

Do furtive predators benefit from a selfish herd effect by living within their prey colony?

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Abstract Protection from predators is a recognized benefit of group living for animals. The selfish herd effect implies that individuals in a central position within the group suffer lower predation than individuals at the edges of the group. The midge, *Aphidoletes aphidimyza*, is a furtive predator that lives within aphid colonies where it benefits from a dilution effect that reduces the incidence of intraguild predation. We hypothesized that the selfish herd effect also contributes to midge survival. In laboratory experiments, we examined the distribution of midge larvae within aphid (*Macrosiphum euphorbiae*) colonies and determined the susceptibility of central and peripheral individuals to lacewing, *Chrysoperla rufilabris*, and coccinellid, *Coleomegilla maculata* larvae, two common intraguild predators. The probability of observing a midge in the central zone of an aphid colony was higher than predicted after a 24-h period. During predation tests, midges and aphids in the peripheral zone were attacked first significantly more often than prey in the central zone of the colony. However, because foraging coccinellid and lacewing larvae rapidly disrupt the cohesion among aphids in the colony, midge mortality was subsequently similar in both zones. We conclude that *A. aphidimyza* preferentially choose the

central position of their aphid prey colonies. Such a preference reduces the probability of becoming the first prey attacked by intraguild predators. The effectiveness of the selfish herd for slow-moving midge larvae would depend on the nature and foraging behavior of the predator, as well as on cohesion of the aphid colony.

Keywords Defensive mechanism · Anti-predator behavior · Intraguild predation · Predatory midge · Indirect effect

Introduction

Defense against natural enemies is one of the main advantages associated with group living. Three types of passive group defenses have been described. First, the encounter effect favors being in groups because the probability of being detected by predators does not increase in direct proportion to group size (Inman and Krebs 1987; Wrona and Dixon 1991). Second, once a predator has localized a prey colony, the dilution effect favors being in a group because the individual's probability of being attacked by a predator decreases (Edmunds 1974; Pulliam and Caraco 1984; Inman and Krebs 1987; Vulinec 1990; Mooring and Hart 1992). Third, the selfish herd effect, first described by Hamilton (1971), states that individuals in a central position in a group suffer lower predation than individuals at the edges of the group, because predators usually concentrate their attacks on peripheral individuals. Selfish herds have been shown to reduce predation (Rayor and Uetz 1990; Romey 1995), parasitism (Mooring and Hart 1992; Fauchald et al. 2007), and kleptoparasitism (Wcislo 1984) in central individuals for numerous systems including mammals (Lingle 2000; De Vos and O'Riain 2010), birds (Watt and Mock 1987; Sadedin and Elgar 1998;

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Quinn and Cresswell 2006), fish (Orpwood et al. 2008), spiders (Rayor and Uetz 1990, 1993), and insects (Foster and Treherne 1981).

The midge *Aphidoletes aphidimyza* Rondani (Diptera: Cecidomyiidae) is a specialist aphidophagous predator (i.e., predator that feed on aphids) that has been reported to attack more than 60 aphid species (Harris 1973). Only the larvae are predaceous, while the adults feed on nectar or honeydew. Females lay their eggs singly or in small clusters on foliage, usually within or close to aphid colonies. Larvae hatch after 2–4 days and almost immediately start feeding on aphids. They use a furtive foraging behavior that triggers little defensive response by its aphid prey (Lucas and Brodeur 2001). There are three larval stages; the final instar pupates in soil. *A. aphidimyza* thus spends its entire larval development within its prey colony (Klingauf 1967).

Eggs and larvae of *A. aphidimyza* are highly vulnerable to intraguild predation (i.e., members of a guild killing and eating another member of the same guild; Polis et al. 1989). Laboratory and field evidence shows that intraguild predation is ubiquitous in the species-rich aphidophagous guild (Rosenheim et al. 1999; Lucas 2005; Gagnon et al. 2011). Aphids typically form contagious aggregates on host plants. Of major significance in the context of intraguild predation, most aphidophagous species have a significant numeric response to aphid density and tend to aggregate in aphid patches, thereby creating favorable situations for interspecific encounters (Brodeur and Rosenheim 2000; Lucas 2005, 2012). *A. aphidimyza* larvae commonly experience unidirectional intraguild predation by ladybeetles (Lucas et al. 1998; Lucas 2012; Gardiner and Landis 2007), lacewings (Lucas et al. 1998), hoverflies (Hindayana et al. 2001), and pirate bugs (Brodsgaard and Enkegaard 1997). Given its high vulnerability to intraguild predators, *A. aphidimyza* is expected to have evolved an array of defensive mechanisms. For instance, confined within an aphid colony, *A. aphidimyza* benefits from a dilution effect generated by its prey, which reduces the incidence of intraguild predation (Lucas and Brodeur 2001). Furthermore, the midge larvae could gain extra benefits by occupying a central position within the aphid colony that entails lower risk of predation (Hamilton 1971).

In this study, we tested the hypothesis that *A. aphidimyza* larvae benefit from a selfish herd effect against predators when developing within aphid colonies. Under laboratory conditions, we first characterized the distribution of midge larvae within aphid colonies. Then, we evaluated how this distribution affects the survivorship of the midge when exposed to two common intraguild predators, the 12-spotted ladybeetle *Coleomegilla maculata lengi* Timberlake (Coleoptera: Coccinellidae) and the green lacewing *Chrysoperla rufilabris* Burmeister (Neuroptera: Chrysopidae).

Materials and methods

C. rufilabris and *C. maculata* were purchased from Groupe Biocontrôle Inc. (Sainte-Foy, Canada) and *A. aphidimyza* from Plant Products Inc. (Montréal, Canada). Predators were reared on the potato aphid, *Macrosiphum euphorbiae* Thomas (Hemiptera: Aphididae). Midge larvae were selected based on their size, and only large individuals (>168 h) were used. Green lacewing (third instar larvae) and 12-spotted ladybeetle (second instar larvae) were used 48 h after molting. To establish aphid colonies on potato plants, early second instar aphids were introduced on the lower surface of a leaf 24 h prior to testing. Clip cages were used to prevent aphids from dispersing and thus to favor cohesion among individuals. The experiments were carried out at 23 °C, 60–70 % relative humidity, under a 16:8 h light:dark photoperiod.

A. aphidimyza distribution

We first described the spatial distribution of midge larvae within 14 aphid colonies containing 13 to 19 individuals. This aphid colony size corresponds to the mean number of aphids observed on potato plants when selected as oviposition sites by *A. aphidimyza* females in a previous experiment (Lucas and Brodeur 1999). Following clip cage removal, a midge larva was introduced at the edge of the colony, as close as possible to the aphids. Insects were observed once at 4, 8, and 24 h, and their position was recorded. A 24-h period allows the midge to explore the aphid colony and select a foraging site (see Lucas and Brodeur 2001). For each observation, the position on a Cartesian coordinate plane of every individual in the colony (including the midge larva) was recorded. In addition, a Voronoi diagram was drawn using the PBSmapping package in R (R Development Core Team 2010) to determine the metric space of each individual. The boundary of the colony was determined based on the position of the individuals at the limits on the four azimuths on the Cartesian plane. If the metric space of an individual overlapped the boundary of the colony, the individual was considered at the periphery of the colony. Conversely, when the metric space of an individual was not overlapping the boundary of the colony, the individual was recorded as being in the central zone (Fig. 1). To test whether the distribution of midge larvae within the aphid colonies results from random or active processes, we compared the observed and predicted probabilities of finding the midge larvae in the central zone of the aphid colonies using Monte Carlo simulation. The predicted probability was obtained by randomly attributing a position (i.e., in the central or at peripheral zone) to each midge larva. The probability that the midge larva would be found in the center or peripheral zone of a given colony was equal to relative surface covered by the central and the peripheral zones in that colony. For example, if the central zone of the aphid colony was 25 %

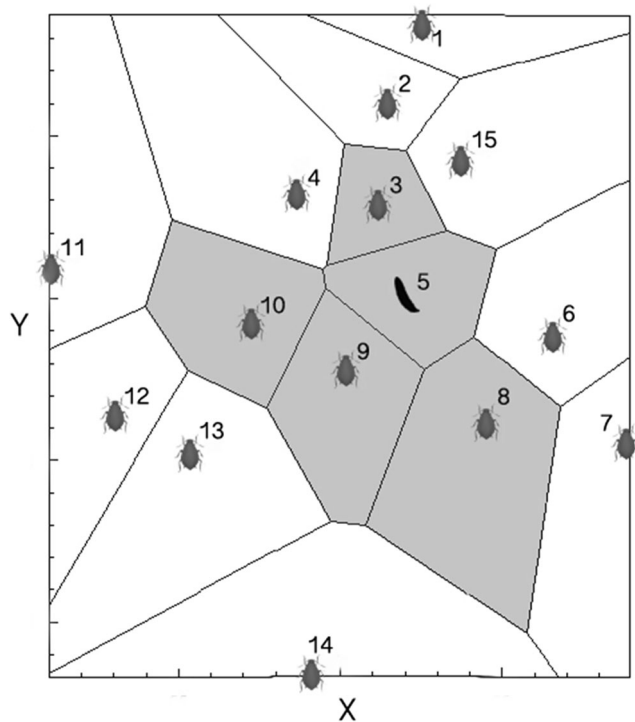


Fig. 1 Voronoi diagram of a colony of aphids and *A. aphidimyza*. Individuals #3, 5, 8, 9, and 10, as well as *A. aphidimyza*, are in the center of the colony and expected to benefit from a selfish herd effect

of the total surface, the midge larva has a 25 % probability to be randomly distributed in the central zone. We ran 1000 iterations of this simulation for each midge larva. For each observation period (4, 8, and 24 h), we obtained the p value associated with the observed probability of finding the midge larva in the central zone of the aphid colony by dividing the number of times the simulation generated a higher probability than the observed one by 1000.

We ran a multiple linear regression to test the effect of the number of individuals in the colony and the time after introduction of midge larva, on the probability of observing aphids in the central zone of the colony. The probability of observing midge larva in the central zone of the colony as a function of the number of individuals in the colony and of time was tested using a generalized linear model for binomial response variables.

Intraguild predation

The second experiment evaluated predation risk of midge larvae foraging in central or peripheral zones of the aphid colony. Colonies of 8 to 22 aphids were established on potato seedlings 24 h before the experiment. The proportion of individuals in the central zone compared to that in the peripheral zone increases with colony size. We thus expected the selfish herd effect to be modulated by colony size. Following clip cage removal, a midge larva was gently introduced as close as

possible (<1 cm) to the aphid colony, using a fine paintbrush. After a minimum of 15 min, when the midge larva had successfully attacked an aphid, the position of insects (midge larva and aphids) in the central and the peripheral zone was determined following the method described above. Tests started with the release of a green lacewing (L3) or a 12-spotted ladybeetle (L2) larva on the petiole of the leaf and ended when the predator left the leaf or killed the midge. Aphid colonies were monitored continuously during the test. The species and the position of the first prey attacked, and the survival of the midge after the test were recorded. Twenty-nine and 33 replicates were carried out for lacewing and ladybeetle, respectively. The probability that a given prey (either midge larva or aphids) was the first prey attacked by the intraguild predator was related to its distribution in the colony (central or peripheral zone), the number of prey in the colony, and the type of prey (midge larva or aphid) using a generalized linear model for binomial data. The analysis pools midge larva and aphids to determine whether the predator selected prey from the central or peripheral zone. However, there is a lack of independence among observations when all individuals of a group are included in the analysis. To overcome this problem, we ran Monte Carlo simulations in which the response variable was randomized within each group. The GLM model was ran 1000 times to generate the randomized response variable, and the p value of each variable was estimated from this distribution. This procedure was run once per predator species.

Twelve-spotted ladybeetle and green lacewing larvae typically disturbed the cohesion among aphids, and consequently, the distribution of prey within the colony changed after the first attack. Thus, we tested the probability that the midge larva survived the first attack as a function of its initial position (central or peripheral zone), colony size, and type of intraguild predator (ladybeetle or lacewing) using a generalized linear model. Explanatory variables were selected using a backward stepwise selection procedure, and only variables with a p value under 0.05 were kept in the models.

Results

A. aphidimyza distribution

Aphid colonies, including a midge larva, initially consisted of 15.86 ± 1.35 (\pm SD) individuals (at time 0), distributed in the peripheral (65.4 %; 10.36 ± 1.22 individuals) or in the central (34.6 %; 5.50 ± 1.16 individuals) zone. Colony size decreased with time following consumption of aphids by the midge (9.63 ± 3.66 individuals after 24 h). Accordingly, the probability of randomly observing midge larvae in the central zone of aphid colonies should have decreased over the 24 h (Fig. 2). In contrast, midge larvae were more frequently observed in the central zone over time (Fig. 2). The difference between

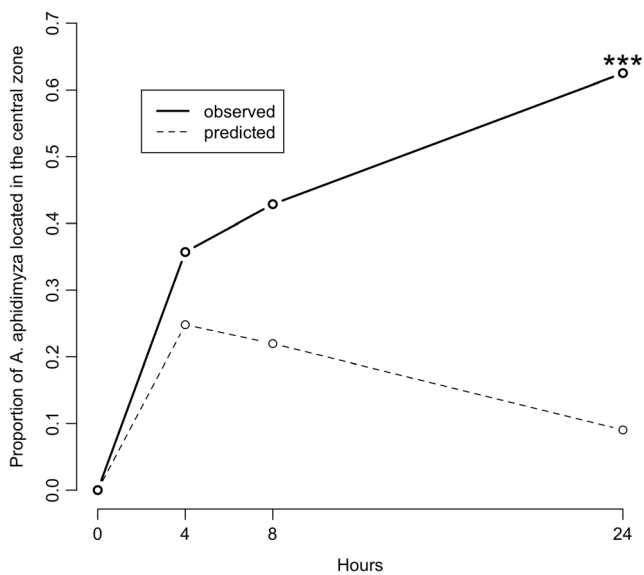


Fig. 2 Proportion of *A. aphidimyza* observed in the central zone of *M. euphorbiae* colony as a function of time after its introduction in the colony (full line). The dotted line represents the predicted distribution of *A. aphidimyza* if distribution was random. Triple asterisks indicate that the difference between observed and expected distribution is statistically significant

observed and predicted *A. aphidimyza* distribution was statistically significant after 24 h (observed=0.63; predicted=0.09; $p < 0.0001$), slightly over the significance threshold after 8 h (observed=0.43; predicted=0.23; $p = 0.07$) and not significant after only 4 h (observed=0.36; predicted=0.31; $p = 0.11$).

Intraguild predation

In tests with green lacewing larvae ($n = 29$), prey colonies (midge larva and aphids) consisted of an average of 15.93 ± 4.88 (\pm SD) individuals; with an average of 32.1 % being distributed in the central zone (Fig. 3). The probability that either the midge larva or an aphid was the first prey attacked by lacewings was significantly lower when it was located in the central zone ($\beta = -1.62$; $p < 0.0001$). Furthermore, for a given individual, the probability of being the first prey captured decreased with colony size ($\beta = -0.04$; $p = 0.003$). Midges and aphids did not differ in their probability of being the first prey captured ($\beta = 0.85$; $p = 0.10$).

The size of prey colonies during tests with 12-spotted ladybeetle larvae ($n = 33$) averaged 16.12 ± 5.21 (\pm SD) individuals (27.2 % being distributed in the central zone) (Fig. 3). Midge larvae and aphid in the central zone of the colonies had significantly lower probability of being the first prey attacked by ladybeetles ($\beta = -1.40$; $p < 0.0001$), and this probability decreased with colony size ($\beta = -0.05$; $p < 0.0001$). There was no difference between midge and aphid in their probability of being the first prey attacked ($\beta = 0.96$; $p = 0.07$).

Survival of the midge larva upon the first attack depended on the intraguild predator species ($\beta = 1.38 \pm 0.58$; $z = 2.40$; $p = 0.02$),

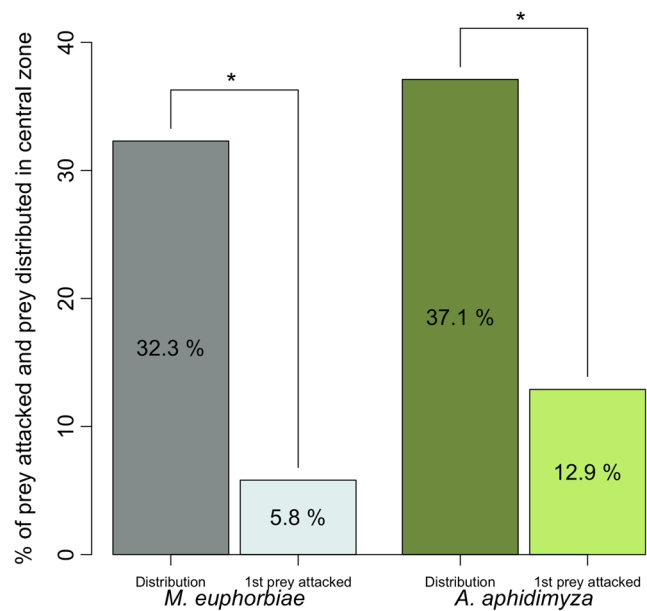


Fig. 3 The probability for both *A. aphidimyza* and *M. euphorbiae* located in the central zone of the colony to be the first prey attacked by an intraguild predator (*C. maculata* or *C. rufilabris* larvae) and the distribution of the prey in the central zone of the colony before the introduction of the intraguild predator. Asterisks indicate that the difference between observed and expected prey being the first attacked first when located in the central zone is statistically significant

with 67.9 % (19 out of 28 midges) surviving in tests with ladybeetles and 34.6 % (9 out of 26 midges) surviving in presence of lacewings. However, the initial position in the colony (center or periphery) prior to the first attack ($\beta = -0.10 \pm 0.63$; $z = -0.15$; $p = 0.88$) and size of the colony ($\beta = -0.06 \pm 0.06$; $z = -1.04$; $p = 0.30$) had no significant effect on the survival of the midge.

Discussion

Furtive predation is a foraging strategy that requires a close relationship between the predator and its prey. Furtive predators differ considerably from active searching or ambush predators in several ways including: morphology, foraging behavior (Fréchette et al. 2008; Sentis et al. 2012 and references therein), response to landscape (Maisonhaute and Lucas 2011), susceptibility to intraguild predation (Sluss and Foote 1973; Lucas et al. 1998), and defensive mechanisms (Lucas and Brodeur 2001). *A. aphidimyza*-exploiting aphid colonies are highly vulnerable to intraguild predation (Lucas et al. 1998) and have evolved an array of defenses. Pupation occurs in the soil, and adults rely on fleeing behavior to escape predation (Harris 1973). Ovipositing females prefer pubescent sites on leaves thus enhancing egg survival (Lucas and Brodeur 1999). *A. aphidimyza* larvae frequently cover themselves with dead aphid corpses to provide camouflage (E. Lucas, pers. observation). Finally, larvae can usurp the communal defensive behavior of

aphids for their own benefit (Lucas and Brodeur 2001) by taking advantage of a dilution effect, which decreases the individual's probability of being attacked once the prey patch has been detected by a predator (Inman and Krebs 1987).

The present study shows that *A. aphidimyza* larvae preferentially occupy the center of the aphid colony. The classical Hamilton's hypothesis of the selfish herd effect predicts that centripetal tendencies would be selected in individuals living with conspecifics (Hamilton 1971). In our study, the motivation behind the centripetal tendency of *A. aphidimyza* larvae could either be to increase foraging efficiency or benefit of additional communal defense, these two hypotheses being not mutually exclusive. Notwithstanding the motivation behind the centripetal tendency of the furtive predator, the incidence of predation was reduced in the center of aphid colonies during the first attack by an intraguild predator. This suggests that the selfish herd effect is complementary to the dilution effect by providing additional protection to *A. aphidimyza*. However, large intraguild predators used in the present study (green lacewing and spotted ladybeetle larvae) disrupted the cohesion of the aphid colony and thereby the benefit from the selfish herd effect over time. Furthermore, aphids also benefit from a selfish herd effect against lacewing and ladybeetle larvae, but the presence of predatory midge in the central zone of the colony eliminates this advantage.

No defense strategy is universal and its effectiveness is determined by the predatory threat (Edmunds 1974). In the present study, furtive predators occupying the central position in their prey colony benefit from the selfish herd only during the first attack by the intraguild predator. Several aphids escaped by dropping off the leaf or by walking away, with 65 and 59 % of the aphids abandoning their feeding sites following a first attack by green lacewing or 12-spotted ladybeetle larvae, respectively. Subsequently, the cohesion of the aphid colony collapsed, thereby increasing the vulnerability of slow-moving midge larva to intraguild predation. Aphid colony cohesion may vary among aphid species and among predators (Losey and Denno 1998a, b), thereby influencing the efficacy of the selfish herd effect. For instance, communal defenses may be more effective against small predators, such as minute pirate bugs (anthocorids) or younger stages of large predators that do not completely destroy aphid colony cohesion. We observed a difference in midge susceptibility to the third instar green lacewing and the second instar 12-spotted ladybeetle after the first attack, *A. aphidimyza* survival being lower in the presence of green lacewing. Similarly, Lucas and Brodeur (2001) observed for *A. aphidimyza* that a dilution effect generated by its aphid prey was effective against the second instar 12-spotted ladybeetles but not in the presence of the third instar green lacewing. The third instar green lacewing differed from the second instar spotted ladybeetle both in size and voracity. Finally, the selfish herd effect may be lost in

the presence of aerial natural enemies like midge parasitoids since they may contact their host from the air directly in the center of the colony. In such cases, the size of the midge's "domain of danger" (Hamilton 1971) should be more important than its position in the aphid colony (central or periphery) (Mooring and Hart 1992).

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Ethical standards All experiments comply with current Canadian laws.

References

- Brodeur J, Rosenheim JA (2000) Intraguild interactions in aphid parasitoids. *Entomol Exp Appl* 97:93–108
- Brodsgaard HF, Enkegaard A (1997) Interactions among polyphagous anthocorid bugs used for thrips control and other beneficials in multi-species biological pest management systems. *Recent Res Dev Entomol* 1:153–160
- De Vos A, O'Riain MJ (2010) Sharks shape the geometry of a selfish seal herd: experimental evidence from seal decoys. *Biol Lett* 6:48–50
- Edmunds M (1974) Defence in animals. Longman Inc., New-York
- Fauchald P, Rodven R, Bardsen B-J, Langeland K, Tveraa T, Yoccoz et al (2007) Escaping parasitism in the selfish herd: age, size and density-dependent warble fly infestation in reindeer. *Oikos* 116:491–499
- Foster WA, Treherne JE (1981) Evidence for the dilution effect in the selfish herd from fish predation on a marine insect. *Nature* 296:466–467
- Fréchette B, Lucas F, Larouche É (2008) *Leucopis annulipes* larvae (Diptera: Chamaemyiidae) use a furtive predation strategy within aphid colonies. *Eur J Entomol* 105:399–403
- Gagnon A-È, Heimpel GE, Brodeur J (2011) The ubiquity of intraguild predation among predatory arthropods. *PLoS ONE* (on-line) 6: e28061
- Gardiner MM, Landis DA (2007) Impact of intraguild predation by adult *Harmonia axyridis* (Coleoptera: Coccinellidae) on *Aphis glycines* (Hemiptera: Aphididae) biological control in cage studies. *Biol Control* 40:386–395
- Hamilton WD (1971) Geometry for the selfish herd. *J Theor Biol* 31:295–311
- Harris KM (1973) *Aphidophagous Cecidomyiidae* (Diptera): taxonomy ecology and assessments of field populations. *Bull Entomol Res* 63: 305–325
- Hindayana D, Meyhofer R, Scholz D, Poehling H-M (2001) Intraguild predation among the hoverfly *Episyrphus balteatus* de Geer (Diptera: Syrphidae) and other aphidophagous predators. *Biol Control* 20:236–246
- Inman AJ, Krebs J (1987) Predation and group living. *Trends Ecol Evol* 2:31–32
- Klingauf F (1967) Abwehr- und Meidereaktionen von Blattläusen (Aphididae) bei Bedrohung durch Räuber und parasiten. *J Appl Entomol* 60:269–317
- Lingle S (2000) Anti-predator strategies and grouping patterns in white-tailed deer and mule deer. *Ethology* 107:295–314

- Losey JE, Denno RF (1998a) Interspecific variation in the escape responses of aphids: effect on risk of predation from foliar-foraging and ground-foraging predators. *Oecologia* 115:245–252
- Losey JE, Denno RF (1998b) The escape response of pea aphids to foliar-foraging predators: factors affecting dropping behaviour. *Ecol Entomol* 23:53–61
- Lucas E (2005) Intraguild predation among aphidophagous predators. *Eur J Entomol* 102:351–364
- Lucas E (2012) Intraguild interactions. In: Hodek I, van Emden HF, Honek A (eds) *Ecology and behavior of the ladybird beetles (Coccinellidae)*. Wiley, pp 343–374
- Lucas E, Brodeur J (1999) Oviposition site selection by the predatory midge *Aphidoletes aphidimyza* (Diptera: Cecidomyiidae). *Environ Entomol* 28:622–627
- Lucas E, Brodeur J (2001) A fox in sheep's clothing: furtive predators benefit from the communal defense of their prey. *Ecology* 82:3246–3250
- Lucas E, Coderre D, Brodeur J (1998) Intraguild predation among aphid predators: characterization and influence of extraguild prey density. *Ecology* 79:1084–1092
- Maisonhaute J-E, Lucas E (2011) Influence of landscape structure on the functional groups of an aphidophagous guild: active-searching predators, furtive predators and parasitoids. *Eur J Environ Sci* 1:41–50
- Mooring MS, Hart BL (1992) Animal grouping for protection from parasites: selfish herd and encounter-dilution effects. *Behaviour* 123:173–193
- Orpwood JE, Magurran AE, Armstrong JD, Griffiths SW (2008) Minnows and the selfish herd: effects of predation risk on shoaling behaviour are dependent on habitat complexity. *Anim Behav* 76:143–152
- Polis GA, Myers C, Holt RD (1989) The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annu Rev Ecol Syst* 20:297–330
- Pulliam HR, Caraco T (1984) Living in groups: is there an optimal group size? In: Krebs JR, Davies NB (eds) *Behavioural ecology: an evolutionary approach*, 2nd edn. Sinauer Associates Inc. Publishers, Sunderland Massachusetts, pp 122–147
- Quinn JL, Cresswell W (2006) Testing domains of danger in the selfish herd: sparrow hawks target widely spaced redshanks in flocks. *P Roy Soc B* 273:2521–2526
- R Development Core Team (2010) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria
- Rayor LS, Uetz GW (1990) Trade-offs in foraging success and predation risk with spatial position in colonial spiders. *Behav Ecol Sociobiol* 27:77–85
- Rayor LS, Uetz GW (1993) Ontogenic shifts within the selfish herd: predation risk and foraging trade-offs change with age in colonial web-building spiders. *Oecologia* 95:1–8
- Romey WL (1995) Position preferences within groups: do whirligigs select positions which balance feeding opportunities with predator avoidance? *Behav Ecol Sociobiol* 37:195–200
- Rosenheim JA, Limburg DD, Colfer RG (1999) Impact of generalist predators on a biological control agent, *Chrysoperla carnea*: direct observations. *Ecol Appl* 9:409–417
- Sadedin SR, Elgar MA (1998) The influence of flock size and geometry on the scanning behaviour of spotted turtle doves, *Streptopelia chinensis*. *Aust J Ecol* 23:177–180
- Sentis A, Lucas É, Vickery WL (2012) Prey abundance, intraguild predators, ants and the optimal egg-laying strategy of a furtive predator. *J Insect Behav* 25:529–542
- Sluss TP, Foote BA (1973) Biology and immature stages of *Leucopis verticalis* (Diptera: Chamaemyiidae). *Can Entomol* 103:1427–1434
- Vulinec K (1990) Collective security: aggregation by insects as a defense. In: Evans DL, Schmidt JO (eds) *Insect defenses: adaptive mechanisms and strategies of prey and predators*. State University of New-York Press, Albany, pp 251–288
- Watt DJ, Mock DW (1987) A selfish herd of martins. *Auk* 104:342–343
- Weislo WT (1984) Gregarious nesting of a digger wasp as a selfish herd response to a parasitic fly (Hymenoptera: Sphecidae; Diptera: Sarcophagidae). *Behav Ecol Sociobiol* 15:157–160
- Wrona FJ, Dixon RWJ (1991) Group size and predation risk: a field analysis of encounter and dilution effects. *Am Nat* 137:186–201