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8 **Carbohydrates complement high protein diets to maximize the growth of an actively**

9 **hunting predator**

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Abstract

In nature, food is often variable in composition and availability. As a consequence, predators may need to seek non-prey food sources. Some predators are known to feed on nectar when food is limited. Nectar and other carbohydrate resources could also be beneficial when prey are more abundant if it helps predators balance protein-biased diets. We tested if an actively hunting predator, the jumping spider, *Phidippus audax*, benefited from liquid carbohydrates when prey were not limited. We also tested if the benefit of carbohydrates varied with the nutrient content of prey (i.e., from protein to lipid-biased). Spiders were reared on one of six live prey, *Drosophila melanogaster*, treatments that ranged from high protein to high lipid. Half of the spiders were given access to a 20% sucrose solution. After two months, we measured spider mass, cephalothorax width, instar duration, percent body fat, survival, and estimated number of prey eaten. Spiders reared on high protein diets with carbohydrates were larger and heavier than spiders on other treatments. Access to carbohydrates also increased percent body fat and survival across prey treatments. Our results suggest that carbohydrates may be a valuable component of spider diets, especially when prey have high protein and low lipid content as is commonly observed in prey in the field. Our results highlight the importance of diet balancing for predators, and that liquid carbohydrates can be an important nutrient to supplement a diet of prey rather than just being an energy supplement during periods of starvation.

Keywords: Jumping spider; Macronutrients; Nutritional ecology; *Phidippus audax*.

42 **Statements and declarations**

43 The authors declare that there are no competing interests

44

45 **Significance statement**

46 Protein and lipid are thought to be the primary nutrients used by predators, including
47 spiders. Yet, some spiders have been observed feeding on carbohydrate-rich nectar from flowers.
48 We tested if the addition of carbohydrates to a high protein or high lipid diet affected the growth
49 of the North American jumping spider, *Phidippus audax*. Spiders grew largest on high protein
50 diets with carbohydrates, demonstrating that plant-based foods rich in carbohydrates can be
51 important for some predators.

52

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60 measuring spiders.

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Introduction

67 The quantity and quality of food consumed has large effects on the growth, reproduction,
68 and survival of animals. Food is often limiting, especially for some predators, and individual
69 food items can be nutritionally imbalanced or biased (Sturner & Elser 2002). Hence, animals can
70 spend significant time foraging and often need to seek multiple food sources to balance their diet
71 (Simpson & Raubenheimer 2012). When given a choice, many animals are capable of selecting
72 food items that maximizes fitness by selecting foods that are nutritionally complementary (Lee et
73 al. 2008, Maklakov et al. 2008). However, in nature free choice among nutritionally
74 complementary foods may not always be possible and, hence, it is important to understand how
75 limited or nutritionally-biased diets affect growth and survival.

76 Macronutrients are used for two broad functions: to fuel metabolism, and to provide
77 building materials for body structures. Carbohydrates and lipid are often the primary source of
78 energy while protein is often used to build new tissue. Protein can also be used as a source of
79 energy (e.g., via gluconeogenesis) if other sources of energy are limited in the diet (Myers and
80 Klasing 1999, Eisert 2011) or as a specialized source of energy (e.g., proline use by some flying
81 insects; Klowden 2007). However, use of protein as an energy source is likely less efficient than
82 other sources of energy (i.e., carbohydrates and lipid), and may produce harmful nitrogenous
83 metabolic byproducts (Klowden 2007). While some animals can substitute macronutrients, like
84 using protein as an energy source, not all animals are capable of macronutrient substitution. For

85 example, cats have a limited ability to digest carbohydrates and cannot use this macronutrient as
86 a substitute for low levels of lipid in their diet (MacDonald et al. 1984, Hewson-Hughes et al.
87 2011). In another example, carbohydrates are a non-substitutable resource for fire ants, with
88 colonies able to increase both brood production and the number of worker when carbohydrates
89 are available compared to colonies with only *ad libitum* lipid and protein from prey (Wilder et al.
90 2011). Understanding whether or how well macronutrients can be substituted, and/or
91 complement one another, is critical for predicting the consequences of food limitation and
92 nutrient imbalances for individuals and populations in nature (Simpson et al. 2006).

93 One factor that has a key influence on the primary nutrients used by animals is the trophic
94 level at which they feed. Herbivores primarily ingest carbohydrate and protein, which are the
95 bulk of the macronutrients in plants, and often consume limited amounts of lipid in their diet
96 (e.g., some seeds). On the other hand, carnivores typically consume diets high in protein and
97 lipid but low in carbohydrate (Russel et al. 2003). While the diets of herbivores and carnivores
98 typically differ, both groups can engage in omnivory, with herbivores consuming animal tissue
99 (White 2011) and carnivores consuming plant material (Wäckers et al. 2005). These deviations
100 from what are considered typical diets for animals within a given trophic level are often thought
101 to be an extreme response to starvation or as part of a coevolved food-for-protection mutualisms
102 (Wäckers et al. 2005, White 2011, Ballova et al. 2015). Yet, recent research suggests that not all
103 animals follow traditional views of being strictly carnivorous or herbivorous and that many, if
104 not most animals, may be somewhat omnivorous (see the extensive review of Coll and Guershon
105 2002). There is a breadth of literature covering food-for-protection mutualisms in which plants or
106 honeydew-producing hemipterans provide carbohydrates to carnivorous insects (e.g., ants and
107 wasps) in exchange for protection (Wäckers et al. 2005), and even some literature on spiders

108 feeding on plants (see Nyffeler et al. 2016). However, further work is needed to resolve the
109 contribution of non-traditional food sources to the diets of animals, especially focusing on the
110 role of plant-based foods in carnivore diets.

111 Spiders provide an interesting system for testing the role of plant-based foods for
112 carnivores. Nearly all spiders are obligate carnivores (but see Meehan et al 2009). Yet, up to 30
113 species have been observed feeding on floral or extrafloral nectar in nature, including species in
114 the wandering spider families Miturgidae, Thomisidae, Anyphaenidae, Corinnidae, and
115 Salticidae (Jackson et al. 2001). In the miturgid spider, *Cheiracanthium inclusum*, supplementing
116 the diet of food-limited individuals with nectar allows them to achieve growth and reproductive
117 rates comparable to individuals fed higher quantities of prey (Taylor and Pfannenstiel 2009).
118 Similar results have been found in the crab spider *Ebrechtella tricuspidata* (Wu et al. 2011), with
119 honey (acting as simulated nectar) increasing survival and decreasing development time. Hence,
120 some spiders appear to be able to use the carbohydrates in nectar to compensate for a lack of
121 overall food availability. However, it remains unclear whether carbohydrates are only a source of
122 nutrition during starvation or if carbohydrates contribute to growth of spiders when prey are
123 more abundant. Furthermore, recent research suggests that the lipid and protein content of prey
124 can have large effects on the growth (Wiggins and Wilder 2018), survival (Jensen et al. 2010)
125 and reproduction (Lomborg and Toft 2009) of spiders and other predators. Macronutrient
126 balance is integral to proper function, yet the availability of these key macronutrients can vary
127 widely in prey (Wilder et al. 2013). As such, carbohydrates would be predicted to be more
128 beneficial to spiders fed protein-biased prey as the carbohydrates could provide a source of
129 energy to substitute for the low lipid content of prey (Noreika et al. 2016). Although, context-
130 dependency in the benefit of carbohydrates for spiders remains to be tested.

131 The overall goal of this study was to test if a common plant-based food, liquid
132 carbohydrates, benefitted the growth of an obligate predator when prey were not limited.
133 Furthermore, we tested if the benefit of carbohydrates varied with the nutritional content of the
134 prey, which can vary widely (Wilder et al. 2013, Wiggins and Wilder 2018). Specifically, we
135 provided the jumping spider *Phidippus audax* with one of six diets of live prey (*Drosophila*
136 *melanogaster*) that varied in their nutrient content (i.e., ranging from low to high lipid:protein)
137 either with or without access to supplemental carbohydrates. We hypothesized that the addition
138 of carbohydrates would have more of a benefit to the growth of spiders fed protein-biased prey
139 than spiders fed lipid-biased prey.

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141 **Methods**

142 **Spider Maintenance:** Spiders used in the laboratory experiments were first generation
143 individuals whose parents were collected as penultimates during October-November 2015 from
144 the old-field community surrounding Sooner Lake Dam, Pawnee Co., Oklahoma. The parent
145 spiders were fed 1-2 appropriately sized crickets, *Acheta domesticus*, and watered twice a week.
146 Parent spiders were paired for mating in mid-December. Spiderlings hatched in mid-January and
147 were raised with their mother until they underwent their first molt. Twelve spiderlings from each
148 females' first clutch (n = 27) were separated into individual containers and given an alpha-
149 numeric identification code (n = 324). Spiderlings were housed in Carolina Biological (Carolina
150 Biological Supply Co., Burlington, NC) fly vials (3.3 cm diameter × 11 cm tall) with 2 cm of
151 Plaster of Paris in the bottom to retain moisture and stoppered with sponge stoppers. The sponge
152 stoppers had a small hole cut in the center. A translucent polypropylene drinking straw stuffed

153 with cotton was inserted into the hole (diameter 5 mm x length 50 mm). The spiders were kept
154 on a 14:10 hour light/dark cycle at a constant temperature of 26 °C.

155 **Prey Nutrient Treatments:** We manipulated the macronutrient content of live prey
156 items, wild type *Drosophila melanogaster*, by raising the flies on media with different nutrient
157 content that allowed us to create six treatments of flies with particular ratios of lipid:protein (as
158 in Jensen et al. 2011). As established in a previous study (Jensen et al. 2011) all the prey diets
159 used Carolina Biological fly media (potato flake) as the base. Casein (milk powder) was added to
160 the media to increase the protein content of the resulting flies or sucrose was added to increase
161 the lipid content of the flies. Casein treatment ratios were 2:3, 1:4, or 1:9 casein to Carolina by
162 mass. Sucrose treatments were either 1:2 or 1:4 sucrose to Carolina by mass, and one treatment
163 was Carolina fly media with no supplemental nutrients. These treatments produce flies with a
164 wide range of lipid:protein content (Table 1) from highly protein-biased (i.e. 2:3 casein:Carolina)
165 to highly lipid-biased flies (i.e. 1:2 sucrose:Carolina) (see Jensen et al. 2011, Wiggins & Wilder
166 2018). Spiders were each fed four flies twice a week. Spiders were allowed twenty-four hours to
167 consume the flies. After twenty-four hours, the flies were counted and released to give us an
168 estimate of how many prey items were consumed. We are using the term estimate because we
169 did not see each fly get consumed and cannot rule out natural deaths or kills without feeding.

170 To determine the role of carbohydrates in spider nutrition, we gave spiders in each diet
171 treatment access to either a 20% sucrose solution (20 g of sucrose into 100ml of water, colored
172 with 5 drops of red food coloring) or tap water (100 ml colored with 5 drops of red food
173 coloring). The solutions were presented via the translucent drinking straws stuffed with cotton.
174 We used red food coloring in both solutions to verify that spiders were drinking the solutions.
175 When spiders drank the food coloring it turned their excreta a red-reddish brown color. Also, the

176 abdomens of the spiders that drank the red solution appeared pinkish. All spiders were given
177 access to water without food coloring twice a week via a light misting when flies were removed.

178 We alternated between providing spiders with liquid solutions and flies. The two were
179 never provided at the same time, as not to allow the flies to drink the sucrose solutions and
180 change their macronutrient contents. The straws with water or sugar water were inserted for
181 seventy-two hours, until the next feeding of flies.

182 **Measurement of Growth:** Spider growth was calculated using multiple measures. First,
183 spiders were weighed on a scale to the nearest 0.01 mg at two months. The first molt following
184 this mass measurement was recorded for date. Molts were collected and measured for a fixed
185 body size, carapace width at the posterior lateral eyes (PLE). We used carapace width alone
186 because the other common size measurement, patella/tibia length, is highly correlated with
187 carapace width (Wiggins and Wilder 2018). Photos were taken of the molts and a micrometer
188 slide using a camera attached to a dissecting microscope and measured with ImageJ software
189 (Rasband 2016) to 0.001 mm. These measurements provide an accurate measure of the size of
190 the spider's body at weighing without undue stress or sacrificing the animal. Some molts were
191 damaged before or during the weighing, slightly decreasing total sample size.

192 **Flies Consumed:** Twenty-four hours after feeding, surviving flies were counted and
193 released. We are able to estimate the number of flies eaten by taking the total flies fed (4 flies
194 twice a week for two months) and subtracting the number of flies released.

195 **Spider Lipid Content:** We analyzed a subset spiders from each treatment ($n = 76$) for
196 lipid content using a gravimetric protocol. Spiders were dried in an oven for 24 hours at 60 C°
197 and weighed to the nearest 0.01 mg. Following the initial dry mass measurement, spiders were

198 washed in chloroform for two consecutive twenty-four hour baths, with the chloroform being
199 changed between baths. The lipids from the spiders were solubilized within the chloroform.
200 After the second bath, spiders were once again dried in an oven for 24 hours at 60 C° and
201 reweighed to the nearest 0.01 mg to obtain the final lean (i.e., lipid-free) mass.

202 **Statistical Analysis:** We used Generalized Additive Models (Woods 2006) to test for
203 effects of prey nutrient content, sugar access, and their interaction on spider growth. Generalized
204 Additive Models are similar to Generalized Linear Models without the assumption of linearity.
205 This allows the response to take a nonlinear form. The GAMs were run in R (R Core team 2014).
206 JMP (SAS Inc. 2016) was also used to analyze survival of the spiders via a parametric survival
207 model with a Weibull distribution analyzing the effects of prey nutrients, supplemental
208 carbohydrates, and the interaction between prey nutrients and carbohydrates on spider survival.
209 JMP was also used for all post-hoc analyses.

210 **Results**

211 **Mass:** There were significant main effects of both carbohydrates ($f_{1,302} = 65.96, p < 0.01$), and
212 prey nutrients ($f_{5,298} = 76.86, p < 0.001$), as well as an interaction between prey nutrient content
213 and carbohydrates on spider mass ($f_{6,297} = 24.11, p < 0.001$) (Figure 1a). We further explored
214 this interaction with post hoc tests. For spiders fed the three highest lipid prey (i.e., highest
215 lipid:protein), there was no significant difference between mass of individuals with or without
216 carbohydrates (Figure 1a). However, the spiders fed the three highest protein prey treatments
217 were significantly heavier when supplemented with carbohydrates (Figure 1a). The difference
218 between spider mass with and without carbohydrates increased as the prey treatments became
219 more protein biased ($f_{1,6} = 10.86, p = 0.03$).

220 **Body Size:** There were significant effects of carbohydrates ($f_{1,278} = 15.50, p < 0.001$), prey
221 nutrients ($f_{6,273} = 21.84, p < 0.001$) and their interaction ($f_{7,272} = 6.61, p = 0.01$) on spider body
222 size, measured as carapace width at PLE (Figure 1b). Post hoc tests showed that on the high
223 protein prey treatments, spiders provided carbohydrates had significantly wider carapaces than
224 those without carbohydrates. There were no differences in carapace width of spiders fed high
225 lipid prey regardless of carbohydrates presence.

226 **Instar Duration:** We measured instar duration for both the 2nd and 3rd instars. We found a
227 significant effect of prey nutrient content for the second instar duration ($n = 279, f_{5,273} = 17.03, p$
228 < 0.001) and a significant interaction between prey nutrients and supplemental carbohydrates (f
229 $_{7,271} = 13.68, p < 0.001$). The main effect of carbohydrates was not significant ($f_{1,277} = 0.12, p =$
230 0.73). Post hoc tests indicated that spiders fed high lipid prey items with available carbohydrates
231 took significantly longer to molt than all other treatment groups. To further explore the
232 interaction effect, we conducted linear regressions of instar duration and prey lipid:protein
233 separately for carbohydrate and no carbohydrate treatments. Linear regression of data from only
234 carbohydrate supplemented spiders showed that individuals molted sooner when fed prey with
235 higher protein content ($n = 138, f_{5,132} = 33.05, p < 0.001$). However, for spiders not provided
236 carbohydrates, there was no effect of prey nutrient content on second instar duration ($n = 141, f$
237 $_{5,135} = 0.09, p = 0.77$) (Figure 1c). We took the same measurements for the 3rd instar duration and
238 found that there were no longer any significant effects of prey nutrients ($n = 109, f_{5,103} = 1.86, p$
239 $= 0.18$), supplemental carbohydrates ($f_{1,107} = 2.20, p = 0.14$), nor the interaction ($f_{7,101} = 0.008, p$
240 $= 0.78$) on instar duration.

241 **Survival:** Of the starting spiders, 199 individuals survived and 108 died (sample size is less than
242 total spiders in the experiment due to some escapes $n = 17$). An effects likelihood ratio test

243 revealed that prey nutrient content did not significantly affect survival ($\chi^2 = 0.08$, $df = 1$, $p =$
244 0.78). However, the presence or absence of supplemental carbohydrates did significantly affect
245 survival ($\chi^2 = 25.97$, $df = 1$, $p < 0.001$), with individuals fed carbohydrates having higher
246 survival. The interaction between prey nutrients and carbohydrates was near significant ($\chi^2 =$
247 3.60, $df = 1$, $p = 0.06$), but no clear conclusions could be drawn (Figure S1).

248 **Spider Lipid Content:**

249 We measured the body fat content of a subset of spiders that survived across all nutrient
250 treatments. We found that the presence or absence of supplemental carbohydrates was the only
251 factor that affected body fat content ($n = 76$, $f_{1,74} = 21.78$, $p < 0.001$), with spiders fed
252 carbohydrates having higher body fat content than spiders not provided carbohydrates (Figure 2).
253 Prey nutrients and the interaction were non-significant ($f_{5,70} = 0.007$, $p = 0.93$; $f_{7,68} = 0.75$, $p =$
254 0.39, respectively).

255 **Total Prey Consumption:**

256 There was a significant effect of prey nutrients ($n = 301$, $f_{5,295} = 6.95$, $p = 0.009$),
257 carbohydrates ($f_{5,299} = 15.71$, $p < 0.001$), and the interaction ($f_{5,293} = 26.13$, $p < 0.001$) on the
258 number of flies consumed by spiders (Figure 3). Post hoc tests revealed that spiders fed high
259 protein diets with carbohydrates ate fewer flies than spiders fed high protein diets with water
260 (Figure 3).

261 **Discussion**

262 Our results demonstrate that carbohydrates can be a valuable component of carnivore
263 diets, especially when carnivores are feeding on high protein prey. Spiders fed the high protein
264 prey and also provided carbohydrates were almost twice as heavy and had wider cephalothorax

265 than spiders in all other treatments. Instar duration was longest for spiders fed carbohydrates and
266 high lipid prey, putting them at a disadvantage but only during the second instar. The effect was
267 no longer present in the third instar. Supplementation with carbohydrates also increased survival
268 and percent body fat across all prey nutrient treatments. We had expected carbohydrates to
269 increase growth, but the large benefit of carbohydrates for spider growth (i.e., carbohydrate fed
270 spiders were > 40% heavier than non-carbohydrate fed spiders on the highest protein treatment)
271 was not expected for such an obligate carnivore. Previous studies have found that spiders,
272 especially actively hunting species, will consume nectar in nature and that nectar can increase
273 survival and growth during periods of limited food availability or starvation (Taylor and
274 Pfannenstiel 2009, Wu et al. 2011). Our results suggest that carbohydrates may be more than just
275 an energy supplement during periods of starvation and that carbohydrates could be an important
276 component of this actively hunting spider's diet during development.

277 The high protein diet with carbohydrates may have provided the ideal situation for spiders: a
278 large amount of protein to build new tissue and carbohydrates to provide a source of non-protein
279 energy for growth. The high protein diet offered the highest amount of protein to invest in new
280 tissues. However, the high protein prey lacked a readily metabolizable energy source. Protein can
281 be catabolized for energy, but doing so is less efficient than extracting energy from
282 carbohydrates or fat. Also, this metabolizes the protein so that it cannot be used to build tissue.
283 The spiders on higher lipid diets also had a balance of protein and non-protein energy (lipid) but
284 they had less overall protein and the addition of carbohydrates would only provide additional
285 energy, which may not have been limiting on this diet. This is similar to what is observed in
286 carabid beetles, where lipids and carbohydrates can be used interchangeably (Noreika et al.
287 2016). The present results suggest that the observations of spiders feeding on nectar in nature

288 may be due to diet choice by the spiders, especially since prey are often protein-biased in nature
289 (Wilder et al. 2013, Wiggins and Wilder 2018).

290 Spiders fed the high protein prey with no carbohydrates ate significantly more flies than
291 spiders fed the high protein prey with carbohydrates. By feeding on more prey, spiders on the
292 high protein treatment could have been either selectively extracting the limiting lipid from many
293 prey (e.g., Mayntz et al. 2005) or consuming large amounts of protein to catabolize some of this
294 protein for energy. Measurement of nutrients in the prey carcasses would have been needed to
295 differentiate between these mechanisms. Regardless, the differences among treatments in fly
296 consumption demonstrate that spiders are able to adjust their foraging behavior to compensate
297 for variation in the nutritional composition of prey or available resources and its potential
298 consequences for growth. Jensen et al. (2011) demonstrated similar compensatory feeding in
299 *Pardosa prativaga* fed prey varying in lipid and protein content and found relatively few effects
300 of diet on spider growth. Compensatory feeding in the absence of nectar could have important
301 implications for understanding spatial and temporal variation in food web dynamics and how it
302 may relate to the availability of floral resources.

303 In addition to providing more energy, there could be a difference in the digestibility of
304 carbohydrates relative to the other major energy source, lipid. For example, studies of fire ants
305 have shown that the addition of liquid carbohydrates (an artificial nectar substitute) increased
306 colony growth even when insect prey, which contained significant amounts of lipid and protein,
307 were available *ad libitum* (Wilder et al. 2011). Also, Toft and Nielsen (2017) have observed
308 differences in carabid beetle metabolism of carbohydrates versus lipids and protein, and found
309 carbohydrates best for replenishing fat reserves post-hibernation. It is possible that carbohydrates
310 may, similarly, be more readily metabolized than lipids by spiders as well. Further work is

311 needed on the metabolic costs of digesting (i.e., specific dynamic action, SDA) different foods
312 and nutrients in spiders and other predators.

313 A previous study using similar fly diets with no carbohydrates found that juvenile *P.*
314 *audax* grew largest on flies with the highest lipid content (Wiggins and Wilder 2018). The
315 present study did not find similar results for the no carbohydrate treatments. Another interesting
316 difference between the studies is that the spiders in the present study at two months of age were
317 larger than spiders in the past study at four months of age (Wiggins and Wilder 2018). There are
318 at least two potential explanations for the differences between the studies. First, the present study
319 provided spiders with more readily available water in wet cotton, whereas the past study only
320 periodically provided a spray of water droplets in containers. Water availability could interact
321 with nutrient content of prey to affect spider growth (McCluney 2017). Second, the maintenance
322 fly cultures used to inoculate our fly treatment cultures were raised in two different ways. In the
323 past experiment, maintenance flies were cultured on only potato flake medium versus the present
324 study where they were maintained on potato flake supplemented with ground dog food. While
325 the flies fed to spiders had similar macronutrient content in both studies, there could have been
326 transgenerational effects of past culture on different media that affected some unmeasured aspect
327 of fly quality. The differences between the past and present studies suggest that while
328 macronutrients can be important factors affecting prey quality, there may be other aspects of
329 prey that can affect predator growth.

330 Across all diets, carbohydrates increased spider survival, with between 20% to 60% more
331 spiders surviving when carbohydrates were present. This survival benefit is likely to be even
332 higher in nature due to the benefit of carbohydrates for increasing lipid reserves. Increased lipid
333 reserves would help spiders during food limitation, which can be often for some species (Wise

334 2006). Studies of a linyphiid spider suggest that they regularly experience periods of starvation
335 of one week or more in nature (Bilde and Toft 1998). Studies of a wolf spider showed that wild-
336 caught spiders had body condition not significantly different from lab-maintained spiders that
337 were fed *ad libitum* and then completely deprived of food for three months (Wilder and Rypstra
338 2008). Lipid reserves are critical for surviving periods of starvation and, regardless of the prey
339 on which they fed, spiders that consumed carbohydrates had higher lipid reserves than spiders
340 that did not have access to carbohydrates.

341 These results demonstrate that carbohydrates can be an important component of spider diets.
342 There are at least two potential ways that spiders may consume carbohydrates in nature: 1) by
343 feeding on pollinators that have recently fed on nectar, and 2) by feeding directly from the plant,
344 either through floral or extrafloral nectaries. It is likely that jumping spiders consume
345 carbohydrates from both of these mechanisms. Jumping spiders and some other wandering
346 spiders hunt prey on flowers, as flowers provide a hotspot of insect activity. Many of the insects
347 captured on flowers will likely have nectar in their guts from recently feeding on other flowers.
348 Some jumping spiders have also been observed feeding directly from nectaries (see Nyffeler et
349 al. 2016). Given the potential benefits of hunting from flowers, it is surprising that jumping
350 spiders are not more specialized for this behavior (e.g., coloration to blend into flowers).
351 Although, this could be due to competition for these hunting locations with other predators that
352 frequently hunt on flowers (e.g., praying mantids, crab spiders). Rather, for jumping spiders,
353 flowers may serve as one of multiple feeding sites used as the spiders actively move through
354 their habitat.

355 **Data Availability:** The datasets generated during and/or analyzed during the current study
356 are available from the corresponding author on reasonable request.

358

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444 Table 1. Fly diet effect on fly body composition and mass \pm SD

Fly diet	Fly body composition (lipid : protein)	Fly mass (mg)
Casein 2:3	0.09	0.31 \pm 0.05
Casein 1:4	0.12	0.34 \pm 0.02
Casein 1:9	0.16	0.32 \pm 0.05
Carolina	0.27	0.34 \pm 0.03
Sucrose 1:4	0.37	0.29 \pm 0.04
Sucrose 1:2	0.43	0.28 \pm 0.03

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Figure Legends

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Figure 1 Growth metrics of spiders after being fed flies, one of six different prey nutrient

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ratios, ranging from high protein to high lipid with and without an available carbohydrate

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source at two months, with post hoc assignments and standard error. a) spider live mass

461

b) posterior lateral eye width c) second instar duration

462

463

Figure 2. Percent body fat from surviving spiders fed one of six different prey nutrient

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ratios with and without an available carbohydrate source. * Denotes groups with too few

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samples for standard deviation.

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Figure 3. Estimated total flies consumed after 2 months of sustained feeding of eight flies

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a week across six different prey nutrient ratios with and without an available

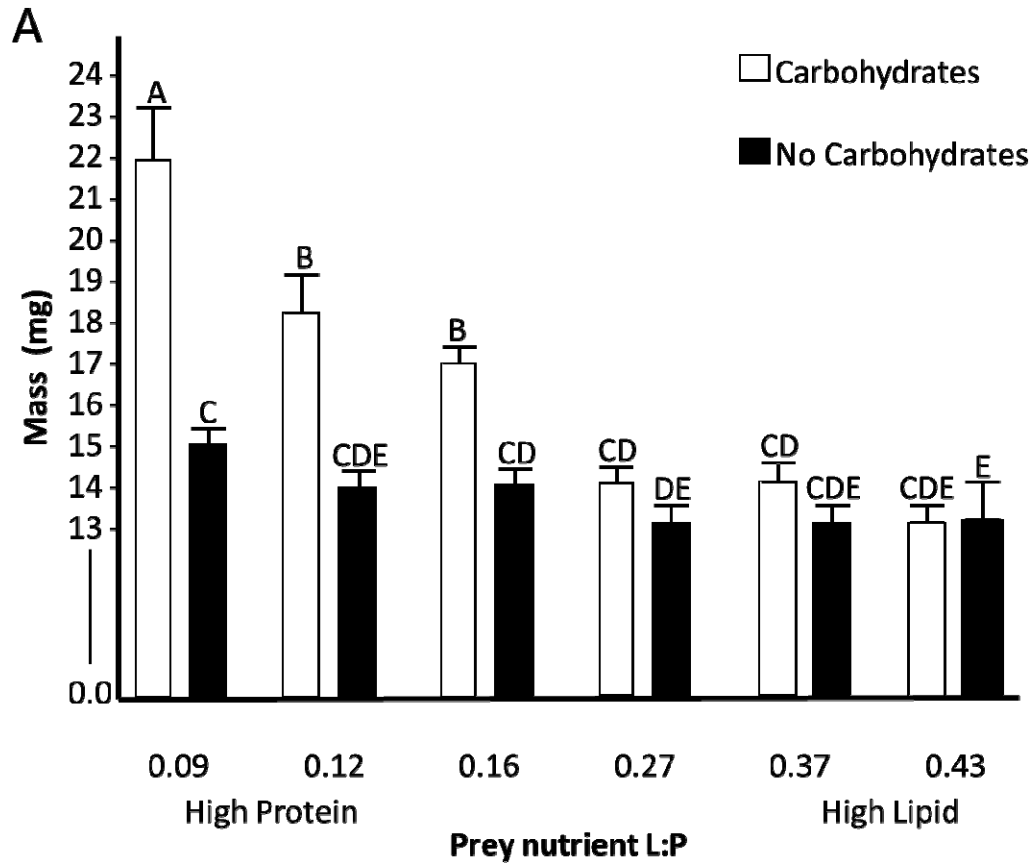
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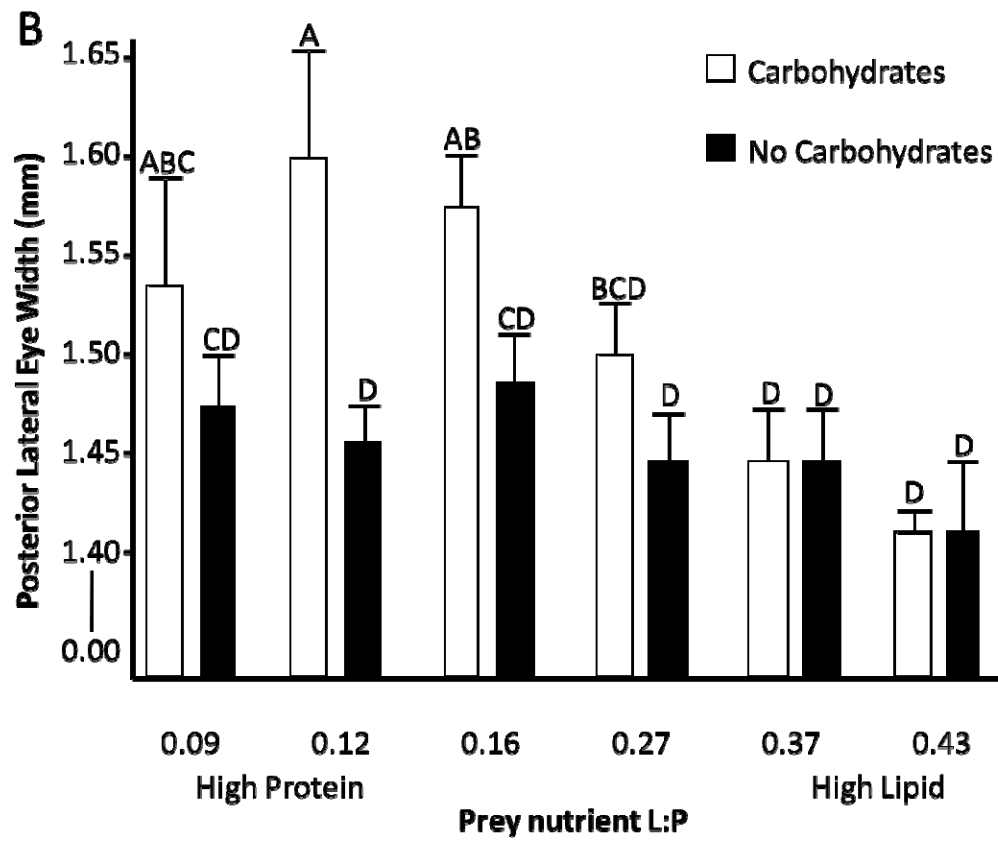
carbohydrate source. Post hoc assignments and standard error are shown above the mean,

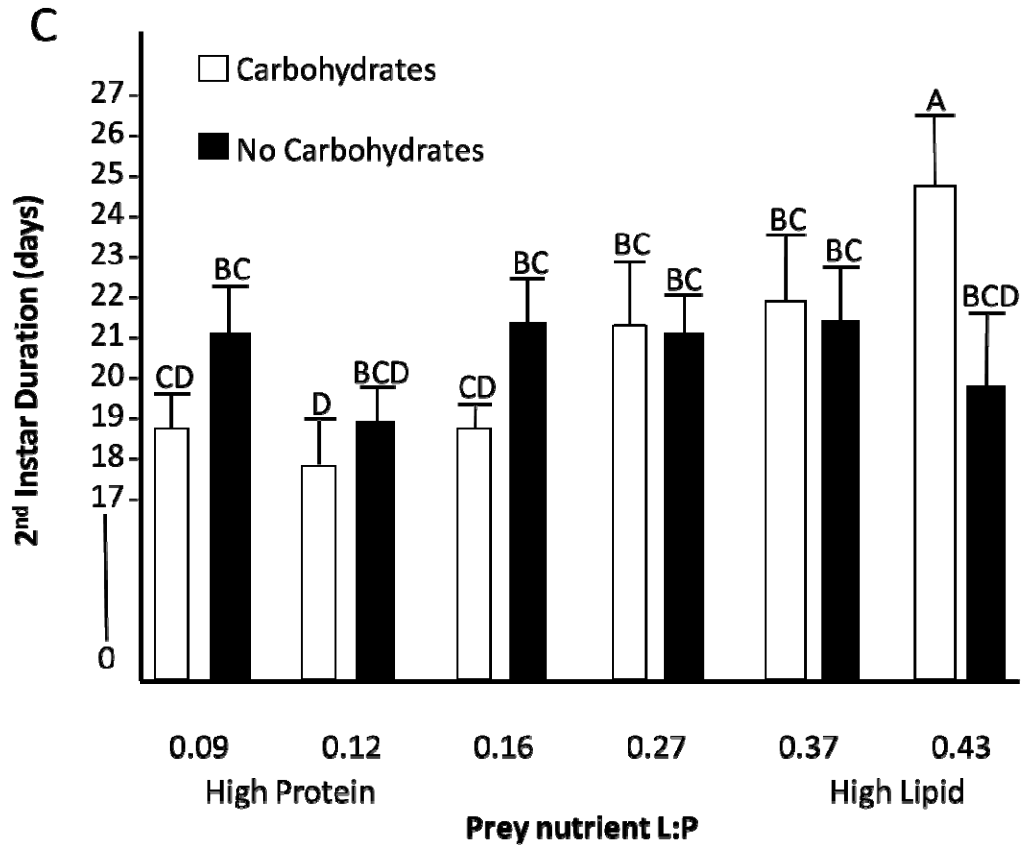
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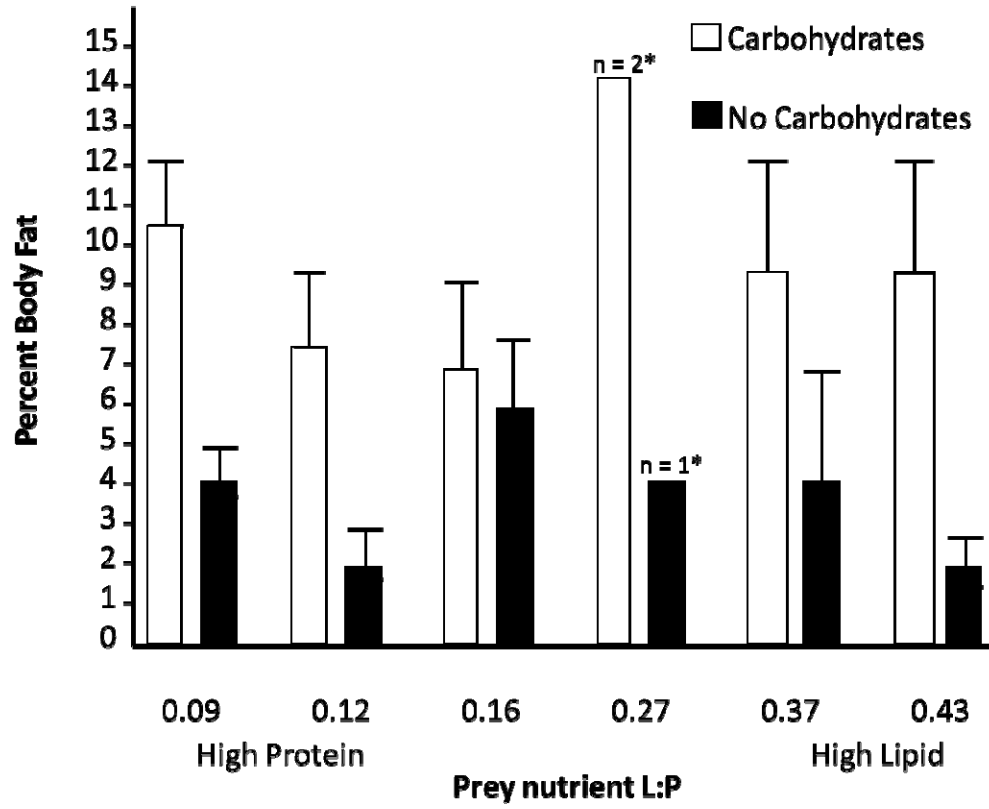


Figure 3

