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Growth and nest hole size preferences in immature southern house spiders (Araneae: Filistatidae): Are they constrained consumers?

James E. Carrel

Over the course of 5 decades of studying arachnids, I have been consistently impressed by the abundance and beauty of the circular webs of southern house spiders, *Kukulcania hibernalis* (Hentz 1842) (Araneae: Filistatidae) that adorn walls, doors, eaves, and other exterior surfaces of most buildings at the Archbold Biological Station in south-central Florida. Until voracious brown anoles (*Anolis sagrei* Duméril and Bibron, 1837; Squamata: Polychrotidae) became commonplace in the late 20th century (http://myfwc.com/wildlifehabitats/nonnatives/reptiles/brown-anole/), I could easily see hundreds of flat, 3–40 cm wide webs every night year round in an hour of searching with a flashlight (Fig. 1). *Kukulcania hibernalis* nest in existing holes and crevices that seem to more-or-less match their size. Radiating from a silken collar inside the nest opening is a distinctive network of dozens of radial threads dotted with "wooly" silk teased by the spider to have properties of Velcro® (Comstock 1965; Gertsch 1979; Edwards & McCanless 2012). Spiders at new sites spend several nights building webs; thereafter they add to the web and repair damage caused by entangled insects (Comstock 1965).

Because *K. hibernalis* use pre-existing holes that they modify slightly with silk, they are classified as "opportunistic secondary animal architects" (Vermeij 2010). Like hermit crabs that must protect their soft bodies by occupying empty gastropod shells (Laidre 2011; Laidre et al. 2012), southern house spiders of all ages, except adult males, must locate unoccupied holes or crevices in human-made structures for protection and for web construction. Furthermore, since they do not exhibit ballooning behavior (Bell et al. 2005), immature spiders dispersing from the maternal nest have to find suitable nest sites within several meters walking distance. This searching behavior with all of its associated risks from dehydration, predation, and parasitism probably is repeated by a spider at least a few times in a year before it reaches maturity.



Fig. 1. Photograph showing "wooly" webs of 2 small and one large *Kukulcania hibernalis* radiating from nest holes on side of a wooden barn at the Archbold Biological Station, Lake Placid, Florida. Scale bar (lower left): 5 cm.

I hypothesized that immature *K. hibernalis* might exhibit size-related preferences for holes to use as nest sites, which would provide evidence that they are "constrained consumers" in an evolutionary sense (Laidre et al. 2012). To evaluate this idea, I performed 2 studies in my laboratory. First, I determined growth patterns in immature spiders during their first 32 weeks of life. Second, I tested whether older, larger spiders show a statistically significant preference for holes of larger diameter than their smaller, younger siblings.

I collected adult female *K. hibernalis* by hand at night in Feb 2001 on walls of buildings at the Archbold Biological Station, Highlands County, Florida (N 27°11' W 81°21'). Spiders were transported to the University of Missouri and maintained individually in plastic jars (9 cm diam. × 10 cm) in the laboratory at ambient temperature (21–24 °C) with a 12:12 h L:D light cycle. Each jar contained a 10 cm long inclined stick to serve as a perch and a 1 cm^3 moistened sponge on the bottom for hydration. I fed spiders a few mealworms (Coleoptera: Tenebrionidae: *Tenebrio molitor* L.) or domestic crickets (Orthoptera: Gryllidae: *Acheta domestica* (L.)) 1–2 times weekly. Additional water was provided at feeding by misting.

Female *K. hibernalis* (n = 12) each produced one egg sac in May or Jun; embryos were allowed to develop in the maternal jar. After emergence in Jul or Aug 2001, I placed each natal jar without a lid inside a large plastic container (21 × 31 × 11 cm) to allow dispersal of ~ 100 spiderlings. The methods of Curtis & Carrel (1999) were followed to rear *K. hibernalis* siblings communally for 32 weeks. Starting at age 1 wk, I regularly fed immature spiders a mixture of wild-type, curly wing, and wingless fruit flies (*Drosophila melanogaster* (L.); Diptera: Drosophilidae).

GROWTH OF IMMATURE SPIDERS

I took 5 unfed *K. hibernalis* spiderlings, age 1 wk, from different parts of the same container and weighed each to the nearest 0.001 mg. After killing by freezing for 1 day, I thawed each spider at room temperature for 1 h, then took the following 8 body measurements to the nearest 0.1 mm under a dissecting microscope using an ocular micrometer: width of abdomen, length of abdomen, width of carapace,

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length of carapace, width of eye mound, length of tibia and patella on left foreleg, width of patella on left foreleg, length of left pedipalp. I repeated these measurements with groups of 5 siblings at ages 2, 4, 8, 12, 16, 20, 24, and 32 wk.

I calculated means and standard errors for the 9 measurements in all 9 spider-age groups. Subsequently, to ascertain growth patterns, I transformed the raw data by $\log_{10}$ and calculated Pearson's correlation coefficient (r) and the slope of the least squares regression curves ± their 95% confidence intervals (CI) for 8 parameters relative to carapace width, a commonly used size standard for spiders (Hagstrum 1971). As reviewed recently by Suter & Stratton (2011), spider growth is only loosely related to passage of time or developmental stage, so it is appropriate to use a sclerotized carapace dimension as an independent variable to assess if growth is allometric or isometric.

As shown in Table 1, from age 1 to 32 wk, immature *K. hibernalis* increased in size according to every bodily measurement. Using log-log transformed data, I found there was a highly significant correlation between each of the 8 parameters relative to width of the carapace, the independent variable ($r > 0.85$, $P < 0.00001$). Regression analysis revealed that 3 growth patterns were isometric (carapace length, patella width, and pedipalp length) whereas 5 were positively allometric (tibia-patella length, eye mound width, abdomen width, abdomen length, and body mass). Hence, parts of the legs, eyes, and abdomen grew disproportionately faster than much of the carapace during the 8 mo long study.

NEST HOLE SIZE PREFERENCE IN IMMATURE SPIDERS

To test whether immature *K. hibernalis* might exhibit preferences for retreats that more-or-less match their body sizes, I presented spiders of different ages with 4 wooden dowels (1.9 cm diam. x 5 cm) having a different size hole (1.6, 3.2, 4.8, or 7.9 mm diam.) centered in the end of each, drilled to a depth of 3.5 cm. The dowels were aligned 1 cm apart from each other in the lid of a clear plastic box (12.5 x 5.2 x 5.2 cm) placed horizontally on its side (Fig. 2). Each dowel extended 1.5 cm into the box, 3 mm above its "floor." After a spider was introduced though a 4.8 mm hole in the top of the box, I could easily observe its location. I constructed 120 sets of dowels and used each set once to avoid cross-contamination and experimental bias.

I selected 30 2-wk old spiderlings from a large cohort produced by a second female and placed them singly in boxes, each having 4 dowels with hole diameters in random order. After 4 days I recorded whether a spider had nested in a dowel hole or was free in the plastic box. I repeated this with 30 spiders, age 8 or 24 wk, taken from the same cohort. Differences in size of nest holes as a function of spider age were evaluated using the Chi square test with Yates' correction for continuity (Krebs 1989).

As *K. hibernalis* spiderlings grew in size during the first 24 weeks of life, they showed a strong preference for larger holes to use as nests (Table 2: $\chi^2_c = 40.86$, df = 8, $P = 0.000002$). In each age class the most used holes had diameters 3–4 times as wide as the mean carapace width and 1.5–2.5 times as wide as the mean abdomen width of resident spiders. Visual inspection revealed that spiders appeared to fit snugly in the preferred holes when they were at rest facing outward, but there was sufficient clearance so they could rise, turn easily around, and walk back into the holes' recesses.

Growth patterns and rules in spiders, the largest group of invertebrate predators, are poorly studied, but in general they follow a geometric progression, known as Dyar's rule (Kleinteich & Schneider 2011; Suter & Stratton 2011). The smooth log-log regression curves actually cloak the discontinuous nature of spider growth mandated by molting of the cuticle from one instar to another. Although I did not record production of exuviae by spiderlings, inspection of data in Table 1 for discontinuities in body measurements suggests immature *K. hibernalis* may have molted 4 times and transitioned through 5 instars during my study: between 1-2, 4-8, 12-16, and 20-24 wk of age.

My limited laboratory study suggests that *K. hibernalis* populations have stage-specific preferences for holes and crevices of different sizes to use as nests. This raises the possibility that under natural conditions, populations of this species may be constrained by the local availability of suitable nest sites. But southern house spiders may be not restricted to holes that are empty; they might, like hermit crabs (Laidre 2011 and references therein), increase their resource base by 'targeting' nests already occupied by conspecifics. Yet this seems unlikely considering how socially tolerant they are with their siblings (Curtis & Carrel 1999). Further experimentation of the sort done previously with hermit crabs is in order.

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Summary

In the laboratory, immature *Kukulcania hibernalis* (Hentz 1842) (Araneae: Filistatidae) exhibited a combination of isometric and posi-

Table 1. Body size as a function of age in immature *Kukulcania hibernalis*. Means ± SEM for groups of spiders ($n = 5$) in each age category from same cohort. Statistics at bottom based on log-log transformed data, using carapace width as the independent variable. Positive allometric growth indicated by asterisks.

Spider age (wk)	Carapace width (mm)	Carapace length (mm)	Patella width (mm)	Pedipalp length (mm)	Tibia-patella length (mm)	Eye mound width (mm)	Abdomen width (mm)	Abdomen length (mm)	Body mass (mg)
1	0.80 ± 0.02	1.03 ± 0.03	0.17 ± 0.01	1.45 ± 0.03	1.19 ± 0.03	0.25 ± 0.00	0.78 ± 0.01	1.1 ± 0.01	1.22 ± 0.02
2	0.80 ± 0.00	1.02 ± 0.01	0.16 ± 0.01	1.36 ± 0.02	1.18 ± 0.02	0.25 ± 0.00	1.15 ± 0.03	1.62 ± 0.03	2.20 ± 0.08
4	0.89 ± 0.02	1.07 ± 0.03	0.16 ± 0.01	1.45 ± 0.02	1.24 ± 0.01	0.25 ± 0.00	1.41 ± 0.06	1.97 ± 0.05	3.32 ± 0.25
8	0.96 ± 0.40	1.22 ± 0.48	0.19 ± 0.07	1.63 ± 0.65	1.49 ± 0.55	0.27 ± 0.11	1.50 ± 0.63	2.17 ± 0.88	4.57 ± 0.81
12	0.96 ± 0.02	1.22 ± 0.03	0.20 ± 0.00	1.76 ± 0.02	1.53 ± 0.03	0.31 ± 0.01	1.69 ± 0.05	2.39 ± 0.10	5.61 ± 0.43
16	1.10 ± 0.04	1.35 ± 0.06	0.23 ± 0.01	2.02 ± 0.12	1.72 ± 0.11	0.37 ± 0.02	1.66 ± 0.03	2.34 ± 0.05	6.30 ± 0.30
20	1.02 ± 0.06	1.32 ± 0.08	0.22 ± 0.01	1.77 ± 0.09	1.62 ± 0.13	0.37 ± 0.04	1.68 ± 0.08	2.29 ± 0.16	5.94 ± 0.91
24	1.13 ± 0.03	1.39 ± 0.05	0.24 ± 0.01	1.97 ± 0.09	1.90 ± 0.08	0.42 ± 0.01	1.99 ± 0.14	2.88 ± 0.21	9.22 ± 1.47
32	1.23 ± 0.03	1.47 ± 0.05	0.23 ± 0.02	2.12 ± 0.12	1.87 ± 0.10	0.43 ± 0.02	2.10 ± 0.07	3.09 ± 0.13	10.82 ± 1.02
Statistics	Correlation	0.943	0.852	0.931	0.952	0.895	0.851	0.88	0.925
	Slope ± 95% CI	0.91 ± 0.11	0.99 ± 0.15	1.01 ± 0.14	1.21 ± 0.09*	1.33 ± 0.23*	1.64 ± 0.39*	1.70 ± 0.38*	4.07 ± 0.53*

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tively allometric growth during the first 32 wk of life according to 9 measures of body size. When given an array of artificial holes to use as nest sites, spiders age 2, 8, and 24 wk tended to select holes proportionate to their body sizes. These findings raise the question of whether populations of *K. hibernalis* in the wild are constrained by the limited availability of suitably sized nest sites.

Key Words: *Kukulcania,* arachnid, laboratory study, growth, allometry

Table 2. Preference of artificial nest holes of difference size as a function of spider size (n = 30/group; 0 mm = spider free in cage). Larger spiders significantly preferred to nest in larger holes (χ^2_c = 40.86, df = 8, P = 0.00001).

	Occupancy by immature spiders (age)		
Hole diam (mm)	2 weeks	8 weeks	24 weeks
0	8	7	6
2.4	14	3	0
3.2	7	12	2
4.8	1	6	13
7.9	0	2	9

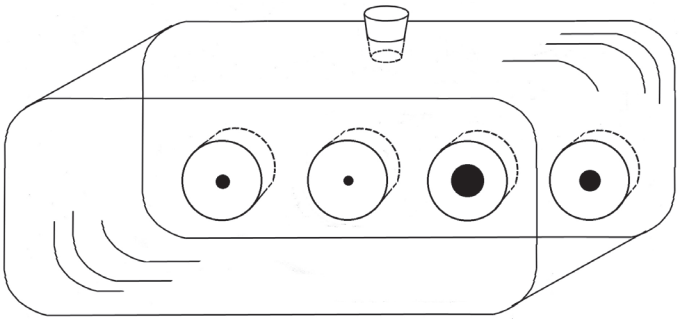


Fig. 2. Scale drawing of clear plastic test chamber. An immature *Kukulcania hibernalis* introduced through the hole in the top could choose to nest in any one of 4 different size holes drilled in wooden dowels (1.9 cm diam.) protruding into the chamber.

Sumario

En el laboratorio, los inmaduros de *Kukulcania hibernalis* (Hentz 1842) (Araneae: Filistatidae) exhiben una combinación de crecimiento isométrico y alométrico positivo durante las primeras 32 semanas de vida según nueve medidas de tamaño corporal. Cuando se les da una serie de cavidades artificiales para su uso como refugio, la arañas con edad de 2, 8 y 24 semanas tienden a seleccionar los agujeros que coinciden con sus tamaños corporales. Estos hallazgos plantean la pregunta de si, en la naturaleza, las poblaciones de *K. hibernalis* se ven limitadas por la disponibilidad limitada de refugios con tamaño adecuado.

Palabras Clave: *Kukulcania*, arácnido, estudio de laboratorio, crecimiento, alometria

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