The effects of relatedness, age differences, family and maternal investment on juvenile cannibalism in the black widow spider, *Latrodectus hesperus*

Kathryn A. Kitchen & J. Chadwick Johnson

Department of Integrated Natural Sciences, Arizona State University at the West Campus

INTRODUCTION

The theory of kin selection emphasizes that an individual's fitness can come from direct and indirect sources (Hamilton, 1964). Whereas direct fitness comes about through one's own reproductive success, indirect fitness benefits are obtained through the survival and reproductive success of one's relatives. In cannibalistic species, directing cannibalism away from related individuals, including siblings, should be favored by kin selection (Pfennig, 1997). The trade off faced by cannibalistic species (i.e. a meal vs. indirect fitness) makes them uniquely suited for kin selection studies. As a result, a wide array of cannibalistic taxa have been used in studies of kin selection (Pfennig, 1997).

Spiders are particularly well suited for such studies given their propensity towards cannibalism and the diversity of social systems seen across spider taxa (Bilde & Lubin, 2001; Wise, 2006). In spiders, there exists a continuum of sociality based upon the frequency of interactions between individuals. This continuum ranges from highly social species that live in communal webs and encounter conspecifics on a regular basis, to solitary species that can have very limited interaction with conspecifics (Roberts *et al.*, 2003). While previous research has demonstrated kin selection in social, sub-social, and solitary wandering spiders (i.e. spiders that live apart from one another but roam throughout the environment, thereby increasing the likelihood of conspecific interactions), solitary web-building spiders, the extreme in asociality, remain to be studied in this respect (Evans, 1999; Bilde *et al.*, 2002; Anthony, 2003).

Here we investigate the role kin selection plays in determining the cannibalistic behavior of a solitary, web-building spider: the Western Black Widow (*Latrodectus hesperus*). In this species, the majority of social interactions occur during the early juvenile spiderling stage (Kaston, 1970). Therefore, we hypothesize that kin selection will cause recently hatched Black Widow spiderlings to cannibalize unrelated individuals more readily than related individuals.

METHODS

We mated twenty-six field-caught, virgin females in the lab to create full sibships for study. Spiders were collected at various urban sites throughout Glendale, Arizona in the Fall and Spring of 2006. Egg sacs were weighed two days prior to hatching and, once egg sacs hatched, the total number of offspring emerging was counted.

Within 2 days of an egg sac hatching, single spiderlings were paired in clear plastic boxes (4 x 4 x 5 cm.) with either a full sibling or with an unrelated spiderling. Paired sibships hatched no more than 5 days apart from each other. For each sibship pairing, 45 boxes were prepared with two spiderlings in each box: 15 related pairs from the first family, 15 related pairs from the second family, and 15 unrelated pairs. Once a week, each box was fed one flightless fruit fly (*Drosophila melanogaster).*

Boxes were checked daily for distance between spiderlings, deaths, cannibalism, and molts. Cannibalism was easily distinguishable from other causes of death as cannibalized spiderlings were found wrapped in silk. After cannibalism occurred the remaining spiderling was fed weekly and followed through its next two molts.

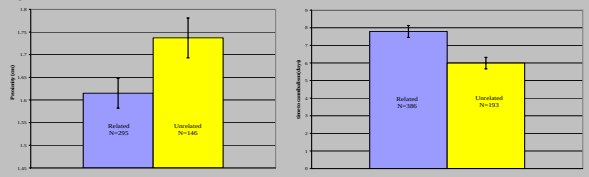
STATISTICAL ANALYSIS

We used one-tailed t-tests to analyze the effect of relatedness on proximity as well as on the average time taken to cannibalize. Additionally, we used analysis of covariance to examine whether maternal investment (e.g. egg sac mass) had any effect on the time taken to cannibalize between related and unrelated spiderlings. To examine family-level variation in cannibalism, we restricted our analysis to related pairings (the family identity of predator and prey was unknown for unrelated pairings), and ran a model III, random effects ANOVA.

RESULTS

As seen in Fig. 1, related spiderlings resided significantly closer to each other than unrelated spiderlings (t=2.16 df=439, p=0.016). In spite of this, related spiderlings took significantly longer to cannibalize each other (t = 3.43, df = 577, p = 0.0005).

Figure 1. The effect of relatedness on cohabitation and cannibalism.



However, several other factors call into question the validity of this relatedness effect. First, among unrelated individuals, despite doing our best to minimize differences in hatch date, age differences between unrelated pairings explained a significant amount of variation in cannibalism (r_{13} = 0.-781, $p_{2\text{-}tailed}$ = 0.002). Greater age differences between spiderlings enhanced the rate of cannibalism between a pair. Repeating the t-test illustrated in Fig. 1 using only the subset of unrelated pairs that differed in age by 2 days or less (n= 9) shows that the effect of relatedness on cannibalism is reduced to a non-significant trend (t = 1.53, df = 517, p = .06).

Second, among related pairings, we found a strong effect of family on cannibalism ($F_{25,360}$ = 15.7, p<.0001). As illustrated in Fig. 2, the rate at which families cannibalized a related individual varied drastically between the 26 sibships studied. As such, related spiderlings emerging from a common egg sac are not independent data points. Thus, we repeated the t-test from Fig. 1 using family averages and found no significant difference in cannibalism between the 13 unrelated pairs and 26 related pairs (t = 1.25, df = 37, p = 0.11).

Figure 2
Family origin affects cannibalism

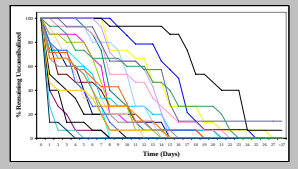
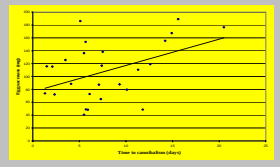


Figure 3
Egg sac mass affects cannibalism



However, this may instead be a product of maternal effects. As seen in Fig. 3, time to cannibalism was significantly influenced by the mass of the egg sac a family emerged from (r_{26} = 0.440, $p_{2\text{-}tailed}$ = 0.025), but was not influenced by offspring number or offspring number/egg sac mass. Heavy egg sacs produced siblings significantly slower to cannibalize one another than lighter egg sacs (r_{26} = 0.44, $p_{2\text{-}tailed}$ = .03). While these larger egg sacs did contain significantly more offspring (r_{26} = 0.99, $p_{2\text{-}tailed}$ < 0.001), they were not better provisioned in terms of egg sac mass per offspring (r_{26} = -0.018, $p_{2\text{-}tailed}$ = 0.932).

DISCUSSION

Our initial results indicated that relatedness promotes cohabitation but deters cannibalism. However, it is premature to conclude that kin selection shapes patterns of cannibalism in black widow spiderlings. Several other factors influence cannibalism in this species. Variation in age differences, family origin and egg sac mass all influenced cannibalism.

Age, and size differences have long been suggested to be factors promoting cannibalism (Elgar & Crespi, 1992). While our inability to mark individual spiderlings made it impossible to determine the exact nature of this relationship, conventional wisdom suggests that larger spiderlings from older families were likely cannibalizing smaller, younger spiderlings. Alternatively, it is not uncommon to observe smaller, food-motivated black widows initiating (and often winning) agonistic encounters with larger, satiated conspecifics (JCJ, pers. obs.). Thus, age differences may promote cannibalism because they allow older, larger spiders a competitive edge and/or because smaller, younger spiders are willing to risk more to win a battle.

Our results indicated that genes and maternal environment shared by siblings are important determinants of cannibalism. While these findings compel us to employ more rigorous quantitative genetic designs in the future to isolate the relative magnitude of genetic and maternal effects on widow behavior, it is nonetheless intriguing to consider the evolutionary implications of a behavioral, ecological trait such as cannibalism being heritable. To the extent that behavioral traits are similar within families behavioral optimization (local adaptation) may be constrained.

In conclusion, future studies will need to do a better job of controlling the effects of variation in age, family origin and maternal investment if they hope to resolve any effect of kin selection. We continue to think this is an interesting question to ask of *L. hesperus.* Urban populations of black widows, are often so densely populated that individual webs overlap, leading to heightened levels of sociality (JCJ, pers. obs.). Under such circumstances, the ability to direct cannibalistic behavior away from kin and towards non-kin may indeed provide substantial indirect fitness benefits.

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