ISSN: 0975-833X

Available online at http://www.journalcra.com

INTERNATIONAL JOURNAL OF CURRENT RESEARCH

International Journal of Current Research
Vol. 13, Issue, 07, pp.18313-18317, July, 2021

DOI: https://doi.org/10.24941/ijcr.41742.07.2021

RESEARCH ARTICLE

INFLUENCE OF KIN SELECTION ON CANNIBALISM IN SUCCESSIVE INSTARS OF Phidippus audax (ARANEAE: SALTICIDAE)

[1,*]Marianne W. Robertson, [2]Daniel M. Delaney, and [3]Casey R. Watson

[1]Department of Biology, Millikin University, 1184 West Main St., Decatur, IL, 62522
[2]Family Medicine Resident, Firelands Regional Medical Center, Sandusky, OH, 44870
[3]Department of Physics, Millikin University, 1184 West Main St., Decatur, IL, 62522

ARTICLE INFO

Article History:
Received 25th April, 2021
Received in revised form
19th May, 2021
Accepted 24th June, 2021
Published online 30th July, 2021

Key Words:
Inclusive Fitness, Kin Selection, Kin Recognition, Cannibalism, Relatedness, Siblings.

Corresponding author:
Marianne W. Robertson

ABSTRACT

Kin selection is common in nature among cannibalistic organisms that have a high kin encounter rate. The jumping spider Phidippus audax (Araneae: Salticidae) has a high, localized population density and is widely distributed. We studied the effects of kinship on cannibalism in the second through the seventh instars of this species. We observed low levels of cannibalism in second instars and high levels in fourth through seventh instars, with no effects of relatedness in those stages. In the third instar, siblings avoided cannibalism, and non-siblings were highly cannibalistic. Starvation results were similar with the only significant difference occurring in the third instar where starvation was significantly higher in related versus unrelated pairs. These results may indicate an age-dependent instinctive response among spiderlings that determines whether or not they will starve rather than confront and attempt to cannibalize their own kin.

Citation: Marianne W. Robertson, Daniel M. Delaney, and3 Casey R. Watson. "Influence of kin selection on cannibalism in successive instars of Phidippus audax (Araneae: Salticidae).*", 2021. International Journal of Current Research, 13, (07), 18313-18317.*

INTRODUCTION

Kin selection and kin recognition are phenomena that occur in taxonomically diverse groups of animals, including mammals (Hauber and Sherman, 2000), birds (Komdeur and Hatchwell, 1999), amphibians (Pfennig *et al*., 1999), insects (Panek and Gamboa, 2000), mites (Schausberger and Croft, 2001), and spiders (Bilde and Lubin, 2001; Roberts *et al*., 2003). Typically, kin selection is dependent upon kin recognition (Roberts *et al*., 2003). Kin selection is expressed in a variety of circumstances, but for many species, it is expressed as differential cannibalism of related versus non-related conspecifics (Pfennig, 1997). Cannibalism is common throughout the animal kingdom (Elgar and Crespi, 1992). In spiders, cannibalism serves multiple functions which include reducing competition (Buddle *et al*., 2003; Wagner and Wise, 1996), increasing energy intake (Hvam *et al*., 2005), and ensuring sperm usage (Schneider and Lubin, 1997, 1998). Additionally, it is often a decision made in a foraging context (Pfennig, 1997; Roberts *et al*., 2003). When an organism selects prey, it is attempting to meet three nutritional goals: maximize energy intake, balance nutrient composition, and minimize toxin consumption (Toft, 1999) and, under some conditions, cannibalism can represent an optimal compromise between these three factors.

Cannibalism also has disadvantages (Nishimura and Isoda, 2004). For instance, in gregarious or social species, where related individuals may encounter each other, inclusive fitness can decline substantially (Dobler and Kolliker, 2011). Since cannibalism of kin decreases inclusive fitness (Crump, 1990; Nishimura and Isoda, 2004), cannibalistic individuals should preferentially eat unrelated individuals when presented with the choice of consuming relatives versus non-relatives (Schausberger, 2004). Thus, the presence of kin recognition should be high in organisms with a high kin encounter rate (Wise, 2006).

Kin recognition is common in many cannibalistic species (Elwood, 1992; Panek and Gamboa, 2000; Pfennig, 1997; Roberts *et al*., 2003; Sadler and Elgar, 1994).

The risk of cannibalizing kin is inversely proportional to dispersal (Pfennig, 1997; Sadler and Elgar, 1994). After dispersal, when an organism does not frequently encounter kin, kin selection would have a minimal effect on inclusive fitness (Grafen 2009). Wise (2006) showed that kin discrimination was present in the spiderlings of a subsocial burrowing wolf spider and not present in spiderlings from nonburrowing, more vagile wolf spiders. Similar results have been found in *Tigrosahelluo*, [*Tigrosa helluo*Brady 2012 (Tmf from *Hogna helluo* (Walckenaer, 1837)], a vagile wolf spider, where kin recognition was present in the pre-dispersal instar and was not present post-dispersal (Roberts *et al*., 2003).

Spiders are primarily obligate predators, and cannibalism is represented in many families (Buddle *et al*., 2003; Roberts *et al*., 2003; Wagner and Wise, 1996; Wise, 2006). Some female spiders sexually cannibalize males during courtship either while copulating or after decoupling (Buskirk *et al*., 1984; Elgar, 1992; Johnson, 2001; Taylor and Jackson, 1999). There are cases of females eating their own eggs (oophagy) (Willey and Coyle, 1992) or young (filial cannibalism) (Wise, 2006). Males of *Stegodyphus lineatus* have been documented killing a female's brood so that she will reproduce again using their sperm (Schneider and Lubin, 1997). In some spiders, juveniles eat their mother before dispersing. Matriphagy is positively correlated with spiderling survival in species such as the Australian thomisid, *Diaea ergandros* (Wise, 2006). Jackson (1977, 1978) reported that 27% of the diet of the jumping spider *Phidippus. johnsoni* consisted of other spiders, and 9% of these were conspecifics**.** Other studies have yielded similar results for jumping spiders, including the primarily araneophagic genus *Portia* (Harland and Jackson, 2000; Wilcox and Jackson, 1998). In some spiders, cannibalism among juveniles might limit species abundance (Roberts *et al*., 2003; Wise, 2006). For example, juveniles of the wolf spider *Pardosa lugubris* may be the primary predators of their species (Edgar, 1969), with juveniles including conspecifics as 29% of their diet (Hallander, 1970). Some, but not all (Hvam *et al*., 2005), cannibalistic spider species examined identify and avoid eating close relatives (Evans, 1999; Bilde and Lubin, 2001; Anthony, 2003; Roberts *et al*., 2003). Kin recognition in spiders is likely a chemically mediated process (Evans, 1999; Miller, 1989). Roberts *et al*. (2003) state that with many chemical compounds found on a spider's body, web, or draglines, chemical communication is one of the most likely pathways for kin recognition.

We examined the jumping spider Phidippus audax (Araneae: Salticidae) from egg sac emergence - the seventh instar to determine whether differential cannibalism of kin versus non-kin occurs throughout successive instars. *P. audax* is distributed throughout most of the United States and has a high localized population density (Jackson, 1978). Egg hatching and emergence from the egg sac are times when spiderlings encounter related conspecifics. We could not examine first instar spiderlings because they are inside the egg sac and relying on stored yolk for nutrition. The second-instar of *P. audax* is the emerging stage consisting of spiders that have been living together within the confines of the egg sac. Although there are not field data on which instar(s) disperse and how far they disperse in nature, early instars may not disperse far enough to avoid kin encounters, so kin selecn, if present, should be adaptive in the early stages of the life cycle.

METHODS

Immature *P. audax* spiders were collected at the Rock Springs Center for Environmental Discovery, Macon Co., Decatur IL. Upon maturity, the spiders were randomly mated and maintained until oviposition. No spider was mated more than once to ensure that clutches would consist of full siblings. Spiderlings (n = 1171) were immediately separated after they emerged from the egg sacs as second instars. A unique identification code was assigned to each individual to record which ones were siblings. Spiderlings were maintained individually in the Millikin University Arachnology Laboratory in clear Petri dishes (10 cm diameter x 1.5 cm depth). When not in trials, each spiderling was provided with water *Ad libitum* via a water-saturated cotton ball and maintained on a feeding regimen (Table 1) limited to *Drosophila melanogaster* to ensure that all spiders ingested the same prey species. As spiders molted and increased in size, they were provided with more prey.

We examined whether *P. audax* was more likely to cannibalize siblings versus non-siblings in the second through seventh instars. Trials could not be conducted beyond the seventh instar due to low sample sizes. On the day of each molt, the mass of each molted spiderling was recorded. Spiderlings that molted within four days of each other and had the same mass (± 0.0001 g) were paired. If more than two spiders were appropriate for pairing, then a drawing was used to randomly determine which two would be paired. We tested 710 spiders, and no spider was used in more than one trial. A minimum of 30 trials were conducted on sibling pairs and on non-sibling pairs within each instar, with the exception of instar 7 which had a limited number of remaining untested spiders when matched for weight (Table 2).

Each trial involved pairing two spiders based on mass and relatedness, putting them in the same Petri dish with a water-saturated cotton ball, and feeding them one wingless fruit fly per day until at least one spider was deceased. Although the nutritional needs of each instar differ, and cannibalism may increase in successive instars as prey proportionally decreases, we held prey number of prey constant in all trials because our research addressed whether sibling versus non-sibling differences would arise, not whether cannibalism rates would change in successive instars.

One spider in each pair was marked ventrally and one dorsally with nontoxic Paper-Mate white-out. A coin flip determined which spider was marked ventrally. If a fruit fly was still alive the subsequent day, a new fruit fly was not introduced. Deceased spiders were examined under a microscope to determine whether death resulted from cannibalism or other causes. A mutilated and deflated appearance, sometimes accompanied by visible puncture wounds, characterized a cannibalized spider, whereas a non-malformed, non-deflated spider with legs that started to curl characterized a spider that died from other causes, such as starvation. A Welch's t-test was used for analysis for related versus unrelated pairings in each instar because it is robust to differences in sample sizes and sample variance (Welsh, 1947). Although IACUC protocol approval is not mandated for invertebrates, we did follow their animal care and use guidelines.

RESULTS

When spiderlings first emerged from the egg sacs as second instars, there was minimal cannibalism with no significant difference between means of related versus unrelated individuals (Table3). When the spiderlings reached the fourth - seventh instars, the percentage of cannibalism reached a plateau of ~75% ± 15% (mean ± SD), which was also statistically consistent for both related and unrelated spiders. However, in the third instar, there is a statistically significant difference between the percentage of cannibalism among related (20.0± 3.65%) versus unrelated (76.7 ± 14.00%) individuals ($p = 2.34 \times 10^{-6}$; $p > 0.05$ for all other instars). Trends were similar for the percentage of deaths, presumably from starvation, in related versus unrelated pairs (Table 4). In the third instar, there is a statistically significant difference between the percentage of starvation events among related (50 ± 9.13%) and unrelated (13.3 ± 2.43%) individuals ($p = 1.95 \times 10^{-3}$). The results are statistically consistent for all other instars ($p > 0.05$). The number of days until death was statistically consistent for both related and unrelated pairs ($p > 0.05$) for all instars.

Table 1. Number of *Drosophila melanogaster* provided to Phidippus audax three times per week as a maintenance diet for spiders not in trials

Instar	Number of fruit flies
2	2
3	3
4	4
5	7
6	9
7	12

Table 2. Number of trials of sibling/sibling pairs and non-sibling/non-sibling pairs tested in second - seventh instars of Phidippus audax

Instar	Number of Sibling Trials	Number of Non-sibling Trials
2	37	62
3	30	30
4	30	31
5	30	30
6	30	30
7	6	9

Table 3. Comparison of the average percent of cannibalized individuals per instar ± SD in related versus unelated pairs of Phidippus audax ($p = 2.34 \times 10^{-6}$ for instar 3*; $p > 0.05$ for all other instars). *Only instar with significant difference between related versus unrelated pairs

Instar	Related (Mean + SD)	Unrelated (Mean + SD)
2	5.41 ± 0.89	3.23 ± 0.41
3*	20.0 ± 3.65	76.7 ± 14.00
4	60.0 + 10.95	71.0 + 12.75
5	73.3 + 13.39	76.7 + 14.00
6	76.7 ± 14.00	70.0 ± 12.78
7	83.3 ± 34.02	77.8 ± 25.93

Table 4. Comparison of the average percent of starvations per instar ±SD in related vs. unrelated pairs of Phidippus audax ($p = 1.95 \times 10^{-3}$ for instar 3*; $p > 0.05$ for all other instars). *Only instar with significant difference between related versus unrelated pairs

Instar	Related (Mean + SD)	Unrelated (Mean + SD)
2	40.5±6.66	37.1±4.71
3*	50.0±9.13	13.3±2.43
4	36.7±6.69	25.8±4.63
5	26.7+4.87	23.3+4.26
6	23.3±4.26	26.7±4.87
7	16.7±6.80	22.2±7.41

DISCUSSION

When spiderlings were young and weak (instar 2), there was a low and statistically consistent percentage of cannibalism events among both related and unrelated pairs. When spiderlings were older (instars 4-7), the percentage of cannibalism events increased but was still statistically consistent among related and unrelated pairs. However, in instar 3, the percentage of cannibalism was significantly lower in related versus unrelated pairs. Starvation results were similar with the only significant difference occurring in instar 3 where starvation was significantly higher in related versus unrelated pairs.

These results may indicate an age-dependent instinctive response among spiderlings that determines whether or not they will starve rather than confront and attempt to cannibalize their own kin. In instar 3, siblings tended to starve rather than cannibalize a significantly larger fraction of the time than non-related individuals. To avoid decreasing inclusive fitness, second instar spiderlings that have not lived independently would be expected to avoid/suppress cannibalism. Similarly, cannibalism was less frequent in second instars of the wolf spider *Tigrosa helluo* compared to the third instars (Roberts *et al.*, 2003). However, the presence or absence of foraging behavior in the second instar becomes important here. If *P. audax* does not forage because they still have sufficient yolk or are too weak for aggressive encounters in the second instar, then it cannot be said that the lack of cannibalism implies kin discrimination during this stage. Rather, it would be due to a lack of feeding in general.

However, if foraging behavior is present in the second instar, then there is evidence for a general avoidance of cannibalism rather than just a lack of feeding. Forster (1977) showed that only 52% of second instar spiderlings of the jumping spider *Trite auricoma* caught prey within seven days. Edwards and Jackson (1994) found that second instar *Phidippusregius* can live 51 days, on average, without food if water is provided, but they required fewer days before molting if provided with both food and water. Thus, *P. regius* does not have to eat as second instar spiderlings; however, if they have the option, consuming insect prey speeds up development. Morse (2000) found that spiderlings of the thomisid *Misumenavatia* emerging from egg sacs in the field seldom caught prey immediately even under high prey densities. We did not quantify feeding rates among different instars, but we did observe that second instars caught fewer prey overall than subsequent instars despite being given fewer prey.

Cannibalism was present in all remaining instars (3-7) with significantly less cannibalistic behavior among related versus unrelated individuals in the third instar. It is interesting that there was significantly higher mortality, presumably due to starvation, in the third instar where cannibalism of kin was low. These data provide an indication of kin recognition by *P. audax* in this instar. Dispersal may be limited in the third instar, thereby leading to the suppressed cannibalism we observed in related pairs at this stage of development.

Following dispersal, *P. audax* has a vagrant lifestyle for nine months of the year (Roach, 1987) before becoming territorial at the penultimate or adult stage (Edwards, 2008). Therefore, even if third instars disperse, they may not have dispersed far enough away from the hatching site to avoid kin encounters, making kin recognition and avoidance of kin cannibalism adaptive via inclusive fitness. Due to *P. audax*'s large home range and generalist prey diet, it is unlikely to encounter kin after dispersal (Lion and Gandon, 2009) at which point cannibalism of conspecifics would be beneficial, but kin discrimination would no longer be expected. In the future, it would be beneficial to perform field observations to determine when in the life cycle P. *audax* spiderlings disperse and to observe the magnitude of differential dispersal distances by various instars for *P. audax*. It would also be interestingto study the effects of kin selection and recognition on sexual cannibalism in adult *P. audax*.

ACKNOWLEDGMENTS

We are grateful to the Millikin University Summer Undergraduate Research Fellowship and the Millikin Biology Department for funding. The authors have no conflicts of interest to declare.

Key Points

We observed low levels of cannibalism in second instars and high levels in fourth through seventh instars, with no effects of relatedness in those stages. In the third instar, siblings avoided cannibalism, and non-siblings were highly cannibalistic. Starvation results were similar with the only significant difference occurring in the third instar where starvation was significantly higher in related versus unrelated pairs. There may indicate an age-dependent instinctive response among spiderlings that determines whether or not they will starve rather than confront and attempt to cannibalize their own kin.

REFERENCES

Anthony, CD. 2003. Kinship influences cannibalism in the wolf spider, *Pardosamilvina*. *Journal of Insect Behavior* 16, 23-36.

Baker, L. 2007. Effect of corridors on the movement behavior of jumping spider *Phidippus princeps* (Araneae: Salticidae). *Canadian Journal of Zoology* 85, 802-808.

Bilde. T. and Lubin, Y. 2001. Kin recognition and cannibalism in a subsocial spider. *J. Evol. Biol.* 14, 959-966.

Buddle, CM., Walker, SE., and Rypstra, A.L. 2003. Cannibalism and density-dependent mortality in the wolf spider *Pardosamilvina* (Araneae: Lycosidae). *Canadian Journal of Zoology* 81, 1293-1297.

Buskirk, RE., Frohlich, C., and Ross, K.G. 1984. The natural selection of sexual cannibalism. *The American Naturalist* 123, 612-625.

Crump, ML. 1990. Possible enhancement of growth in tadpoles through cannibalism. *Copeia* 2, 560-564.

Dobler, R. and Kolliker, M. 2011. Influence of weight asymmetry and kinship on siblicidal and cannibalistic behavior in earwigs. *Animal Behaviour* 82:667-672.

Edgar, WD. 1969. Prey and predators of the wolf spider *Lycosalugubris*. *Journal of Zoology* 159, 405-411.

Edwards, GB. (2008. Anecdotal field notes on Florida *Phidippus*(Araneae: Salticidae), with notes on territoriality in *P. regius*. *Peckhamia* 66, 96-100.

Edwards, GB. and Jackson, RR. 1994. The role of experience in the development of predatory behavior in *Phidippusregius*, a jumping spider (Araneae: Salticidae). *New Zealand Journal of Zoology* 21, 269-277.

Elgar, MA. 1992. Sexual cannibalism in spiders and other invertebrates. Pp. 128-155. *In* Cannibalism: Ecology and evolution among diverse taxa. (M.A. Elgar & B.J. Crespi, eds.). Oxford University Press, New York.

Elgar, MA. and Crespi. BJ. 1992. Cannibalism: Ecology and evolution among diverse taxa. Oxford: Oxford University Press.

Elwood, R. 1992. Pup-cannibalism in rodents: Causes and consequences. Pp. 299-322. *In* Cannibalism: Ecology and evolution among diverse taxa. (M.A. Elgar & B.J. Crespi, eds.). Oxford University Press, New York.

Evans, TA. 1999. Kin recognition in a social spider. *Proceedings of the Royal Society B: Biological Sciences* 266, 287-292.

Forster, LM. 1977. Some factors affecting feeding behavior in *Trite auricoma*spiderlings (Araneae: Salticidae). *New Zealand Journal of Zoology* 4, 435-443.

Grafen, A. 2009. Review: Formalizing Darwinism and inclusive fitness theory. *Philosophical Transactions of the Royal Society B* 364, 3135-3141.

Hallander, H. 1970. Prey, cannibalism, and microhabitat selection in the wolf spiders *Pardosachelata* O. O. Muller and *P. pullata*Clerck. *Oikos*. 21, 337-340.

Harland, DP., and Jackson, RR. 2000. Cues by which *Portia fimbriata*, an araneophagic jumping spider, distinguishes jumping-spider prey from other prey. *The Journal of Experimental Biology* 203, 3485-3494.

Hauber, ME. and Sherman, PW. 2000. The armpit effect in hamster kin recognition. *Trends of Ecology and Evolution* 15, 349-350.

Hvam, A., Mayntz, D., and Nielsen, RK. 2005. Factors affecting cannibalism among newly hatched wolf spiders (Lycosidae, *Pardosaamentata). The Journal of Arachnology* 33, 377-383.

Jackson, RR. 1977. Prey of the jumping spider *Phidippusjohnsoni* (Araneae: Salticidae). *Journal of Arachnology* 5, 145-149.

Jackson, RR. 1978. Life history of *Phidippusjohnsoni* (Araneae, Salticidae). *Journal of Arachnology* 6, 1-29.

Johnson, JC. 2001. Sexual cannibalism in fishing spiders (*Dolomedes triton*): an evaluation of two explanations for female aggression towards potential mates. *Animal Behavior* 61, 905-914.

Komdeur, J. and Hatchwell, BJ. 1999. Kin recognition: Function and mechanism in avian societies. *Trends of Ecology and Evolution* 14, 237-241.

Lion, S, and Gandon, S. 2009. Habitat saturation and the spatial evolutionary ecology of altruism. *Journal of Evolutionary Biology* 22 (7), 1487-1502.

Miller, GL. 1989. Subsocial organization and behavior in broods of the obligate burrowing wolfspider*Geolycosaturricola* (Treat). *Canadian Journal of Zoology* 67, 819-824.

Morse, DH. 2000. Flower choice by naïve young crab spiders and the effect of subsequent experience. *Animal Behaviour* 59, 943-931.

Nishimura, K., and Isoda, Y. 2004. Erratum to evolution of cannibalism: referring to costs of cannibalism. *Journal of Theoretical Biology* 228, 293-302.

Panek, LM. and Gamboa, GJ. 2000. Queens of the paper wasp *Polistesfuscatus*(Hymenoptera: Vespidae) discriminate among larvae on the basis of relatedness. *Ethology* 106, 159-170.

Pfennig, DW. 1997. Kinship and cannibalism: Understanding why animals avoid preying on relatives offers insights into the evolution of social behavior. *BioScience* 47, 667-675.

Pfennig, DW. and Frankino, WA. 1997. Kin-mediated morphogenesis in facultatively cannibalistic tadpoles. *Evolution* 51, 1993-1999.

Pfennig, DW., Collins, JP., and Ziemba, RE. 1999. A test of alternative hypotheses for kin recognition in cannibalistic tiger salamanders. *Behavioral Ecology* 10, 436-443.

Roach, SH. 1987. Observations on feeding and prey selection by Phidippus audax (Hentz) (Araneae: Salticidae). *Environmental Ecology* 16, 1098-1102.

Roberts, JA., Taylor, PW., and Uetz, GW. 2003. Kinship and food availability influence cannibalism tendency in early-instar wolf spiders (Araneae: Lycosidae). *Behavioral Ecology and Sociobiology* 54, 416-422.

Sadler LM. and Elgar, MA. 1994. Cannibalism among amphibian larvae: a case of good taste. *Trends of Ecology and Evolution* 9, 5-6.

Schausberger, P. 2004. Ontogenetic isolation favours sibling cannibalism in mites. Animal Behaviour 67, 1031-1035.

Schausberger, P. and Croft., BA. 2001. Kin recognition and larval cannibalism by adult females in specialist predaceous mites. Animal Behavior 61, 459-464.

Schneider, JM. and Lubin, Y. 1997. Infanticide by males in a spider with suicidal maternal care, *Stegodyphus lineatus* (Eresidae). Animal Behavior 54, 305-312.

Schneider, JM. and Lubin, Y. 1998. Intersexual conflict in spiders. *Oikos* 83, 496-506.

Taylor, PW. and Jackson, RR. 1999. Habitat-adapted communication in *Trite planiceps*, a New Zealand jumping spider (Araneae, Salticidae). *New Zealand Journal of Zoology* 26, 127-154.

Toft, S. 1999. Prey choice and spider fitness. *Journal of Arachnology* 27: 301-307.

Von Schantz, T. 1984. Spacing strategies, kin selection, and population regulation in altricial vertebrates. Wiley 42, 48-58.

Wagner, JJ. and Wise, DH. 1996. Cannibalism regulates densities of young wolf spiders: Evidence from field and laboratory experiments. *Ecology* 77, 639-652.

Welch, DL. 1947. The generalization of ‘Student’s’ problem when several different population variances are involved.*Biometrika* 34, 28-35.

Wilcox, RS., and Jackson, RR. 1998. Animal Cognition in Nature. San Diego, California. Academic Press, Print.

Willey, MB. and Coyle, FA. 1992. Female spiders (Araneae: Dipluridae, Desidae, Linyphiidae) eat their own eggs. *Journal of Arachnology* 20, 151-152.

Wise, DH. 2006. Cannibalism, food limitation, intraspecific competition, and the regulation of spider populations. *Annual Review of Entomology* 51, 441-465.

****