

Scavenging throughout the life cycle of the jumping spider, *Phidippus audax* (Hentz) (Araneae: Salticidae)

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Abstract. *Phidippus audax* (Hentz 1845), a common North American jumping spider, is a visual predator that uses its highly developed eyesight to detect and forage actively for prey. We demonstrate that *P. audax* can survive throughout its life cycle as a scavenger. We separated 600 spiderlings into eight treatments examining all combinations of three different variables: live versus dead prey, substrate present versus substrate absent, and large versus small arenas. Over the course of the study, we recorded survival rates, instar durations, and carapace widths. Our results indicate that *P. audax* can survive solely on a diet of dead prey, but at significantly lower survival rates and with longer instar durations than spiders fed on live prey. Scavenging spiders, however, exhibited no significant difference in carapace widths when compared to predators. Choice tests conducted on adults indicate that spiders raised as either predators or scavengers exhibit no significant differences in prey choice when given the option of live or dead prey.

Keywords: Dead prey, mortality, habitat complexity, development

Jumping spiders (Salticidae) are active predators that feed on a wide variety of prey. Their enlarged anterior-median eyes and secondary eyes provide them with heightened sensitivity to visual stimuli (Land 1971). Individuals first orient toward prey, then stalk or actively chase it to within a few centimeters, and then attempt a strike (Forster 1982a; Foelix 1996). Active predation is the strategy most widely studied in salticids (Givens 1978; Hill 1979; Forster 1982a; Freed 1984; Nyffeler et al. 1990; Richman & Jackson 1992; Jackson & Pollard 1996), however, alternative types of feeding behaviors do occur in this family. These alternative behaviors include araneophagy (Harland & Jackson 2000; Jackson 2000; Rienks 2000; Jackson et al. 2002; Penney & Gabriel 2009), herbivory (Meehan et al. 2009), indirect vertebrate blood feeding (Jackson et al. 2005), myrmecophagy (Jackson et al. 1998; Clark et al. 2000), nectivory (Ruhren & Handel 1999; Jackson et al. 2001), and prey stealing (Jackson et al. 2008). Our study focuses on scavenging in the salticid *Phidippus audax* (Hentz 1845).

Scavenging by spiders is not widely reported in the field; however, it has been demonstrated in the laboratory. For example, wolf spiders (Lycosidae) preferentially feed on aged, dead prey items over live prey when given the choice (Knost & Rovner 1975). Female *Theridion evexum* Keyserling 1884 (Theridiidae) collect and store dead prey in their webs, and when spiderlings emerge, they feed upon both old and newly acquired dead prey items (Barrantes & Weng 2008). The brown recluse spider, *Loxosceles reclusa* Gertsch & Mulaik 1940 (Sicariidae), also feeds on dead prey items (Sandidge 2003; Cramer 2008; Vetter 2011).

Scavenging in jumping spiders has also been demonstrated. Wolff (1986) starved 13 adult *Salticus scenicus* (Clerck 1757) females for five days and then presented them with dead house flies as prey. House flies given to starved spiders had significantly lower post-trial weights than house flies given to well-fed spiders, indicating that the starved spiders fed on the dipteran prey. Although Wolff (1986) demonstrated that starved salticids have the potential to feed on dead prey,

scavenging has never been demonstrated throughout the life cycle of any spider species. We examined scavenging in a jumping spider, *P. audax*, to determine if a highly visually-oriented predator could survive solely on dead prey throughout its life cycle.

In the present study we examined three possible variables: prey type, habitat complexity (presence or absence of substrate), and arena size. We predicted that spiders raised as scavengers would have lower survival rates than predators due to the lack of visual cues provided by dead prey. As a corollary, we hypothesized that scavengers would exhibit longer instar durations and smaller carapace widths than predators due to reduced prey consumption. We predicted that the addition of substrate and increased arena size would further hinder scavengers' ability to detect dead prey and thus further reduce their survival rate. Because the combination of added substrate and increased foraging area better reproduces the spiders' natural environment, adjusting these conditions enabled us to test the prospect of scavenging in the field, and the effects that changes within an environment might have on scavengers.

METHODS

We collected eleven gravid female jumping spiders, *P. audax*, from the Rock Springs Center for Environmental Discovery in Macon Co., Decatur, IL USA (39.817713° N, 89.00932° W) in the spring of 1998. We housed each gravid female individually in a petri dish (15 cm diameter × 1.5 cm height) until oviposition. Eight females successfully oviposited in the lab. We removed 600 spiderlings (mean = 75, SE = 14.87, range = 6–104) and housed each in a separate petri dish (10 cm diameter × 1.5 cm height) until spiderlings were randomly separated into groups.

We randomly separated the 600 spiderlings into eight groups of 75 with the following treatments: live versus dead prey, large (15 cm × 1.5 cm) versus small (10 cm × 1.5 cm) arena size, and substrate present (10 g of peat moss in large arenas and 4.5 g of peat moss in small arenas) versus substrate absent.

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Table 1.—Feeding regime for *Phidippus audax* in instars 2–8. Note that instar 1 is spent within the egg sac.

| Instar | No. of prey introduced | Prey species |
|--------|------------------------|--------------------------------|
| 2 | 2 | <i>Drosophila melanogaster</i> |
| 3 | 4 | <i>D. melanogaster</i> |
| 4 | 6 | <i>D. melanogaster</i> |
| 5 | 1 | <i>Musca domestica</i> |
| 6 | 2 | <i>M. domestica</i> |
| 7–8 | 3 | <i>M. domestica</i> |

Spiders were kept at room temperature under a 12:12 photoperiod regime. We fed spiders three times per week, removed uneaten prey, and supplied fresh water via soaked cotton balls. We introduced prey at an approximate distance of 13 cm from the spider in large arenas and 8 cm away in small arenas. For prey, we used fruit flies, *Drosophila melanogaster*, or house flies, *Musca domestica*, depending on spider instar (Table 1). For scavenging treatments, we killed prey immediately prior to feeding. We lightly crushed fruit flies, and we killed house flies by applying pressure to the prothorax with forceps. We used organic, sphagnum peat moss as a substrate to simulate a more natural environment. The peat moss was kept dry during the course of the study and not replaced.

Throughout the life cycle of each spider, we recorded the date of every molt and the date of death when applicable. At the end of each instar, we removed exuviae and preserved them in 80% ethanol for later measurement of carapace widths. Carapace widths were recorded using a Meiji microscope fitted with an ocular micrometer. Five of the spiders were removed from the study because of unrecorded molt dates. Voucher specimens were deposited in the Millikin University Arthropod Collection.

When spiders reached maturity, we conducted a choice test to determine which prey type (live versus dead house fly) spiders would select. For these choice tests, we introduced two prey items simultaneously ≥ 7.0 cm in front of the spiders' cephalothorax in a large (15 cm \times 1.5 cm) arena. We ran choice tests for approximately 20 min or until capture, and then recorded prey choice. We tested a total of 226 spiders: 144 raised as predators and 82 raised as scavengers.

Statistical analysis.—To determine the effects of scavenging on *P. audax*, we recorded survival rates, instar durations and carapace widths throughout their development, and choice of live versus dead prey as adults. To isolate differences arising from each of the 3 environmental variables (prey type,

presence or absence of substrate, and arena size), we used a Cox Regression survival analysis with survival (yes or no) as the dependent variable and prey type (live or dead), substrate (yes or no), arena size (large or small), their three-way interaction and their two-way interactions as independent predictor variables.

To determine the effects of the prey type, substrate, and arena size on instar duration, we completed a General Linear Mixed Model (LMM) with instar duration as the dependent variable and instar, prey type, substrate type, arena size, and all two-way and three-way interactions as independent variables. Spider identity was included as a random variable.

Choice test results were analyzed within each group, predators and scavengers, using the chi-square goodness-of-fit test against a null expectation of 50:50. In addition, we used a chi-square contingency test to determine whether the proportion of predators that chose live prey differed from the proportion of scavengers that preferred live prey. In all cases, *P*-values of less than 0.05 were considered statistically significant.

RESULTS

Of the initial sample of 600 spiderlings, we successfully raised a total of 226 *P. audax* to maturity, with 144 raised as predators on live prey and 82 as scavengers on dead prey (Table 2; Fig. 1).

Survival.—There was a statistically significant three-way interaction among prey type, substrate type, and arena size with regards to survival ($\beta = 0.951$, Wald $\chi^2 = 4.714$, *df* = 1, (exp) $\beta = 0.386$, *P* = 0.030). The β is the logistic coefficient for each predictor variable (i.e. arena size, substrate type, or prey type) and represents the expected amount of change in survival when changing from one condition to the other within the predictor. The Wald test (and accompanying *P*-value) is useful in evaluating whether or not the logistic coefficient (β) is different from zero. Finally, the (exp) β represents the instantaneous relative risk of death, at any time, for a spider with one treatment for one variable compared with an individual with the other treatment for that variable. To gain an understanding of the nature of the interaction, we ran separate Cox Regression analyses within each of the two arena sizes.

Within the small arenas, differences in survival between spiders fed different prey types were dependent upon substrate type (two-way interaction of prey type and substrate type; $\beta = -1.173$, Wald $\chi^2 = 15.527$, *df* = 1, (exp) $\beta = 0.310$, *P* < 0.001). Because of the significant interaction term within small

Table 2.—Total number of *Phidippus audax* assigned to each treatment, total number of spiders raised to maturity, and percent survival in each of the eight treatments.

| Prey type | Substrate type | Arena size | #Assigned to treatment | #Raised to maturity | % survival |
|-----------|----------------|------------|------------------------|---------------------|------------|
| Live | Empty | Large | 75 | 43 | 57 |
| Live | Empty | Small | 75 | 34 | 45 |
| Live | Substrate | Large | 75 | 32 | 42 |
| Live | Substrate | Small | 75 | 35 | 46 |
| Dead | Empty | Large | 75 | 28 | 37 |
| Dead | Empty | Small | 75 | 42 | 56 |
| Dead | Substrate | Large | 75 | 2 | 0.02 |
| Dead | Substrate | Small | 75 | 10 | 13 |

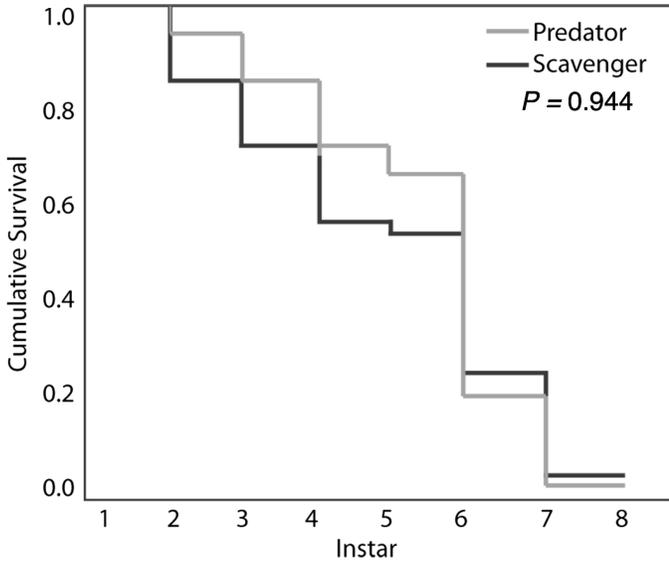


Figure 1.—Survival curve based on Cox Regression for *Phidippus audax* raised on live prey (predator) or dead prey (scavenger). There was no significant main effect of prey type on survival ($P = 0.944$).

arenas, we ran a separate Cox Regression within small arenas with substrate and small arenas without substrate. Within small arenas with no substrate, there was greater survival to subsequent instars with dead prey ($\beta = 0.578$, Wald $\chi^2 = 8.36$,

$df = 1$, $P = 0.004$, (exp) $\beta = 1.783$; Fig. 2a). Conversely, within small arenas with substrate, there was greater survival to subsequent instars with live prey ($\beta = -0.564$, Wald $\chi^2 = 6.320$, $df = 1$, $P = 0.012$, (exp) $\beta = 0.569$; Fig. 2b).

Within the large arenas, differences in survival on different prey types were dependent upon substrate type (two-way interaction of prey type and substrate type; $\beta = 1.797$, Wald $\chi^2 = 28.077$, $df = 1$, (exp) $\beta = 6.032$, $P < 0.001$). Because of the significant interaction term within large arenas, we ran a separate Cox Regression within large arenas with substrate and large arenas without substrate. Within large arenas with no substrate, there was no significant difference in survival between spiders with live prey or dead prey ($\beta = 0.231$, Wald $\chi^2 = 1.285$, $df = 1$, $P = 0.257$, (exp) $\beta = 1.260$; Fig. 2c). Within large arenas with substrate, however, there was greater survival to subsequent instars among spiders with live prey ($\beta = -1.736$, Wald $\chi^2 = 34.916$, $df = 1$, $P < 0.001$, (exp) $\beta = 0.176$; Fig. 2d).

Sex comparisons in mature predators and scavengers: Of the 595 spiderlings used in this study, 117 males and 99 females successfully reached maturity. However, adding the variable ‘sex’ resulted in poorer models in all cases, and there was no difference in survival between males and females in the presence of the other three variables ($P > 0.198$ in all cases).

Instar duration.—There were significant three-way interactions of instar, prey type, and substrate type ($F_{1,1595} = 13.682$, $P < 0.001$; Table 3) and instar, prey type, and arena size

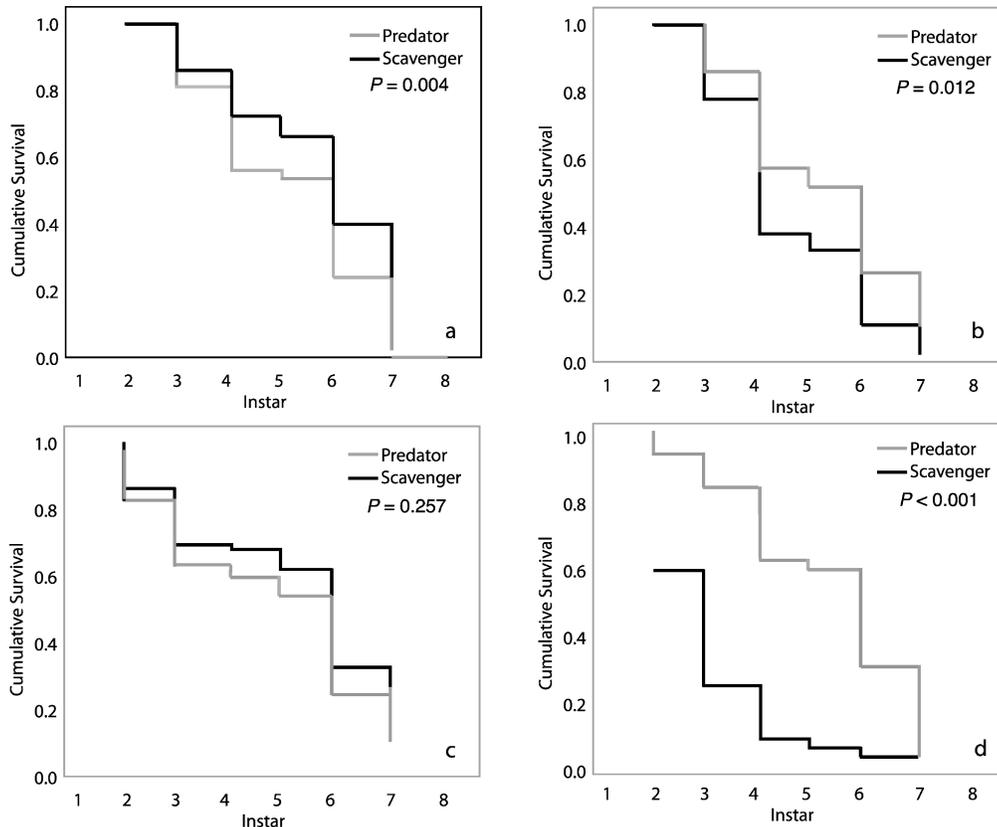


Figure 2a–d.—Differences in survival for *Phidippus audax* raised on live prey (predator) or dead prey (scavenger) in a) small arenas without substrate ($P = 0.004$); b) small arenas with substrate ($P = 0.012$); c) large arenas without substrate ($P = 0.257$); and d) large arenas with substrate ($P < 0.001$).

Table 3.—Results from a General Linear Mixed Model with instar duration as the dependent variable and spider identity as a random variable. Random variable (Spider ID): Wald $Z = 28.249$, $P < 0.001$ (retained in all models).

| Variable | <i>df</i> | <i>F</i> | <i>P</i> |
|-------------------|-----------|----------|----------|
| Instar | 5, 1595 | 148.863 | <0.001 |
| Prey type | 1, 1595 | 81.492 | <0.001 |
| Habitat | 1, 1595 | 45.681 | <0.001 |
| Arena size | 1, 1595 | 4.351 | 0.178 |
| Instar*Prey | 5, 1595 | 18.913 | <0.001 |
| Instar*Habitat | 5, 1595 | 3.835 | 0.137 |
| Instar*Arena | 5, 1595 | 1.083 | 0.247 |
| Prey*Habitat | 1, 1595 | 53.919 | <0.001 |
| Prey*Arena | 1, 1595 | 2.352 | 0.577 |
| Habitat*Arena | 5, 1595 | 6.799 | 0.146 |
| Instar*Prey*Hab | 1, 1595 | 13.682 | <0.001 |
| Prey*Hab*Arena | 5, 1595 | 0.149 | 0.7 |
| Instar*Prey*Arena | 5, 1595 | 6.006 | <0.001 |

($F_{5,1595} = 6.006$, $P < 0.001$; Table 3). The significant three-way interactions of instar and prey type with substrate type and arena size indicate that instar duration is dependent upon multiple variables; therefore, to determine the nature of the interactions, we used subsequent LMM's to analyze the effects of instar and prey type as well as the two-way interactions of instar and prey type within each of the possible combinations of arena size and substrate type. The random variable, spider identity, was also significant (Wald $Z = 28.249$, $P < 0.001$), therefore, it was used in all subsequent analyses.

Within small arenas and no substrate, there was a significant interaction between instar and prey type ($F_{5,511} = 6.473$, $P < 0.001$); therefore, we ran a separate LMM within those with dead prey and found a significant difference in instar duration among instars with a general pattern of increasing instar duration from instar 2 (14.94 days) to instar 7 (63.95 days; Fig. 3a). The second LMM, within live prey, revealed a similar pattern, with an increase in instar duration from instar 2 (12.46 days) to instar 6 (52.6 days), however, instar 7 was slightly lower than instar 6 (51.7) creating the significant interaction term. In general, instar duration is shorter with spiders given live prey within small arenas and no substrate (Fig. 3a).

Within small arenas with substrate, there was again a significant interaction between instar and prey type, and a subsequent LMM within spiders given dead prey revealed a significant difference in instar duration among instars, with a general pattern of an increase in instar duration from instar 2 (23.6 days) to instar 7 (91.5 days; Fig. 3b). Exceptions were an increase in instar duration in instar 4 to 64.59 days, followed by a decrease in duration to 52 days in both the 5th and 6th instars. The second LMM, within live prey, again showed a general increase in instar duration from instar 2 (13.8 days) to instar 7 (47.15 days; Fig. 3b). The interaction term, then, is a product of the increase in instar duration to 64.59 days in the dead prey group's 4th instar. Again, overall, spiders given live prey had shorter instar durations than those given dead prey within small arenas with substrate (Fig. 3b).

Within large arenas without substrate, there was a significant interaction between instar and prey type, and a subsequent LMM within spiders given dead prey revealed

a significant increase in instar duration from instar 2 (17.46 days) to instar 4 (43.68 days). However, there was a plateau in instar duration for the subsequent instars (Fig. 3c). From an LMM within spiders given live prey, we found a significant increase in instar duration from instar 2 (11.2 days) to instar 7 (51.85 days). Again, spiders given live prey, in general, had shorter instar durations than those given dead prey (Fig. 3c).

Within large arenas with substrate, there was another significant interaction between instar and prey type. Therefore, we ran a separate LMM within spiders with dead prey and found a significant increase from instar 2 (17.34 days) to instars 4 and 5 (89.25 days and 76.5 days, respectively). Only one spider in this group survived to instar 6 (instar duration of 37 days) and no spiders in this group survived to instar 7. From the second LMM within spiders given live prey, there was a significant increase from instar 2 (14.76 days) to instar 7 (70.64 days; Fig. 3d). Again, overall, spiders given live prey consistently had shorter instar durations than those given dead prey (Fig. 3d).

Sex comparisons: We initially used a LMM that included sex as an independent variable, but there was no significant interaction between other independent variables and sex ($P > 0.114$ in all instars) nor was there a significant difference between males and females with regards to instar duration ($P > 0.182$). Given the low percentage of spiders surviving to an instar where sex could be determined and that there were no significant interactions or main effects of sex, adding sex to the LMM substantially reduced the power of the analysis. Therefore, sex was not included in the final analyses of the differences in instar durations.

Carapace widths.—Overall, as spiders matured, carapace widths were not significantly different among the eight treatments in any of the instars ($P > 0.05$ in all cases).

Choice tests.—Whether raised as predators or scavengers, spider choice of prey type differed from random (i.e., 50:50). Among predators, 117 chose live prey, while 27 chose dead prey ($\chi^2 = 56.25$, $df = 1$, $P < 0.001$). Among scavengers, 62 chose live prey, while 20 chose dead prey ($\chi^2 = 38.03$, $df = 1$, $P < 0.001$). There was no significant difference in the proportion of predators (117/144) and scavengers (62/82) that preferred live prey ($\chi^2 = 0.283$, $df = 1$, $P = 0.595$).

DISCUSSION

Spiders can survive on dead prey alone but face costs, such as lower survival rates and longer instar durations. Additionally, the two independent variables of substrate/no substrate and large/small arenas had significant effects on scavenging spiders.

Survival.—With the addition of substrate in both small and large arenas, scavengers exhibited lower survival rates. Our results are consistent with those of previous studies. *Phidippus audax* has been observed to hunt mainly on upper, well-lit areas of vegetation, such as leaves and branches, as well as on the sides of houses and fence posts (Givens 1978; Carducci & Jakob 2000). It therefore stands to reason that the dark substrate color and the lack of visual stimuli from dead prey hindered the spiders' ability to find dead prey items and would both have a significant, negative impact on the spiders' survival rates and instar durations. This indicates a low

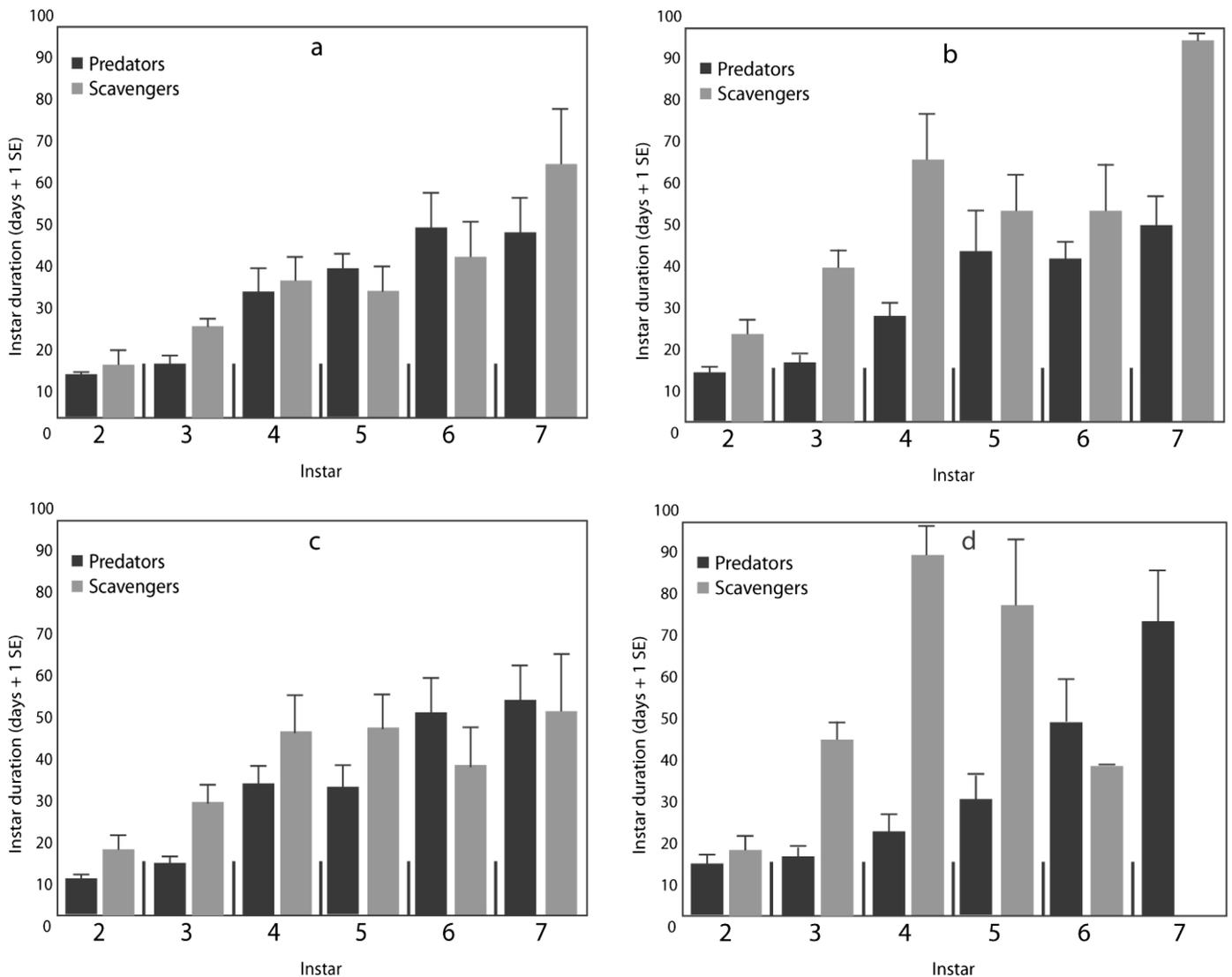


Figure 3a–d.—Differences in instar duration for *Phidippus audax* raised on live prey (predator) and dead prey (scavenger) in a) small arenas without substrate; b) small arenas with substrate; c) large arenas without substrate; and d) large arenas with substrate.

probability of successful scavenging by *P. audax* in nature, where the foraging area is substantially larger and substrate is varied and abundant. In the smaller foraging area, spiders had a greater likelihood of finding dead prey by chance.

We found an interesting exception to the trend of lower scavenger survival rates for treatments involving empty arenas. While predators and scavengers in large, empty arenas had statistically similar survival rates, scavengers had significantly greater survival to subsequent instars than predators in small, empty arenas. These results are somewhat counterintuitive, but a possible explanation is that scavenger *P. audax*, within a smaller foraging area, could have encountered and began feeding upon dead prey items more quickly than predator *P. audax* could capture and begin feeding on live prey. In accord with our results, when predatory waterbugs *Microvelia macgregori* Kirkaldy (Hemiptera: Veliidae) held in water-filled arenas, were given dead prey items, *D. melanogaster*, the waterbugs began feeding when they came across a dead prey item (Jackson & Walls 1998). Wolf spiders often

took dead prey as a meal if given the option, even if live prey items were present (Knost & Rovner 1975). The jumping spider, *Trite planiceps* Simon 1899 fed on freshly killed squashed flies, if left overnight in their arenas (Forster 1982b). In the latter case as well as in our study, the scavenging spiders may have detected minor residual movements from the freshly killed flies that prompted them to attack and feed.

Instar duration.—On average, scavengers had longer instar durations. Scavengers raised in substrate-filled arenas, both large and small, exhibited the longest instar durations, presumably due to difficulty in finding prey. Our results are consistent with the literature. Pholcid spiders, *Holocnemus pluchei* (Scopoli 1763), developed significantly faster and often underwent fewer molts when they were given a prey diet that allowed them to reach their satiation point (Jakob & Dingle 1990). Alternatively, when prey were limited, the orb-weaving *Zygiella-x-notata* (Clerck 1757), had longer instar durations, a correspondingly longer development time, and reduced adult

weight (Mayntz et al. 2003). In addition, spiders reduce their metabolic rates during long periods of food deprivation and consequently survive longer (Anderson 1974; Greenstone & Bennett 1980), which in turn may result in longer instar durations.

Although *P. audax* are naturally active predators feeding on a wide variety of live prey, we have shown for the first time that these spiders are capable of surviving from egg sac emergence to maturity solely on a diet of dead prey, albeit with lower survival rates and longer instar durations. In addition to acquiring nutrients from the dead prey, spiders raised as scavengers may have also used metabolic defense mechanisms to survive. For example, in a time of prey shortage, spiders will exhibit a high tolerance to starvation by lowering metabolic rates and using their abdomens to store large quantities of lipids that can be used slowly until the prey shortage ends (Anderson 1974; Greenstone & Bennett 1980; Iida 2005). Further research should be conducted to better understand the types of nutrients being obtained from freshly killed or desiccated prey items. Whatever the nutrients are, our results indicate that at least some jumping spiders were able to survive by further breaking down dead prey items (Givens 1978; Cohen 1995; Foelix 1996; Morse 1998).

Carapace widths.—Overall, as spiders matured, we found that carapace widths were not significantly different among the eight treatments from instar to instar. Predators and scavengers grew comparably, regardless of their prey type. With regard to scavenging, these results may indicate that even though we reported significant differences in mortality and instar duration, individuals were able to reach average size. Correspondingly, the orb-weaver, *Zygiella x-notata*, experienced longer instar durations when prey was limited, but these prey shortages did not negatively impact growth within an instar. Additionally, spiders fed low quality prey experienced higher instar growth ratios by utilizing the longer instar durations to gain more weight (Mayntz et al. 2003). The wolf spider *Pardosa prativaga* (L. Koch 1870) experienced longer instar durations when food restricted or fed nutritionally insufficient prey items. However, when available prey was more abundant, spiders were able to catch up on any lack in growth and development (Jespersen & Toft 2003). Although the ability to stay within an instar for longer periods of time to grow to average size may be beneficial in the long run, in the short run it would make scavengers more susceptible to predators in the wild.

Choice tests.—Because spiders raised both as predators and scavengers preferred live prey as adults, *P. audax* exhibited its instinctive predatory behavior regardless of the diet on which it was raised. However, it is important to note that 47 spiders did choose dead prey. This result could simply be due – at least in part – to spiders finding and feeding on dead prey before detecting live prey. Corroborating this hypothesis, wolf spiders (Knost & Rovner 1975) and jumping spiders (Forster 1982b) will feed on dead prey if they happen to come into contact with it while foraging.

Our results indicate that *P. audax* can be reared as a scavenger throughout its entire life cycle, but at certain costs to the organism. Whether or not scavenging occurs in the field is largely unknown. Much of the research conducted on scavenging has been carried out in a controlled laboratory setting (Knost & Rovner 1975; Wolff 1986; Cramer 2008),

where many of the variables can be restricted to much narrower ranges than those that prevail in the natural world. Because *P. audax* is a highly visual predator that actively hunts for prey, scavenging may be a way to supplement food intake during times of prey shortage. Further research should also be conducted to determine the effects of a multi-prey diet on scavenging as an alternative feeding strategy.

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