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ORIGINAL ARTICLE

Cannibalism in the pea aphid, *Acyrthosiphon pisum*

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Abstract Previous observations of cannibalism have been made in the aphid *Acyrthosiphon pisum* (L.): this article seeks to quantify factors contributing to such behaviors. We observed and quantified the responses of a number of clones and life stages to varying levels of starvation, in the form of increasingly desiccated *Vica faba* L. plants (receiving 50, 25, or 10 mL every second day) or a complete absence of host plant. We found that, while the longest incidences of cannibalism are carried out by juveniles ($F = 3.45$, $P = 0.019$, df $= 3$) and targeted at adults, the starvation treatments had the most significant effect on the prevalence of cannibalism in mature *A. pisum* ($F = 2.24$, $P = 0.025$, df $= 9$). Furthermore, there was no difference between the prevalence or duration of cannibalistic activities within and between different clones ($P \geq 0.05$ in all cases), though juveniles were more likely to target unrelated aphids ($V = 6\,112$, $P = 0.011$), and spent more time feeding on aphids from the same culture ($V = 6\,062$, $P = 0.018$).

Key words *Acyrthosiphon pisum*, *Aphididae*, behavior, cannibalism, kin selection, modularity

Introduction

Far from being an aberrant behavior resulting from stress in captivity (Dionne, 1985; Dixon, 2000; Nishimura & Isoda, 2004), cannibalism has been frequently observed *in vivo* (Fox, 1975; Polis, 1981) in multiple taxa ranging from single-celled ciliates (Wicklow, 1988) to primates (Watts & Mitani, 2000). Thus so far, there has been only a single formal report (Banks *et al.*, 1968) of apparently cannibalistic activity in the Aphididae, however, and this is nearly 5 decades old. Hence, the aim of this article is to take a fresh look at the behavior as it has been observed in the apterous viriginoparae of *Acyrothosiphon pisum* (L.), to confirm this report and others (Aal-Harbi, personal communication, 2010; Leather, personal observation, 2010, 2011; Desjonqueres, 2012; Cooper & Leather, unpublished data), and to determine the circumstances under which this behavior occurs.

Given the phytophagous nature of aphids and their dependence on a high phloem sap pressure (Dixon, 1998), the extent to which *A. pisum* is capable of cannibalism might be questioned (see Fig. 1). First, cannibalism has been observed in a number of species previously thought purely vegetarian (most famously the great apes; Watts & Mitani, 2000). Second, aphids possess a relatively powerful cibarial pump, with which they can imbibe unpressurized fluids (Lowe, 1967; Dixon, 1998). Third, aphids of several species have been known to probe unusual substrates; including human flesh (Takahashi, 1930; Aoki & Kurosu, 2010; Leather, 2013).

A number of the common factors affecting the prevalence of cannibalism can be ruled out immediately: sexual cannibalism is impossible as the behavior has only been observed in parthenogenic virginoparae (Buskirk *et al.*, 1984; Simon *et al.*, 2002; Leather, 2011), and changes in density alone are an unlikely controlling factor, as colonies of *A. pisum* can grow quite dense without any discernible intraspecific predation (personal observation). It

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Fig. 1 Juvenile aphid engaged in purported cannibalistic behavior. Folded antennae indicate feeding behavior (Hardie & Powell, 2000).

is also unlikely that this is incidental cannibalism of the type common in filter feeders (Polis, 1981) as, in a reversal of the norm (Agarwala & Dixon, 1992; Elgar & Crespi, 1992), much of the reported cannibalistic activity has taken the form of early instars feeding on more mature stages (Al-Harbi, personal communication, 2010; Cooper & Leather, unpublished data; Leather, personal observation, 2010, 2011).

Therefore, the most likely controlling factor is variation in the quantity or quality of the nutrition on offer (Polis, 1981; Dionne, 1985; Bortolotti *et al.*, 1991; Agarwala & Dixon, 1992; Via, 1999; Simpson *et al.*, 2006). This conclusion is supported by the low-nutrient situation in which the initial observation of cannibalism was made in *A. pisum* (Banks *et al.*, 1968). Furthermore, the normal aphid diet is nutritionally unbalanced, being very high in sugars but low in amino acids, most of the latter are nonessential types, and present in unsuitable proportions to fuel growth and reproduction (Sasaki *et al.*, 1990; Douglas, 1993, 1996, 1998; Ashford *et al.*, 2000). Therefore, many aphid species form mutualisms with bacteria such as *Buchnera aphidicola* (Munson *et al.*, 1991; Douglas, 1996, 1998; Moran *et al.*, 2003; van Ham *et al.*, 2003), where sucrose is exchanged for the nutritional components lacking from phloem sap (Dixon, 1998; Douglas, 1998). Hence, logic would suggest that in situations where sucrose is unavailable, cannibalism becomes selectively advantageous as it may permit the acquisition of sufficient nutrients, in the correct ratios, to fund the survival and generation of alate virginoparae and the clone's escape from a nutrient-poor situation; an example of what is called the lifeboat mechanism (Polis, 1981; Meffe & Crump, 1987; van den Bosch *et al.*, 1988). Presumably cannibalistic behaviors have not been widely observed to date either because behavioral studies of aphididae tend to take place on healthy plants, or because the cost-benefit ratio of cannibalism is poor where sucrose is plentiful. The latter could be because of the energy expenditure involved in operating the cibarial pump, or because the yield of nutrients does not match that provided by the symbiotes, as the aphid digestive system may not be able to process some proteins and lipids, though evidence is mounting that *A. pisum* possesses some capacity to disassemble proteins and peptides (Cristofoletti *et al.*, 2003), possibly as an adaptation to combat plant defense peptides, though perhaps also suggestive of a long history of cannibalism in the species.

It has also been suggested that a form of kin selection might play a role in cannibalism among *A. pisum* (Al-Harbi, personal communication, 2010; Leather, personal observation, 2010), more specifically that cannibalistic individuals have been observed to either feed preferentially, or to be permitted to feed solely upon members of the same clone. While selection has generally favored mechanisms to suppress such activities amongst kin (Pfennig *et al.*, 1999; Schausberger & Croft, 2001), it has been known for parents to allow themselves to be consumed by offspring where to do so would promote offspring survival and fitness (Polis, 1981). Furthermore, the clonal nature of parthenogenically generated aphid lines such as those under observation means that clones are better considered not as groups of kin, but as members of a single, highly dispersed individual (a genet) composed of multiple genetically identical units (ramets; Janzen, 1977; Tuomi & Vourisalo, 1989). Hence, selection would be at the level of the clone (individual selection, rather than kin selection), and behaviors improving the survival of the genet (such as passivity in the face of cannibalism by other ramets) would be selected for, even those which result in the deaths of individual ramets. The main problem with this theory is that there is no known kin-recognition mechanism in aphids, even in the highly territorial, gall-forming, Pemphigidae (Abbot *et al.*, 2001; Foster, 2002), though, given the above, it is likely one would be selected for if starvation and cannibalism were frequent.

There are two hypotheses that this study wishes to test, based on the above body of theory and our own observations. First, it is hypothesized that reduced dietary quality increases the rate of cannibalism. Second, that the targets of cannibalism will tend to be more related to the cannibalizing individual than would be expected if the target was random. Hence that the target individual is more likely to be from the same culture or the same clone (cultures may consist of multiple clonal lines), and that these individuals will be cannibalized for a longer period.

Materials and method

In order to culture the *A. pisum* necessary for this experiment, a number of *Vica faba* L. (var Witkiem Manita; Tozer Seeds) were grown from seed in general purpose compost with John Innes, under natural light supplemented with mercury vapor bulbs (12 : 8-h diurnal cycle) at 20 °C until they reached the 8-leaf stage. Each plant received 50 mL of water every second day. The *V. faba* were distributed in 4 culture cages, and individuals from one of three aphid cultures (green and pink cultures collected from *V. faba*, var. The Sutton at Silwood in 2007 and kept on *Pisum sativum* L., and μ181); a culture collected by York University from *P. sativum*; single collections from field conditions were introduced to each cage (such that there were 2 cages containing the green culture, and one each containing the other cultures). It is very likely that each culture contains multiple clones (groups of genetically identical virginoparae), though different clones may not be related. The newly established subcultures were left for a week so as to allow the aphid populations to increase in size.

In order to test the effect of starvation and genetics on the prevalence of apparently cannibalistic behaviors, the procedures given below were followed. First, a number of *V. faba* were grown from seed, as above, until they had 8 leaves. The following watering treatments were then applied: 50 mL (control), 25 or 10 mL every second day, for 7 d. Since aphids consume a largely fluid diet, reducing the water content of plants ought to reduce their nutritional suitability. At the same time clones were segregated by isolating several adult aphids from each culture in clip-cages (constructed as in MacGillivray & Anderson, 1957) on separate *V. faba* until they produced 2 first-instar offspring.

The adult (Kin, or K) aphid were then dusted with either blue or pink fluorescent powder, as will its offspring (Juvenile Blue [JB] and Juvenile Pink [JP]). The kin group was then placed in either an empty 3-cm Petri dish or in a Petri dish attached to one of the plants treated as above, along with an aphid (Non-Kin or NK), randomly chosen from either the same culture (hence possibly a member of the same clone as the kin group: there is no nondestructive way to be certain, ahead of time) or a different culture, dusted with fluorescent powder of opposing color to that used on the K aphid. The 4 assembled aphids were confined to a mature, fully expanded, healthy (undamaged, unblemished, noncholorotic), leaf of one treated plant using the base of a 3-cm-diameter Petri dish (the leaf must be of sufficient size to fill the footprint of the dish), held in place by a 3-cm stainless steel alligator clip, secured to a retort stand with temporary adhesive (Blu-tack; Bostik). After a 15-min acclimatization period, the assembled aphids were manually observed for an hour and the frequencies and durations of the following behaviors or states in the 4 observed individuals recorded: stationary (S), walking (M), and cannibalism (CP, if on a pink aphid, or CB, if on a blue aphid, so as to avoid any unconscious bias concerning whether or not the aphid attacked is known to be from the same clone from the cannibal or not). This was repeated for a total of 12 times for each possible combinations of clones (9 in total) and 30 times for each treatment. In order to avoid any bias resulting from environmental fluctuations, the combinations of cultures were rotated so that the same combination is not in use over 2 consecutive days and 1 replicate of each treatment (4 replicates per day) was performed each day. These will also be rotated so that no 1 treatment is performed at the same time each day. Observations were performed in a laboratory at temperatures of 25 °C and under natural light, between the hours of 10:00 and 14:00.

For each aphid the following parameters were recorded: mean duration spent in motion, stationary, probing the substrate and cannibalizing (for the purpose of this experiment, defined as having mouthparts in contact with another individual, and antennae folded back over the abdomen; Hardie & Powel, 2000), proportion of time spent performing the above behaviors, and the identity of the target of, and duration of, any incidents of cannibalism. All proportions were arcsine transformed before analysis. The effects of clone combination and aphid identity (a combination of aphid age and dust color) on the duration and proportion of events (cannibalism, probing, motion, etc.) observed within the arenas were analyzed using a nested ANOVA (nested thusly: combination of cultures/treatment applied to arena/aphid identity). The effect of aphid age, color, and relatedness (expressed as cultural and clonal identity) on the tendency of individuals to cannibalize or be targeted were examined using a Wilcoxon Rank Sum test. All possible interactions were tested and eliminated if nonsignificant.

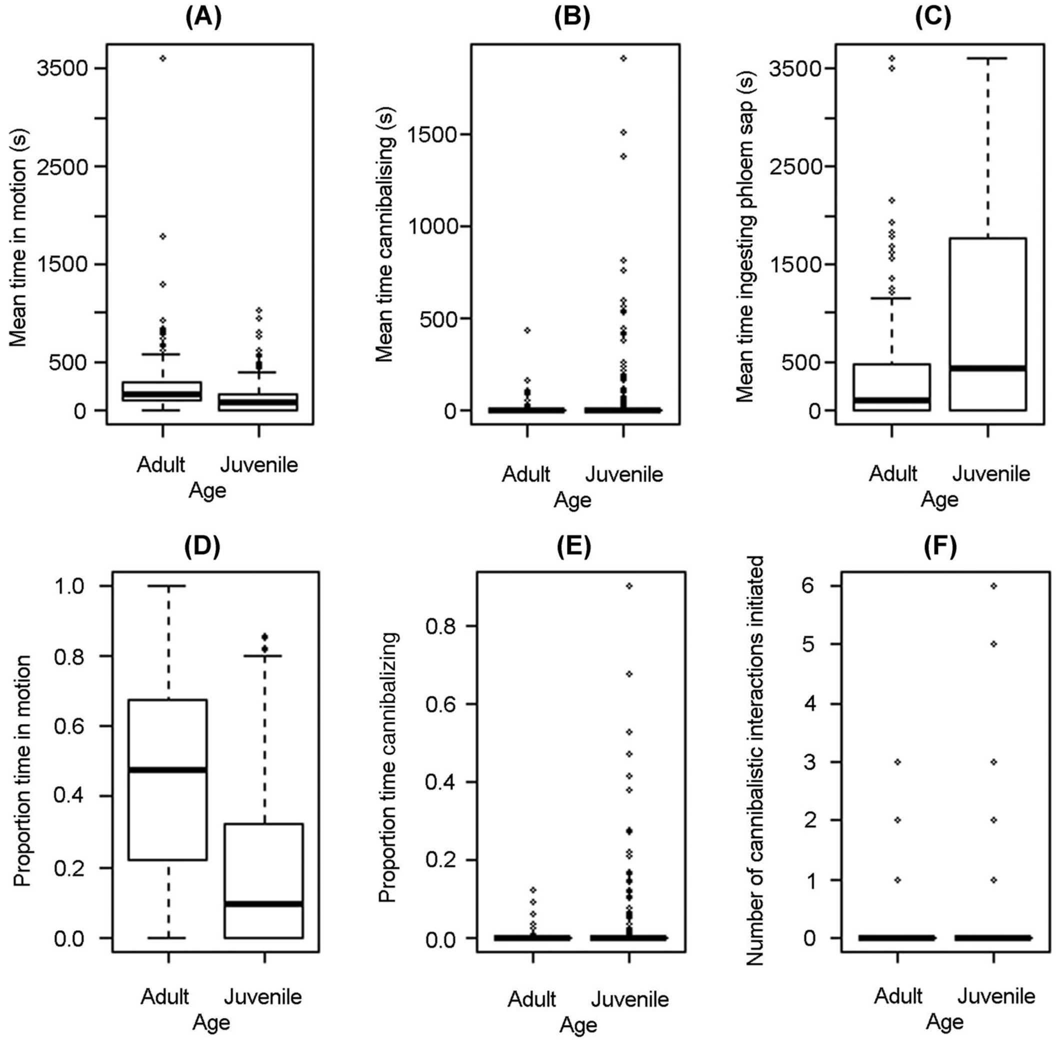

Fig. 2 The effect of *A. pisum* maturity on (A) mean duration spent in motion (s) ($F = 3.47$, $P = 0.018$, df = 3), (B) mean duration engaged in cannibalism (s) ($F = 3.45$, $P = 0.019$, df = 3), (C) mean duration engaged in ingesting phloem sap (s) ($F = 5.34$, $P \leq 0.001$, df = 3), (D) proportion of observed time spent in motion ($F = 8.04$, $P \leq 0.001$, df = 3), (E) proportion of observed time engaged in cannibalism ($F = 4.79$, $P \leq 0.001$, df = 9), (F) number of cannibalistic interactions initiated ($F = 2.64$, $P = 0.05$, df = 3).

Results

The effect of reduced nutrient quality

The analysis of the experimental data proves interesting. First, (see Fig. 2) there is a significant effect of age on behavior: juveniles tend to spend significantly lower mean durations and mean proportions of time mobile ($F = 3.47$, $P = 0.018$, df = 3; $F = 8.04$, $P \leq 0.001$, df = 3), significantly greater mean durations and mean proportions of each replicate engaged in cannibalistic interactions ($F = 3.45$, $P = 0.019$, df = 3; $F = 4.79$, $P \leq 0.001$, df = 9) and a significantly greater proportion of time, on average, probing the leaf surface ($F = 5.34$, $P \leq 0.001$, df = 3), than adults. There is also a significant ($F = 2.64$, $P = 0.05$, df = 3) effect of age on the mean number of cannibalistic interactions that occur in each replicate; specifically the juveniles tend to initiate a greater number of cannibalistic interactions, on average, than adults. No significant effect of the treatment alone was detected, but there is a significant interaction effect between the effects of age and treatment (Fig. 3) on the proportion of time spent involved in cannibalistic interactions ($F = 2.24$, $P = 0.025$, df = 9) and a near-significant effect on the mean time spent in motion ($F = 1.48$, $P = 0.08$, df = 9). Specifically, variation in the levels of nutrient

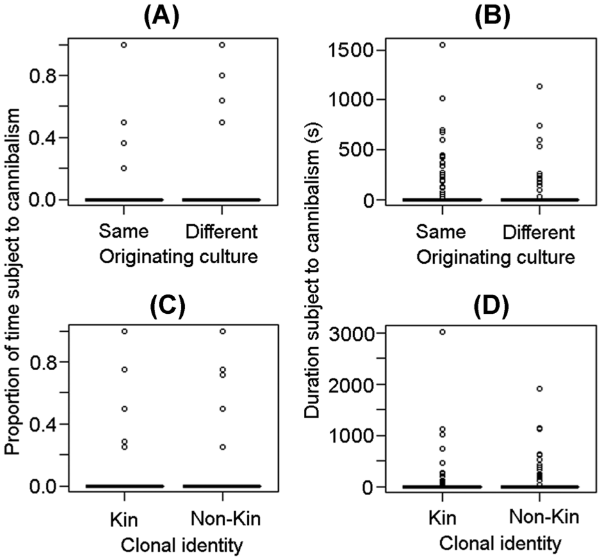

Fig. 3 The effect of originating culture and clonal identity on the proportion of observed time and the mean duration (s) an individual is subject to cannibalism. (A) $V = 6\,112$, $P = 0.011$, (B) $V = 6\,062$, $P = 0.018$, (C) $V = 5\,402$, $P = 0.77$, (D) $V = 5\,409$, $P = 0.72$.

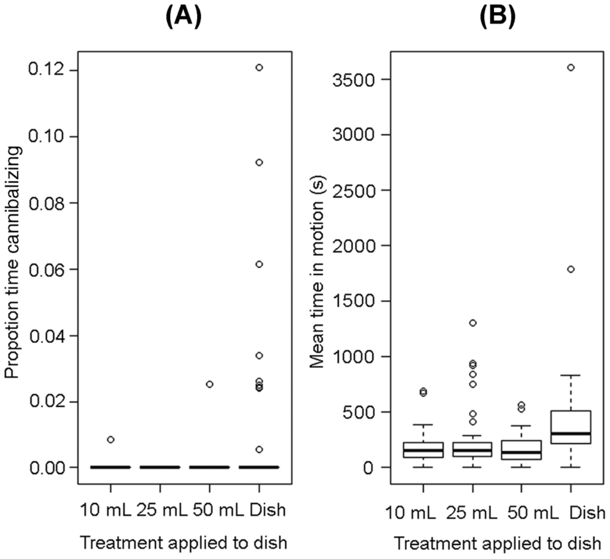

Fig. 4 The effect of nutritional deprivation in adult *A. pisum* on (A) the proportion of observed time engaged in cannibalism ($F = 2.24$, $P = 0.025$, df $= 9$), (B) mean duration spent in motion (s) ($F = 1.48$, $P = 0.08$, df $= 9$).

quality has a greater effect on the behavior of adults than on the behavior of juveniles, and decreases in quality tend to increase the proportion of time spent cannibalizing, and the slightly increase means time spent moving. No other significant effects were detected.

On this basis it is possible to accept the alternate hypothesis concerning the effect of starvation on the frequency, if not duration, of cannibalistic behaviors, if only in adult individuals.

The effects of kinship and culture

Looking more closely at the recorded incidents of cannibalism, it is possible to determine the following. First, the target in all cases of cannibalism was adult. Second, there is no significant effect ($V = 52.5$, $P = 0.08$) of the color of powder applied to the aphids on any aspect of cannibalism. Third, looking at interactions initiated by juveniles (for whom this is a choice test) and combinations where all aphids came from the same culture (so that differences in interactions between cultures do not affect the results), there is no significant difference in the proportion of cannibalistic interactions directed at aphids either immediately related to the cannibal or chosen randomly from the same culture ($V = 5\,402$, $P = 0.77$; see Fig. 4). Nor is there any significant difference in the duration of cannibalistic interactions ($V = 5\,409$, $P = 0.72$). Finally, (again looking at juveniles, but this time all combinations of cultures) a significantly greater numerical proportion of cannibalistic interactions is directed at aphids from different cultures ($V = 6\,112$, $P = 0.011$), but cannibalistic interactions where both individuals are from the same culture tend to last significantly longer than interactions where this is not the case ($V = 6\,062$, $P = 0.018$). Hence, while we cannot accept the hypothesis that more related individuals (individuals from the same culture or clone) are more likely to be the target of cannibalism, we can accept the hypothesis that these individuals are likely to be cannibalized for greater mean durations than those that are not.

Discussion

Based on the results of our observations, we can safely state that, at least for adults, there is some effect of nutrient deprivation on the frequency and duration of cannibalism, as is seen in a number of other insect species such as *Harmonia arxyridis* (Snyder *et al.*, 2000), *Tribolium castaneum* (Via, 1999), and *Dicyphus Hesperus* (Laycock *et al.*, 2006); and rather more generally in the animal and protozoan kingdoms (Polis, 1981). We can also reasonably well state that while the behavior exists at a low level regardless of the availability of nutrients, it undergoes a great increase in frequency when other sources of nutrition are absent. This correlates well with the observations made by Banks *et al.*, (1968); who state that the behavior tended to be observed on host plants that were very nearly deceased. The most logical explanation for this pattern is that the apeterous *A. pisum* are not discriminating feeders and will tend to probe and consume any cellular material that displays an appropriate molecular composition (they are oligophagous, and aphids have been known to sequester secondary metabolites; Sandstrom, 1994; Kazana *et al.*, 2007), but that in the absence of nutrients they will tend to be more mobile and hence more likely to encounter conspecifics (Polis, 1981). Furthermore, the relative rarity of the conditions under which cannibalism occurs at anything more than a low level will have consequences for section. Specifically, the strength of selection and rate of evolution on alleles, behavior, and physiology related to cannibalism is likely to be weak, unless there is a significant selective benefit or cost attached to said variation (Ricklefs & Miller, 2000). The latter is not impossible, particularly as *A. pisum* is autoecious on the Fabacae; Williams & Dixon, 2007), which are relatively vulnerable to the consequences of drought and disease (by comparison with the woody hosts of many other autoecious aphid; (Williams & Dixon, 2007); cannibalism might permit a clone of aphids to survive long enough to produce alates and move to a new host if the current host fails (the lifeboat mechanism; van den Bosch *et al.*, 1988).

A number of questions arise from the above results, however; the first of which we will confront is the fact that all the targets of observed cannibalism were adults. In the case of cannibalistic interactions between adults, this is likely because juvenile individuals are too small a target to be easily grappled by adults, and furthermore represent a relatively small payout for the energy expended in securing them (personal observation). In the case of juveniles, adults represent a superior target because the small size of the juveniles used in the experiment means that once they have successfully mounted an adult they are largely out of the adult's "arc of fire" in terms of defensive kicking and grappling, which they are not when targeting an individual of similar size (Polis, 1981; Pfennig *et al.*, 1999). This is not to say that adults are without defense; the frequent repositioning of juveniles during cannibalistic attempts may suggest some form of clotting mechanism is in action, though it is equally likely that cannibalizing individuals move once they have exhausted the liquid contents of an area, and adults were several times observed to remove cannibals by grooming them off.

Variation in size might also account for the paradoxical observation that juveniles not only probe the *V. faba* leaves for longer but are more given to cannibalism; the relatively small size of the juveniles would result in a low rate of phloem sap uptake compared to adults, therefore they would require a longer period to exhaust the phloem sap in a particular area and not be stimulated to move so often by resource depletion.

A combination of the above is a likely explanation for the observation that changes in nutrient availability only affect the incidence of cannibalism in adult *A. pisum*. First, the higher rate of uptake, and probable higher nutrient requirements of adult aphids, would mean that the effects of nutrient deficiency on behavior would be obvious at higher levels of nutrient availability in adults than juveniles. Second, the relative energy expenditure and risk involved in intra-adult cannibalism (Agarwala & Dixon, 1992; Elgar & Crespi, 1992) indicates that the cost-benefit ratio is unlikely to become favorable except at the highest levels of nutrient deprivation.

The lack of significant difference in the intra/interclone rates and durations of cannibalism may result from the effects of colony adaptation to caged conditions. Specifically, there is initially high mortality and low fecundity within wild populations introduced to culture conditions, due to the strong selection pressures resulting from these conditions (Boller, 1972; Chambers, 1977); it is entirely possible that adaptation to the conditions in which they are reared has reduced the number of clones in each culture to one or very few. If this is true then it is highly probable that, in situations where all individuals are from the same culture, they are also from the same clone and thus that the adults are equally likely to become the targets of cannibalism. It is not possible to confirm or deny this theory with the current data set; future work might include microsatellite analyses in order to establish the relatedness and genetic diversity of experimental colonies and ramets or utilize experimental colonies freshly collected from the field.

A further discrepancy between our hypothesis and the results exists; namely, that while juveniles are more likely to initiate cannibalistic interactions against ramets from different cultures, they spend greater average durations cannibalizing ramets from the same culture. It is likely that this results from an interaction between the different selective consequences of cannibalism between cultures for the cannibal and the target individual. Specifically, while it is more selectively advantageous for the cannibalizing ramet to attack other clones than it is to attack ramets from the same clone (as they gain resources without effecting the survival and reproduction of their own clone), permitting cannibalism by members of different clones is deleterious for the target (as they lose resources, suffer damage, and their clone gains no benefits; Polis, 1981). Consequently, selection should favor a mechanism whereby individuals preferentially cannibalize other clones and resist cannibalism by the same, but permit cannibalism by genetically identical ramets (Pfennig *et al.*, 1999). The main problem with this hypothesis, indeed with any hypothesis concerning the effect of kinship on aphid cannibalism, is that there is no recognized kin recognition mechanism, even among the immensely territorial gall-forming Pemphigidae (Abbot *et al.*, 2001; Wool, 2004). This is not to say that such a mechanism cannot exist in *A. pisum*; a line whose members avoid kin-cannibalism will tend to come to dominate, hence the trait will speared rapidly and a significant selective advantage will be attached to it (Pfennig *et al.*, 1999). On the basis of work in social insects such as ants, where an ability to establish the relatedness of an individual is of great selective importance (Carlin & Hölldobler, 1986; Foster *et al.*, 2006; Hughes *et al.*, 2008), and because a kin-recognition mechanism based on familiarity or colony odor would probably not function well given the life history and behavior of aphid colonies (personal observation), it seems likely that the mechanism in question, at least for juveniles to recognize adults of the same or a related clone, would be dependent on per clone differences in either cuticular hydrocarbons or volatiles released by symbionts (Liang & Silverman, 2000; Wagner *et al.*, 2000). This is certainly something that would bear further investigation.

The penultimate thing that was not as expected was that the combination of cultures used in each replicate does not appear to have a marked effect on aphid behavior. This probably results from a fundamental flaw in the assumptions inherent in the hypothesis concerning the differences between cultures. Namely, it had been assumed that different cultures would have been subject to different selection pressures in the past, and would therefore behave somewhat differently either as a direct or indirect (plieotropic) result of this. Looking at the history of the cultures and current practices used to maintain them, it does not seem likely that this is the case: the Silwood cultures are subject to entirely the same procedures, which do not differ too greatly from those used at York. All 3 cultures were also cultured on exactly the same species of plant (*P. sativum*) prior to use in this experiment, and given the planktonic nature of alate aphids (Blackman, 1974; Dixon & Kindlmann, 1999) it is not a certainty that aphids collected from different parts of the United Kingdom are locally adapted. Only the pink culture can be said to be genetically different from the other cultures used in this study with any degree of certainty, and on the basis of the results it does not appear that these differences have any significant effect on the behaviors examined here.

The last problem, and one that certainly bears confronting, is the sheer volume of unexplained variation visible in the data. Given that almost all possible sources of such variation were either controlled, or taken into account in the analysis, the origin of this variation is somewhat mysterious. The only likely explanation is that variation in droughting and drought response between the plants used in the experiment affected the level of nutrients available to the aphids. This variation is probably the result of rearing plants grown from seed in a greenhouse, as opposed to in a CT room, where the temperature and humidity are more constant. Future attempts to study cannibalism in aphids would do well to take this into account, and to establish clonal lines of host plants in order to remove any effect of genetic variation between plants.

Finally, there are a number of questions raised by this experiment that should be investigated in future. First, and most importantly, it was not possible at this juncture to definitively prove that the behaviors observed were cannibalistic, not merely extended probing, though the conditions under which it has been observed to occur (Banks *et al.*, 1968) suggest cannibalism is more likely. Future workers might wish to approach this problem either by looking for the transfer of specific diet-administered sugars or radioactive isotopes between the target and any individuals cannibalizing it, or by recording electrical penetration graphs from aphids performing cannibalistic behaviors. The former is probably more easily done, as the behavior of aphid stylets and cibarial pumps during cannibalism is not yet understood, and therefore it is not possible to predict with any great certainty what waveforms would be evident during such an experiment. Second, the results gathered here have suggested that some form of kin-recognition mechanism has evolved in *A. pisum*. Given that no such mechanism has been previously noted in any aphid species, even in those where such a mechanism would be extremely selectively favorable (Although some aphids show a limited form of eusociality; Aoki & Makino, 1982; Kurosu & Aoki, 1988; Aoki & Kurosu, 2010) it seems important that this be followed up.

In conclusion, the quantity of nutrients available within the environment can be said to have an effect on the prevalence of cannibalistic behaviors in *A. pisum*, though only in extreme cases of nutrient deficit. That there appears to be a kin selection aspect to the behavior has moderately important implications for the study of interactions between individual aphids, especially in solving the problem of the absence of kin-recognition methods in the taxon.

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Disclosure

The authors declare that they have no conflicts of interest.

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