2002), defensive adaptations, and vulnerable body parts (Curio 1976), the predator must be capable of adopting different capture strategies (Edwards & Jackson 1994; Jackson et al. 1998).

Predation strategies in the Salticidae vary according to prey type (Curio 1976), particularly in the myrmecophagous and araneophagous (stenophagous) species (Jackson & Hallas 1986). Members of his family present plasticity in this regard (Forster 1977): they can change their predation strategy to suit prey size, speed, movement type and presence/absence of wings (Harland & Jackson 2004). When spiders recognize that prey can escape by flying, jumping, or through rapid movement, the attack is launched from a greater distance than it is with prey having lower escape capabilities (Bartos 2002). Due to their highly developed vision (Land 1969; Harland & Jackson 2000), salticid spiders are capable of recognizing their prey based on shape (Edwards & Jackson 1994; Jackson et al. 1998; Harland & Jackson 2001), size and color (Gardner 1966), body markings (Harland & Jackson 2001), mobility, and even by the presence of wings (Edwards & Jackson 1994; Bartos 2002).

An additional factor that influences hunting behavior is the hunger level of the predator (Gardner 1966; Forster 1977), because this is closely related to selectivity of prey type (Jackson et al. 1998; Jackson 2000), quantity of food eaten, and latency of reaction to the stimulus (Gardner 1966; Forster 1977). However, information regarding hunger level is relatively scarce in the context of salticid predation (Gardner 1964, 1966; Foster 1977; Persons 1999). Jackson et al. (1998) found that prey selectivity in ant-eating jumping spiders disappears with high levels of hunger. Hungry spiders also capture more prey at a faster rate (Gardner 1965). A perspective that has not been explored is how the condition (hunger as an internal factor) of the predator affects prey capture efficiency. In addition, the extent to which hunger affects spider behavior, in terms of time spent in each phase of the predation strategy and failure rates, remains unknown.

We hypothesize that hunger level not only could affect reaction time to prey and capture efficiency, but also could modify other aspects of predatory behavior, such as predation strategy. In particular, hungry spiders are expected to adopt a simple and rapid predation strategy (with a lower probability of success), while spiders without hunger will exhibit a specific and more complex predatory strategy (with a higher probability of success). This deliberate change in capture strategy could demonstrate that decision-making by the spider can be influenced by hunger level.

In this study, we examined three levels of hunger in spiders: a minimum hunger level (1 day without food), an intermediate hunger level (7 days without food), and an high hunger level (15 days without food) in which spiders displayed low energy but were still able to capture prey (during pilot observations we recorded a 30.2% mortality rate in spiders under this treatment, while in the other two treatments, involving 1 and 7 days without food, no mortality was recorded).

Furthermore, if a spider's need to eat precludes the use of a specific capture strategy, it could be possible to determine whether spiders are capable of selecting a simple and direct strategy. Such a strategy would have a high risk of failure (without crouching) as a result of being the fastest method by which to obtain food, as opposed to adopting a specific, more prolonged strategy, but one with a greater probability of capture.

In this study, we examined how hunger affects prey selection and attack rate in the salticid spider *Corythalia albicincta* (F. O. Pickard-Cambridge 1901). We predicted that the spiders would attack prey with high escape risk from a greater distance than prey with low escape risk (Bartos 2002), and also that the spiders would capture prey with high escape risk by adopting a strategy that involves a short time of latency, followed by a rapid attack with no pursuit. In contrast, low-mobility prey would be harder to identify, since salticids respond more readily to movements, but capture would not be rushed (Jackson et al. 2002; Nelson et al. 2004). Finally, the spiders would modify their predation behavior according to hunger level. Satiated spiders would wait longer to capture prey and would adopt a predation strategy that is specific to prey type, while hungry spiders would react more quickly to the stimulus and would not follow any specific strategy in response to different prey types.

METHODS

Study species and prey type.—*Corythalia albicincta* (Araneae: Salticidae) is found in North and Central America (Platnick 2014). Adults are approximately 0.5 cm in length. Both females and males have similar patterns of coloration. Females are a few millimeters larger with a more rounded and wider abdomen than the males. The males present a more pointed abdomen and yellow pedipalp tips. *Corythalia albicincta* lives in moist soil with abundant leaf litter and can be found on rocks or logs under the shade of tropical vegetation.

Mass-reared *Acheta domesticus* were obtained from the herpetarium of the Benemérita Universidad Autónoma de Puebla. House cricket nymphs (first and second instar only: 5–10 mm in length) were used as prey in the experiments, along with larvae and adults of *Drosophila melanogaster*. The latter were mass-reared in crystal vials in the laboratory (25° C ± 4.8 °C; ambient relative humidity). Both larvae (3–4 mm) and adults (2.5–3 mm) were fed with a specialized culture of flour, yeast, sugar and carrageenan (bancodemoscas.fciencias.unam.mx).

We selected these as prey because, in addition to being easily available, they represent a range of different shapes and are of a suitable size for capture by the spiders. Furthermore, they differ in terms of movement patterns (continuous or discontinuous movements and flight) and speed. Larvae move very slowly, while crickets advance constantly and occasionally jump and flies remain immobile for long periods of time then suddenly fly for a few seconds before landing to remain immobile again. The average speed of movement ± standard error (measured as the distance travelled in one minute, within the area used for the experiment) for larvae was 1.78 ± 0.46 cm/min, $n = 20$; for flies was 30.79 ± 1.21 cm/min, $n = 20$; and for crickets was 39.70 ± 1.11 cm/min, $n = 20$ (speed was measured from the sum of the distances calculated between points, located every 5 s in a Cartesian plane over one minute). Flies and crickets do not differ significantly in this regard (following comparison of larvae, fly and crickets with ANOVA, Tukey multiple comparisons test, $\alpha = 0.05$).

Collection site.—Adult salticids were collected by hand, between 20 April and 12 June 2011, in the municipality of Pantepec, Puebla (20° 46.88′N and 97° 75.70′W; 640 m; INEGI 2011). In the laboratory, the spiders were fed with two fruit flies once a week for approximately three weeks prior to initiating the experiments (Edwards & Jackson 1994; Jackson et al. 1998) in order to acclimatize the specimens to laboratory conditions and to standardize their levels of satiation. Voucher specimens of *C. albicincta* were deposited in the Instituto de Biología of the Universidad Autónoma de México.

Observations.—We conducted the experiments under laboratory conditions (25 ± 4.8 °C, 12:12 light-dark cycle, ambient relative humidity) between 15 June and 12 August 2011. Each test was conducted between 09:00 and 16:00 h.

Predation behavior was monitored in a white acrylic container (11.5 × 15 cm at the base, 25 × 28.5 cm at the top, measurements proportional to those of the video camera screen, and 5 cm in height, with 45° sloping sides), with a removable dividing wall in the middle. This container was larger than those used in other experiments, in which Petri dishes of 9 cm diameter were used (Forster 1977; Edwards & Jackson 1993, 1994; Jackson et al. 1998). To record the spatial behavior of the spiders, a 0.5 cm grid was drawn on the sides and bottom of the container. To facilitate observation, the container was closed with a transparent acrylic lid. Individual spiders and prey were randomly placed on either side of the container. With a wire, we gently pushed the spider directly from the vial to one side of the container and placed the prey at the other side. In the case of prey, larvae were extracted from the crystal vial. For flies and crickets, we isolated one individual in a smaller plastic vial and then placed the vial upside-down over the container with its acrylic lid slightly opened, allowing the prey to enter the container. The dividing wall was removed after one minute and the spider predation behavior patterns recorded for 15 minutes thereafter. All trials were recorded with a video camera (Kodak Easyshare, Z8612 1S, 8.1 megapixels). The method used to record the behavioral patterns was continuous focal sampling, defined as observation of a single individual over a defined period of time.

On analysis of the video recordings, the behavioral variables identified were:

(1) Latency, defined as the time from the beginning of the video recording (starting from the moment at which the internal container division was removed) until the spider detected the prey (Martin & Bateson 2004).

(2) Jumping distance of the spider when capturing prey, calculated from the position of both individuals on the container grid using a system of x and y coordinates. With this procedure, we defined the positions of both spider and prey prior to the attacking jump, then calculated the distance between the two points on a Cartesian plane.

(3) Number of failures before a particular prey was captured and the jumping distance of each failure. This variable, as a measure of capture efficiency, could be related to the internal condition of spiders (hunger level). Gardner (1966) stated that hunting finishes with the jump, but we observed that there could be failed jumps that imply the spiders starting again from the beginning of the sequence of hunting behavior.

(4) Orientation (seconds), defined as beginning when the spider suddenly orientated its cephalothorax towards the prey, before making an approach.

(5) Approach (seconds), defined as the movement made by the spider in order to get closer to the prey. This takes place after the orientation phase, but before the prey moves away from the spider, so the prey is immobile even if the spider is approaching it.
(6) Pursuit (seconds), defined as the movement of the spider chasing the fleeing prey, in one or more movement sequences. This takes place once the prey is moving away from the approaching spider.
(7) Crouching, the final stage, quantified as the time spent motionless by the spider prior to jumping to capture the prey. This stage is distinguished by the fact that the spider flexes the limbs, inclining the cephalothorax slightly forward.
(8) Average speed, defined as the distance moved by the spider within a time period of one minute, during the period of observation of the spider.

Latency helps to determine the moment when the first physical or visual interaction takes place between predator and prey. This value can change depending on different variables, such as the degree of mobility or visibility of the prey. According to Forster (1977), latency represents the stage of searching for prey: when latency finishes, the hunting stage begins.

The other interaction phases were determined according to the primary patterns described by Forster (1977): orientation, pursuit and capture. However, for the purposes of this study, the stage of orientation was considered to be attention because, within the stage of pursuit, following was considered to be pursuit while running/walking was considered to be approach, differing in the sense of whether the prey is mobile or not. Time spent stalking was included in pursuit, or in approach when pursuit did not take place. In addition, since the secondary units of pre-crouch and crouch were not used by the spider in that order and were sometimes executed more than once, we amalgamated these two stages into crouching.

The predation stages of orientation, approach, pursuit and crouching were only recorded when the spiders captured prey; i.e., if the trial featured more than one attempt to catch prey, the last interaction between spider and prey was recorded. Spiders that had not captured their prey within the 15 minutes of observation were fed that day and then starved once again for the previously assigned starvation period. Each spider was exposed to the experiment as many times as necessary until the prey was caught, each time leaving the spider without food for the allotted starvation period prior to each observation. All of the unsuccessful trials were excluded from the data and only the single successful trial was used for analysis of all the variables (including number of failures). The mean number of trials (± SD) per spider was 1.82 (± 1.06), $n = 90$. In addition, the frequency of trials per spider was as follows: one trial for 48 spiders, two trials for 19 spiders, three for 17 spiders, four for 3 spiders and five trials for 3 spiders. The mean number of jumps (± SD) per spider per 15 min trial was 1.23 (± 0.978, max = 10).

Experimental design and statistical analyses.—The experiment consisted of a fixed factor design comprising prey type (cricket, adult fly, fly larva) and starvation period (1, 7, 15 days). The statistical model considered the main effects of, and the interaction between, these two factors. Each treatment combination consisted of ten replicates, making a total of 90 spiders recorded. Each spider was subjected to only one treatment of the possible nine hunger/prey type treatment combinations. Treatment combinations were assigned at random. Bifactorial analysis of variance was applied to both jumping distance and the distance moved by the spider. Tukey multiple comparison tests were carried out in order to identify which treatment combinations differed significantly from other treatments (Zar 1984). Number of failures was analyzed with a generalized linear model, with a Poisson error distribution and loglink function, since the data were counts (Crawley 2007). In cases where the fit was over-dispersed, the statistical model was adjusted via the quasi-likelihood method with the square root of the response variable as a link and the variance as the square of the mean (Crawley 2002). To determine whether the incidence of capture (as a binary variable) depends on jumping distance, prey type and hunger level, we analyzed the data with a binary logistic regression, with incidence of capture as the response variable and distance, prey type and hunger level as the independent variables (Crawley 2007). This analysis allowed us to determine the probability of failure to capture prey; and, in cases when all independent variables were significant, at least nine different curves were generated (representing the nine treatment combinations) with each defined by slope and intercept. The data used for this analysis were incidence of capture with the first jump in order to avoid pseudo-replication.

Following analysis of the frequency of failures, the full model (containing the principal term, and the second and third order interactions) was simplified in order to obtain the minimum appropriate model, deleting the terms of lower degree of significance step by step, starting with the interaction then eliminating individual terms (see Quinn & Keough 2002 and Crawley 2007 for further details).

A survival analysis was applied to all the timed variables, using Accelerated Failure Time Models (Fox 2001). This analysis is used when the duration of an event (*failure time data*) is required, and enables us to compare the curves of probability of occurrence for an event influenced by time (in this particular case, the probability of a spider to remain within a determined predatory stage) (Pyke & Thompson 1986). These data were analyzed with an accelerated failure time regression model (Fox 2001).

We used the Akaike Information Criterion (AIC; Crawley 2007) to determine whether the data fit an exponential, logistic, lognormal, log-logistic or Weibull distribution, because it is an indicator of the model that best explains the fit of the data to the model. Particular differences in each treatment level were analyzed using the contrast method. Due to the fact that the contrast method did not compare all possible combinations (there are $k - 1$ orthogonal contrasts, with k the number of levels of each treatment), we applied the *treatment contrasts* method, which compares pairs of treatments not only explicitly, but also implicitly (Crawley 2007).

All analyses were conducted using the program R.12.2 (R Development Core Team 2011), considering $\alpha = 0.05$. Survival analysis was conducted in combination with the "survival" package (Therneau & Lumley 2011).

RESULTS

Jumping distance.—Jumping distance to capture prey differed significantly among the three prey types. The shortest

Table 1.—Factorial ANOVA of jumping distance of *C. albicincta* as a function of hunger level (H) and prey type (P). % = percentage of variation explained by each term of the model.

	df	SS	*F*	*P*	%
Hunger (H)	2	0.563	0.79	0.456	1.305
Prey (P)	2	12.811	17.99	<0.0001	29.67
H × P	4	0.965	0.68	0.609	2.236
Error	81	28.830			66.782
Total	89	43.171			

distance was for the larvae, followed by the flies and the greatest jumping distance was for the crickets (Table 1, Fig. 1).

Hunger level did not influence jumping distance and there was no influence of the interaction between hunger level and prey type. Prey type explained the highest percentage of the variability in jumping distance (Table 1). Failure to capture prey was influenced by jumping distance and prey type, but not by hunger level (Fig. 2). According to the analysis of contrasts, the intercept was the same between crickets and flies ($z = 0.802$, $P = 0.422$), but differed significantly in the larvae ($z = 2.942$, $P = 0.003$). Figure 2 shows that the probability of the spiders failing to catch prey is greater for prey of high escape risk (crickets or adult flies).

Failure to capture prey.—Prey type, hunger level, and the interaction between these significantly influenced the frequency of failures to capture prey (Table 2). Contrast analysis showed that spiders starved for 7 and 15 days did not differ in terms of number of failures (1.14 ± 0.25 and 1.56 ± 0.24, respectively, $z = 0.99$, $P = 0.319$); however, those that were starved for 1 day presented significantly more failures than those that were starved for 7 and 15 days (2.90 ± 0.39, $z = 2.07$, $P = 0.038$; Fig. 3). There was no significant difference in the frequency of failures to capture flies and crickets (1.70 ± 0.24 and 3.0 ± 0.33, respectively, $z = 1.63$, $P = 0.101$), but the frequencies of failure for both these treatments were significantly greater than those involving the larvae (0.06 ± 0.04, $z = 3.72$, $P = 0.0002$, Fig. 3). Prey type explained the majority of the variability in the frequency of failures (Table 2).

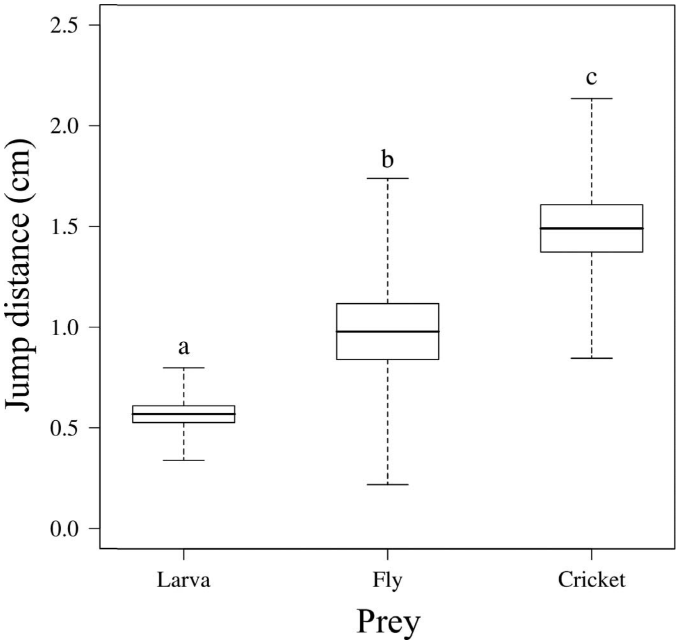

Figure 1.—Jumping distance of *Corythalia albicincta* when capturing different types of prey. Horizontal lines represent mean distances, the top and bottom of each box represent one standard error and the whiskers represent one standard deviation. Different letters above each box denote significant differences between the groups of data according to a Tukey multiple comparisons test.

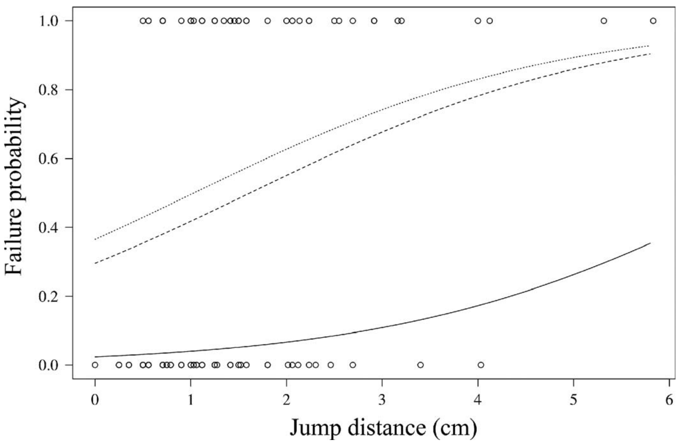

Figure 2.—Relationship between jumping distance and the probability of failing to capture larva (continuous line), cricket (dotted line), and fly (dashed line). The dependent variable shows the frequency of successes and failures, where 1 = success and 0 = failure.

Regarding the interaction between the two variables, the number of failures to capture larvae differed among the three hunger level treatments, being higher with 1 day compared to 7 and 15 days of starvation; all failure frequencies with larvae were the lowest among the prey types. Against flies, failures were higher after 1 and 7 days of starvation than after 15 days. Considering only 1 and 15 days of starvation, we found the same pattern with the crickets: failure frequency was higher after 1 day than after 15 days of starvation; however, the 7 day treatment presented the lowest failure frequency in the crickets. The previous description with larvae pattern made the interaction of hunger and prey type significant.

Mean movement speed of the spiders.—Mean speed of the spiders during the interaction with the prey provided (from latency to the jump) did not differ among the three hunger levels or among prey types. There was also no effect of the interaction between these two factors (Table 3). The overall mean speed was 13.31 ± 2.59 cm/min.

Predation phases.—Based on the AIC value, the error distribution that best fitted latency was exponential. According

Table 2.—Result of a generalized linear model of number of prey capture failures of *C. albicincta* as a function of prey type (P) and hunger level (H). % = percentage of variation explained by each term of the model.

	df	Deviance (χ^2)	*P*	%
Hunger (H)	2	10.310	0.005	5.336
Prey (P)	2	52.757	<0.0001	27.305
H × P	4	10.092	0.038	5.223
Error	81	120.05		62.134

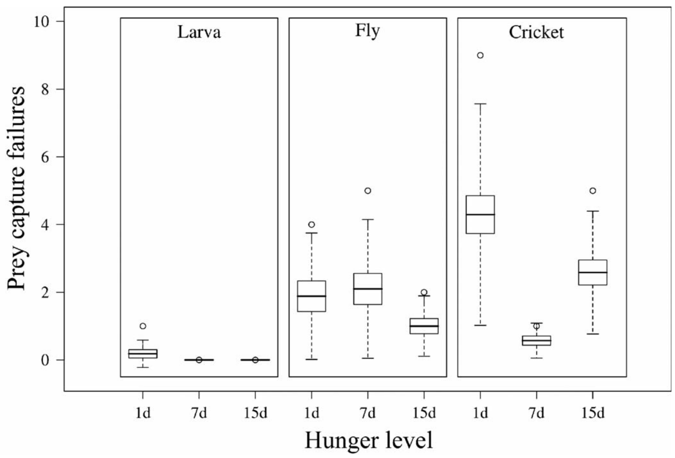

Figure 3.—Average number of failures to capture prey by *Corythalia albicincta* with prey type and different hunger levels. Horizontal lines represent mean distances, the top and bottom of each box represent one standard error, the whiskers represent one standard deviation and the white circles represent the maximum in each treatment.

to the regression failure time model, we observed that the probability of failing to detect prey within a given time differed according to prey type, but not for the three levels of hunger (Table 4). The probability of failure to detect a cricket was the same as the probability of failure to detect a fly (z = 1.433, P = 0.152) and declined rapidly from the start until, at approximately 200 s, the probability was 0.066. The probability of failing to detect a cricket was significantly lower than that of failing to detect a larva (z = 5.547, $P < 0.001$, Fig. 4a).

Time spent in the attention phase fitted a log-normal error distribution. The probability of a spider remaining in the attention phase differed according to prey type (Table 4), but not for level of hunger. The probability of not approaching the crickets was the same as the probability of not approaching the flies (z = 1.329, P = 0.184) and declined abruptly from the first to the fifth second, then reduced more slowly until 14 s, where the probability remained almost constant at 0.133. However, the probability of not approaching the larvae differed from that of not approaching the crickets (z = 1.747, P = 0.008) and declined less rapidly from the first to the third second before declining gradually until maintaining a constant value of 0.033 after 25 s (Fig. 4b).

Prey type explained most of the variability in orientation time, while hunger level had no significant effect (Table 4).

According to the AIC value, the Weibull distribution best fitted the error distribution in the approach phase. The probability of remaining in the approach phase was the same for all three prey types and for the three levels of hunger (Table 4) and decreased rapidly from the first to the third second before steadily declining until the 43rd second.

Table 3.—Factorial ANOVA of spider movement speed as a function of prey type (P) and hunger level (H). % = percentage of variation explained by each term of the model.

	df	SS	*F*	*P*	%
Prey (P)	1	8.5	0.060	0.806	0.106
Hunger (H)	2	75.5	0.269	0.764	0.950
P × H	2	309.4	1.106	0.338	3.894
Error	54	7551.0			95.050
Total	59	7944.2			

Table 4.—Result of survival analysis for each predation stage (latency, orientation, approach, pursuit, and crouching) and the complete interaction (total interaction time) of *C. albicincta* and the percentage of variation explained by each term of the statistical model (%).

	df	χ^2	*P*	%
LATENCY				
Hunger (H)	2	2.316	0.314	0.212
Prey (P)	2	57.215	<0.0001	5.260
H × P	4	2.698	0.061	0.248
Error	81	1025.469		94.278
Total	89	1087.700		
ORIENTATION				
Hunger (H)	2	0.186	0.911	0.035
Prey (P)	2	9.046	0.011	1.714
H × P	4	3.659	0.454	0.693
Error	80	514.857		97.557
Total	88	527.749		
APPROACH				
Hunger (H)	2	0.208	0.901	0.063
Prey (P)	2	4.540	0.103	1.386
H × P	4	1.240	0.871	0.378
Error	80	321.425		98.170
Total	88	327.414		
PURSUIT				
Hunger (H)	2	0.198	0.905	0.037
Prey (P)	2	0.525	0.769	0.098
H × P	4	0.358	0.985	0.066
Error	80	534.676		99.798
Total	88	535.758		
CROUCHING				
Hunger (H)	2	1.424	0.490	0.294
Prey (P)	2	9.707	0.008	2.007
H × P	4	2.400	0.662	0.496
Error	80	469.923		97.2
Total	88	483.456		
TOTAL INTERACTION TIME				
Hunger (H)	2	0.449	0.798	0.058
Prey (P)	2	25.115	<0.0001	3.294
H × P	4	4.069	0.396	0.533
Error	80	732.614		96.112
Total	88	762.248		

For the pursuit phase, the AFT model with logistic distribution was used. We found that the probabilities of pursuing a prey and not crouching were the same, regardless of prey type.

The spiders presented the same probabilities of remaining in the pursuit phase within a given period of time, regardless of hunger level. As with the approach phase, no variable had a significant effect on the time spent in pursuit (Table 4).

In the crouching phase, the Weibull distribution error was used with significantly different probabilities of not capturing prey, depending on prey type; the same probability of capture existed when attacking larvae and crickets (z = 0.415, P = 0.678). In this case, the probability declined abruptly until 17 s

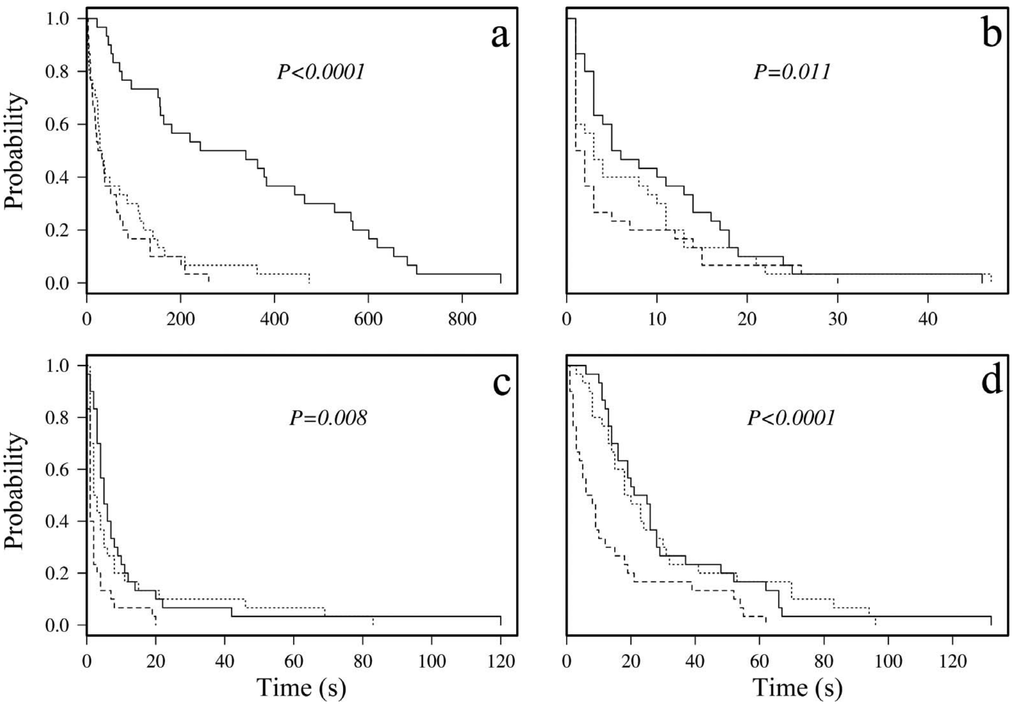

Figure 4.—Survival analysis curves for predation stages in *Corythalia albicincta* when capturing larva (continuous line), cricket (dotted line), and fly (dashed line); (a) location of prey (latency), (b) orientation phase, (c) crouching phase, and (d) the entire interaction.

and remained constant after 20 s, with a value of 0.1. In contrast, the probability of not capturing the flies declines abruptly until 8 s, with a value of 0.066, and differed significantly from the probability of capturing crickets (z = 2.666, P = 0.008; Fig. 4c).

For each hunger level, the probability of not capturing a prey item within a given time was the same among prey treatments. Prey type explained 9.7% of the variability in the duration of attack time (Table 4).

Total time of interaction with larvae was the same as with crickets (z = 0.595, P = 0.552). It declined rapidly until 30 s, but then decreased more steadily until 68 s. This differed from the probability that the spider continued in interaction with the flies (z = 4.335, $P < 0.0001$), dropping abruptly for 20 s and then declining constantly until 55 s, where the probability value was 0.033 (Fig. 4d).

Total time of interaction did not differ with hunger level, and the variability in total interaction time was best explained by prey type (Table 4).

Total interaction time, analyzed with an AFT of log-normal distribution, differed according to prey type. Total interaction time between spiders and flies was 14.6 ± 3.33 s, whereas the interaction times with the larvae and crickets were 30.41 ± 4.28 s and 29.73 ± 4.88 s, respectively. Figure 5 shows the proportions of the predation phases relative to total interaction time, excluding latency. The orientation, approach, and attack phases each varied between 25 and 34% with larvae and crickets. In contrast, in the fly treatment, the spiders spent more time in the orientation stage (43.8%) than in the other stages. Time spent in pursuit was very short in the interaction with all three prey types (9.52% crickets, 2.85% larvae, and 3.5% flies; see Fig. 5).

DISCUSSION

Jumping distance.—Forster (1977) found that the majority of successful jumps against flies (89%) were performed between 2.1 and 5 mm from the prey; the mean capture jump was 4.2 mm, which represents 2.5 times the spider's body length (1.75 mm). This proportion of jump distance is similar to that observed in *Corythalia albicincta,* which jumps 2.47 times its body length (excluding jumps for larvae), with a mean jump distance of 12.35 mm and body length of 5 mm.

The spiders adopted a longer jumping distance with high escape risk prey (flies and crickets) and a shorter jumping distance with the low escape risk prey. Edwards & Jackson (1993) found that seven species of *Phidippus* jump a greater distance to capture flies than when capturing loopers, and that the low efficiency of *P. pulcherrimus* Keyserling 1885 could be due to the fact that its jumping distance is the shortest among the *Phidippus* species, giving prey an opportunity to detect the spider and escape. This may indicate that the spiders modify

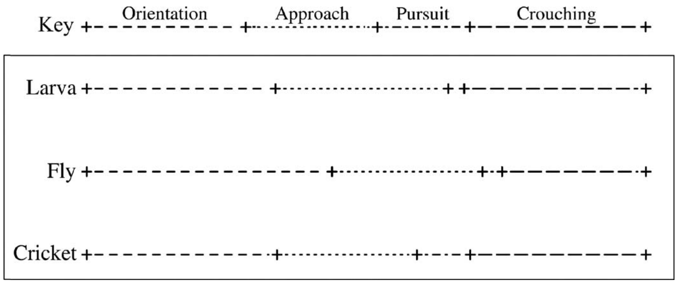

Figure 5.—Proportion of each predation stage of *Corythalia albicincta* relative to total interaction time for each prey type. To increase the detail of hunting behavior, latency is not included.

their jumping distance according to the capacity of the prey to escape. Edwards & Jackson (1994) also observed that jumping distance in *Phidippus regius* C. L. Koch 1846 was greater with prey of high escape risk, while Bartos (2002) found the same results with the attacking distances of *Yllenus arenarius* Menge 1868.

Despite the fact that the crickets and flies present different movement patterns, both are of comparable overall speed and have the same probability of escape (Fig. 2). The difference in jumping distance observed between these prey types may be due to differences in their size. Bartos (2002) explained that spiders perform longer jumps to capture larger prey than they do for smaller prey, even when the capacity to escape is equal in both prey types (Lepidoptera larvae and Thysanoptera, in this case). Edwards & Jackson (1994) did not find these differences in jumping distance related to prey size, but attribute these observations to the fact that, with certain large prey, the spiders attacked from a short distance but outside the field of vision of the prey. Another variable that can influence this difference in jumping distance is that flies remain immobile for much of the time but when they do move, they either do so over short distances or by flying long distances in a short time; conversely, crickets move constantly, albeit at a slower pace than flies. Given the fact that flies spend more time immobile, spiders have a greater probability of getting close to the optimum distance for capture before the fly can escape. With crickets, however, adjustment of jumping distance is more difficult because of their constant movement, and therefore the spider is more likely to attack even when the cricket is beyond the optimum distance. This is supported by the fact that shorter jumping distances imply higher probabilities of capturing prey because the attack becomes more accurate with reduced distance between spider and prey. Bartos (2002) explained that spiders may be capable of evaluating the risk of the prey escaping and the distance of the jump. That is, there is a trade-off between distance and energy cost: short jumps imply low energy cost and a more precise attack, but a higher probability for the prey to escape if it detects the spider prior to the attack.

Jumping distance was found to be unaffected by hunger level. Similar results were found by Edwards & Jackson (1994): young *Phidippus regius* individuals of different hunger levels (starvation periods of 10, 12, 14, and 21 days) attacked prey from similar distances. However, knowing that spider behavior can change only with very long periods of starvation, because they have physiological adaptations to limited feeding opportunities and starvation (Persons 1999), it is possible that even 15 days of starvation is insufficient time to lower the spider's condition. Bartos (2002) thus observed a negative relationship between spider hunger level and jumping distance. This author used recently field-captured spiders in which the only indicator of hunger level was the relative size of the abdomen (smaller abdomen indicating a higher level of hunger) and, in all likelihood, featuring spiders with more than 15 days of starvation. Nevertheless the defined starvation periods of our study enabled us to make more accurate inferences regarding the relationship between spider hunger level and predation behavior.

Failure to capture prey.—In general, there were fewer failures to capture prey with the spiders that had been starved for 7 and 15 days (0.65), than for those that had been starved for just 1 day (1.23). Edwards & Jackson (1994) found that 73.3% *of Phidippus regius* spiderlings successfully captured prey 10 days after leaving the cocoon, while 66.6% were successful after 12 days, and 94.1% were successful after 14 days. This increase in the number of successful captures shows a certain relationship with spider hunger level, although this can be masked by the fact that spiderlings at 10 and 12 days are in a dispersion phase and spiders at 14 days are more prone to capture prey. There are a limited number of studies relating to hunger and capture success; for example, Wells & Bekoff (1982) found that coyotes are more efficient at capturing prey with increasing hunger. This may suggest that when the spiders are not very hungry, loss of prey does not imply a serious risk. On the other hand, as hunger increases, the necessity to feed becomes more important and a higher probability of success in prey capture is therefore required.

In the current study, a prey with low escape risk (such as a larva) is easier to capture than a fly or a cricket. With flies, spiders failed to capture at 1 and 7 days of starvation but became more efficient after 15 days of starvation; consequently, we infer that spiders are more accurate in capturing their prey, as discussed above in the general interpretation. Against crickets, spiders with 1 day of starvation were the least efficient at capturing prey and the pattern from 1 to 7 days of starvation is the same as against flies and larvae; however, the increase of failures after 15 days of starvation can be explained by the fact that crickets are more difficult to capture. According to Persons (1999), spiders may be able to cope with low energy levels when capturing larvae and flies, but this condition renders them unable to capture crickets as efficiently as other prey.

Edwards & Jackson (1994) observed a relationship between capture success and prey type; spiderlings failed more frequently when they attacked flies (only 41% of spiders captured flies at the first attempt) than when they attacked larvae (81% of spiders captured lepidopteran larvae at the first attempt). Forster (1977) found that 54% of the spiders that tried to capture flies (*Drosophila melanogaster*) were successful. We found similar results, since the spiders failed more often to capture crickets and flies than larvae, and they failed more with crickets after 15 days of starvation than with flies and larvae.

Contradictory results were found by Givens (1978); this author observed that both male and female spiders fail more when attempting to capture adult beetles than beetle larvae (*Dermestes tardarius*), but both were more difficult to capture than flies. Spiders gave up trying to capture beetles after the first attempt but often successfully captured flies after the first attempt: female spiders were more persistent than males. Beetle larvae appear to be more difficult to capture than fly larvae, possibly due to the effect of mechanical or chemical defense mechanisms.

In summary, *C. albicincta* used different predation strategies depending on prey characteristics (morphology and mobility); if the spiders were to attack crickets and flies in the same manner, there would probably be differences in the number of failures and thus in the probability of capturing these prey types.

Duration of predation behavior stages.—Regarding latency to orientation towards the prey, the increased time spent by spiders finding larvae than crickets or flies may be due to the fact that larvae present very low mobility: jumping spiders are more likely to be attracted by fast movements (Edwards & Jackson 1994) and immobile prey do not elicit hunting behavior in spiders (Forster 1977). Moreover, the larvae were also camouflaged against the light colored container walls. Pekár (2004) found that latencies did not vary with prey type in zodariid spiders (*Zodarion rubidum* Simon 1914 and *Zodarion germanicum* C. L. Koch 1837); however, in this study, latency was quantified by measuring the time from the start of the experiment to the moment of capture, which makes any comparison with our results very difficult.

The duration of the predation behavior stages of *C. albicincta* differed in each of the three prey types, as did the total duration of the interactions and the proportions of certain stages relative to the total time. Spiders invested a similar amount of time identifying, approaching and capturing larvae, but *C. albicincta* took longer to identify larvae than other prey. This is due to the characteristics of the larvae (size, mobility and coloration). A short time was expected for capturing this type of prey but it was observed that, even at identification stage, the spiders take some time to recognize the larvae as prey. In relation to this, Forster (1977) suggested the possibility of two different phases to the identification of prey; one in the orientation stage and the other in the pursuit to crouching stages. With crickets, spiders invested the same amount of time in orientation, approach and attack stages, which may be due to the fact that the movement of the crickets is almost constant and only varies in terms of the direction of movement, conferring uniformity to the duration of the predation stages. However, the process of orientation took more time than the other predation stages (34% of total interaction time), perhaps because crickets move too much and it is consequently difficult for the spider to initiate the approach stage. With flies, most of the interaction is invested in the orientation phase (43% of total interaction time), possibly because flies remain immobile for much of the time, making detection difficult. However, once the prey is identified, it is approached and attacked in half the time spent in the orientation phase. Additionally, less time was spent in the crouching phase with the fly than with crickets and larvae. Flies accounted for the lowest total predation time of all three prey types, while the total interaction time of crickets and larvae was equal; this is similar to that found by Edwards & Jackson (1994), who stated that flies were captured more quickly than loopers. Dill (1975) found that spiders tend to stalk prey when they are small and of low mobility, while Forster (1977) observed that, depending on the velocity of the fly, spiders can accomplish the pursuit stage by running, walking or stalking. However, Pekár (2004) found that capture times were equal for different prey types. The explanation for this discrepancy may be that Pekár considered capture time to encompass all of the predation stages, but also latency to orientation. Latency is very temporally variable and, out of the predation time, this could affect the variance of the total interaction time with the capture time masked by the latency.

None of the predation stage durations differed among the three starvation treatments. Gardner (1964) recorded probabilities to perform the predation stages of orientation, pursuit, crouching and jumping and observed that sequences of behavior in spiders did not change with hunger level. This means that predation strategy is not modified by hunger; however, the reduced number of failed captures observed in the spiders that were starved for a longer period could be due to the fact that the spiders are more cautious hunters when they are hungry. We found that hunger does not influence the variable total interaction time. Gardner (1966) found that spiders with 7 days of starvation capture prey faster than spiders with 1 day of starvation ($n = 32$). Edwards & Jackson (1994) found that spiders with 21 days of starvation had shorter latency periods than spiders with 10, 12 and 14 days without food ($n = 10$). We think that the sample size of this study ($n = 10$) may have affected these results and significant differences among hunger treatments were therefore not found, although Edwards & Jackson (1994) utilized similar sample sizes.

As can be seen, predation strategies are generally fixed and unaltered by factors such as spider hunger level. Edwards & Jackson (1994) demonstrated that predation strategies are not learned but innate in the spiders; however, they claim that capture efficiency depends directly upon experience. In terms of efficiency, it benefits the spider to maintain a specific predation strategy, even though it may be very hungry, since it represents the strategy with the highest probability of a successful capture. Theoretically, we could speculate that if the spider were to modify its predation strategy, e.g., by approaching and attacking the prey in a very short time or by trying to capture a fly without crouching, the probability of a successful attack would diminish, with the subsequent risk that the spider would fail to obtain any food. Our findings support the idea that predatory strategies are specific for each prey type but remain unaltered by hunger level.

In this study, we used duration of the predatory stages to define and characterize predatory strategies. While this is a different method from that used in previous works, we consider that analyzing the duration of hunting stages allows us to relate predatory behavior and hunger level, considering that time is related to the energy expenditure of an organism (Givens 1978, Ydenberg et al. 2007).

In conclusion, we observed that (1) *C. albicincta* employs different predation strategies depending on a particular prey type, (2) the spiders fail to capture prey less frequently with increasing hunger, and (3) spider hunger level does not influence predation strategy.

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