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When the aggressiveness degree modifies the intraguild predation magnitude

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HIGHLIGHTS

- Aggressive predators have great potential as biological control agents. However, they might also display higher intraguild predation rates.
- Two artificially selected lines of the omnivorous bug *Nabis americoferus* (one aggressive and one docile) were used to test the implication of aggressiveness within IGP interactions.
- We demonstrated that intraguild predation events are positively correlated to aggressiveness.
- We also showed that docile predators are more prone to behavioral adjustment.

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ABSTRACT

In agroecosystems, intraguild predation (IGP) is an ecological interaction that can reduce the effectiveness of biological control programs. Since aggressiveness is correlated with a higher attack rate, it is suspected to influence IGP occurrence. To understand the consequences of increased aggressiveness on the IGP, we used two artificially selected lines of the generalist predator, *Nabis americoferus* (one aggressive and one docile). We hypothesized that IGP is positively correlated to aggressiveness. Individuals of *N. americoferus* were tested individually with an intraguild prey (IGPrey), *Orius insidiosus,* and in the absence or presence of an extraguild prey (XGPrey), third instars of *Lygus lineolaris*. Firstly, the attack rate of *N. americoferus* on *O. insidiosus* was recorded for 15 min and then the IGP after a period of 24 h. We found that aggressive individuals performed a higher attack rate and IGP than docile ones even with the presence of XGPrey. Whereas docile individuals did not display a strong IGP in the absence of XGPrey, it increased significantly when they were introduced. Our results suggest that IGP is positively correlated to a high aggressiveness. Additionally, it seems that docile individuals are more prone to adjust their behavior according to environmental conditions. Finally, the implications of aggressiveness degree for the predator–prey dynamic is discussed.

1. Introduction

In agroecosystems, pests' natural control relies upon the dynamic and interactions among predatory species (Crowder and Jabbour, 2014). While the outcome of these interactions can be modulated by most environmental conditions (e.g., prey and predator density, structural complexity of the environment, voltinism) (Crowder and Jabbour, 2014), studies on animal behavior suggest that animals personality is among one of the major forces driving the ecological dynamic of ecosystems (Réale et al., 2007; Sih et al., 2012). Animal personality describes the idea that most individuals display different but consistent and repeatable behaviors over time and context (Réale et al., 2007). Since there are intraspecific variations of animal personality, their behavioral type can be placed along continuums such as the bold/shy continuum or the aggressiveness continuum (Réale et al., 2007). This leads individuals within a species to behave differently when faced with similar conditions (Sih et al., 2004; Réale et al., 2007; Michalko et al., 2021).

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Aggressiveness, which defines the readiness of an individual to display agonistic reactions toward others (Réale et al., 2007), is correlated to the tendency of an individual to further explore its environment (Verbeek et al., 1996), to attack more (Hedrick and Riechert, 1989; Yasuda et al., 2001), to be bolder (propensity to take risks) (Réale et al., 2007; Bell and Sih, 2007; Sih et al., 2012; Michalko et al., 2021) and to have a higher foraging rate in comparison to docile individuals (Pintor et al., 2009). They can also display wasteful killing (Maupin and Riechert, 2001) and are known to be less selective concerning prey (Michalko et al., 2021). For instance, two predators of the same species will not prey on the same prey species depending on their respective aggressiveness degree (Michalko et al., 2021). These characteristics give aggressive individuals a trophic niche wider than that of docile individuals (Michalko et al., 2021) and can make them more competitive for food acquisition (Bolnick et al., 2003, 2011; Sih et al., 2012). Aggressive individuals can therefore significantly alter the spatial and structural dynamics of populations in an ecosystem (Michalko and Pekár, 2017; Michalko et al., 2021).

Since highly aggressive individuals behave differently in their environment compared to docile individuals, their interactions with other predators should also differ (Réale et al., 2007; Michalko and Řežucha, 2018). For instance, intraguild predation (IGP) is an interaction that could be influenced by the intraguild predators (IGPredator) aggressiveness (Polis et al., 1989; Lucas, 2012; Sih et al., 2012). IGP is an agonistic interaction that occurs between competitors sharing a common ressource where one or both individuals are preying or attacking each other (Polis et al., 1989; Gagnon et al., 2011). It usually happens when mutual preys are scarce, when preying upon intraguild prey (IGPrey) represents no risks for the intraguild predator (e.g., against larval instars or smaller predators), when defending feeding areas or when suppressing a competitor (Polis et al., 1989; Lucas and Maisonhaute, 2019). But attacking another predator can lead to injuries, sublethal effects (e.g. behavioral changes, physiological changes) or death (Lucas, 2005; Lucas and Maisonhaute, 2019). Docile individuals that are shyer, more selective and risk-aversive are less likely to engage in IGP (Michalko and Řežucha, 2018). Moreover, in most cases, the presence of an extraguild prey (XGPrey) is known to reduce the tendency of an IGPredator to attack an IGPrey (Rosenheim et al., 1995; Lucas et al., 1998; Brodeur and Rosenheim, 2000; Nóia et al., 2008; Lucas and Rosenheim, 2011). But the consequences of prey availability combined with the aggressiveness degree on the frequency of IGP is also not yet known.

In order to understand whether intraspecific variation in aggressiveness and availability of XGPrey generates different IGP rates, we worked on a trio of sympatric hemipterans species involved in IGP interactions. The IGPredator *Nabis americoferus* Carayon (Hemiptera: Nabidae) is a large-size omnivorous bug native to North America and the subject of growing attention for its use as a potential biocontrol agent (Perkins and Watson, 1971; Cabello et al., 2009, LaFlair, 2022). The IGPrey is the Anthocorid *Orius insidiosus* Say (Hemiptera: Anthocoridae) and was chosen due to the numerous preys species it has in common with *N. americoferus* such as aphids, thrips, mites, lepidopteran eggs, or young instars of bigger prey like mirids (Coll and Ridgway, 1995; Laflair, 2022). Finally, the XGPrey is the tarnished plant bug, *Lygus lineolaris* Palisot de Beauvois (Hemiptera: Miridae), a pest that attacks more than 120 different types of crops such as tobacco, cotton, apples or strawberries (Young, 1986) and that is also a common prey of both the IGPrey and IGPredator (Coll and Ridgway, 1995; Laflair, 2022).

The objectives of the study were i) to estimate the impact of docility/aggressiveness on the IGP magnitude of *N. americoferus*, ii) to evaluate the impact of the availability of XGPrey on the IGP magnitude of aggressive and docile individuals of *N. americoferus*. The first hypothesis is that the IGP intensity is positively correlated with aggressiveness. The second hypothesis is that the IGP intensity will decrease in the presence of XGPrey both for aggressive and docile IGPredator, and that the reduction will be greater for docile individuals.

2. Materials and methods

2.1. Entomological material and artificial selection

To establish the colony of *N. americoferus* and begin the artificial selection, 219 individuals were collected from various regions of Quebec and Ontario (Canada) during the summer of 2019. After having assessed the aggressiveness degree of every individual, docile individuals were separated from their aggressive counterpart in order to create two lines which were then independently bred. The selection process was repeated for three generation for both lines (Royer et al., 2022). Then, the aggressiveness degree of both lines increased and decreased respectively through the inbreeding process due to a lack of available individuals for the selection process requirements (Royer et al., 2022). The present study used sixth-generation individuals of both lines after their distinction in terms of aggressiveness degree had been statistically confirmed. For full information on the selection process, please refer to Royer et al. (2022). Every individual was reared on eggplants *Solanum melongena* and were fed eggs of the flour moth, *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae). The other two species, *O. insidiosus* and *L. lineolaris*, (without artificial selection) were reared by the Centre de Recherche Agroalimentaire de Mirabel (CRAM). Livestock maintenance was carried out once a week and was maintained in standard abiotic conditions (25 °C; 70 % RH; 16L:8D).

2.2. Intraguild predation: Experimental design and data collection

The IGP intensity was evaluated in laboratory conditions (25 °C; 60 % RH; 16L:8D). Prior to the experiment all *N. americoferus* were starved for 24 h to stimulate their predatory behavior and to standardized their hunger state. They were placed individually in a plastic jar (8 cm x 8 cm x 6 cm) that contained a piece of lettuce to provide a source of water. A total of 30 individuals from each line were individually tested. Individuals from the same line were separated into two groups: 15 of them were confronted with three *O. insidiosus* (IGPrey) whereas the other 15 had three *O. insidiosus* and five third instars of *L. lineolaris* (XGPrey). Two other control treatments of 15 repetitions each were also carried out: one group with only three *O. insidiosus* and the other with three *O. insidiosus* and five third instars of *L. lineolaris*. Specifically, the choice to use third instars of *L. lineolaris* was made so that the nymphs were large enough that predation would only be carried out by *N. americoferus*. During the 15 min following the introduction of the IGPrey and XGPrey, the number of attacks by *N. americoferus* towards *O. insidiosus* was recorded. The microcosm was then closed for 24 h. After this time period, the mortality of *N. americoferus*, *O. insidiosus* and *L. lineolaris* were evaluated.

2.3. Statistical analysis

The experiment included two types of response variables: the number of attacks by *N. americoferus* towards *O. insidiosus* and the mortality of both *O. insidiosus* and *L. lineolaris*. No *N. americoferus* were found dead after 24 h. The two explanatory variables are the behavioral type of *N. americoferus* (i.e., aggressive or docile line) and the presence or absence of XGPrey. Results were analyzed with R software (R Core Team, 2020) using a generalized linear model (GLM) following a binomial distribution for IGP because the mortality rate was constrained between zero and five for *L. lineolaris* and zero and three for *O. insidiosus*. Therefore, to comply with a binomial distribution, this part of the dataset has been transformed by dividing the number of dead *O. insidiosus* by three and the number of dead *L. linerolaris* by five. Following the transformation, the dataset of the IGP was ranged from 0 to 1. As the attack rate had no constrained values, it was analyzed with GLM model for Poisson distributed data. For every model, an interaction was used between the two explanatory variables.

3. Results

3.1. Attack rate on the intraguild prey

In the absence of XGPrey, the attack rate of *N. americoferus* on *O. insidiosus* was significantly higher for the aggressive line (β ± s.e. = -2.35 ± 0.74; z-value = − 3.17; *p*-value = 0.001) with an average of 1.4 (±0.41 s.e.) attacks per 15 min and 0.13 (±0.09 s.e.) attacks per 15 min, for the aggressive line and the docile line respectively (Fig. 1.). In the presence of XGPrey, the attack rate of *N. americoferus* on *O. insidiosus* was not statistically different between the aggressive line and the docile line (β ± s.e. = -0.20 ± 0.37; z-value = -0.556; *p*-value = 0.578).

For the aggressive line, the "presence of XGPrey" did not have a significant influence on the attack rate (β ± s.e. = -2.27 ± 0.33; z-value = -0.82; *p*-value = 0.41). However, in the presence of XGPrey, the attack rate of the docile line significantly increased (β ± s.e. = 2.14 ± 0.82; z-value = 2.58; *p*-Value = 0.009) as it went from 0.13 (±0.09 s.e.) attacks per 15 min to 0.86 (±0.09 s.e.) (Fig. 1.).

3.2. Intraguild predation intensity

In the absence of XGPrey, the IGP's intensity was significantly lower in the docile line (β ± s.e. = -1.84 ± 0.59; z-value = -3.118; *p*-value = 0.003) with an average of 1.73 (±0.23 s.e.) *O. insidiosus* killed per day for the aggressive line and 0.53 (±0.23 s.e.) kills per day for the docile line (Fig. 2.). In the presence of XGPrey, the IGP rate of *N. americoferus* on *O. insidiosus* was not statistically different between the aggressive and the docile line (β ± s.e. = -0.26 ± 0.49; z-value = -0.536; *p*-value = 0.596).

The presence of XGprey did not significantly reduce the IGP for the aggressive line (β ± s.e. = -0.27 ± 0.51; z-value = -0.529; p-value = 0.6). However, for the docile line, in the presence of XGPrey, the IGP rate significantly increased (β ± s.e. = 1.57 ± 0.78; z-value = 2.02; *p*-Value = 0.048) as it jumped from 0.53 (±0.23 s.e.) to 1.33 (±0.25 s.e.) (Fig. 2.).

3.3. Mortality rate of the extraguild prey *Lygus lineolaris*

Individuals of the aggressive line killed an average of 3.0 (±0.33 s.e.) XGPrey and individuals of the docile line 3.0 (±0.33 s.e.). There are no significant differences (β ± s.e. = 0.54 ± 0.40; t-value = 1.34; *p*-value = 0.19) between the results of the two lines.

3.4. Mortality rate in control treatments

In the control treatments, one *O.insidiosus* died in the situation where they were alone and two where they were accompanied by *L. lineolaris*. These results are significantly lower than the mortality rates found in the aggressive (β ± s.e. = 3.98 ± 0.85; t-value = 4.68; *p*-value > 0.0001) and docile treatment (β ± s.e. = 3.00 ± 0.85; t-value = 3.51; *p*-value = 0.0007). Similarly, two *L. lineolaris* were found dead in the control treatment which is a significantly lower result than the mortality rate registered in the aggressive (β ± s.e. = 4.00 ± 0.83; t-value = 4.82; *p*-value > 0.0001) and docile treatment (β ± s.e. = 4.54 ± 0.83; t-value = 5.42; *p*-value > 0.0001).

4. Discussion

Our results support our first hypothesis which was that the IGP intensity is positively correlated with aggressiveness. On the contrary, our second hypothesis that the IGP would decrease in the presence of XGPrey was not supported, neither by aggressive, nor by docile IGPredators. Furthermore, IGP intensity of the docile increased in the presence of XGPrey infirming that the reduction will be greater for docile individuals.

Many authors tried to point out the role of aggressiveness within IGP interactions. But in most cases, different IGPredator species, that either differ in size, or life strategy, or where at least one of them is an invasive species, were compared (Polis et al., 1989; Lucas et al., 1998; Schausberger and Croft, 2000; Michalko and Pekár, 2017; Escudero-Colomar et al., 2019). By comparing individuals of the same species that were artificially selected for their aggressiveness and docility (Royer et al., 2022), we were able to isolate this trait and show its positive correlation to IGP events. Our experiment also supports the idea of behavioral syndrome, stating whereby some traits like aggressiveness are correlated to many behaviors (Sih et al., 2004). In addition to a higher tendency for IGP, aggressive individuals tend to attack more often than docile individuals.

On one hand, the introduction of XGPrey had no effect on the IGP rate of the aggressive line since it remained constant and high. It has already been observed that IGP level can remain constant independently of the XGPrey availability (Lucas et al., 1998). This usually happens when the intraguild predator faces no risk of preying upon the IGPrey, which, considering the size difference between *N. americoferus* and *O. insidiosus*, is the case (Lucas et al., 1998). Nevertheless, as the docile

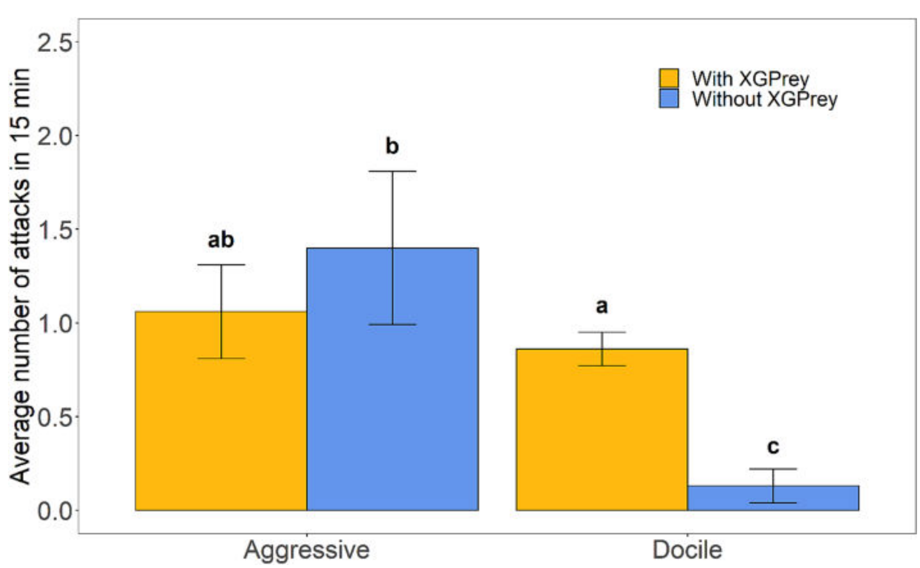

Fig. 1. Attack rates of the docile and the aggressive lines of *N. americoferus* toward *O. insidiosus* in 15 min and depending on the presence (orange) or absence (blue) of extraguild preys (*L. lineolaris*). Letters represent statistically significant differences between the four treatments.

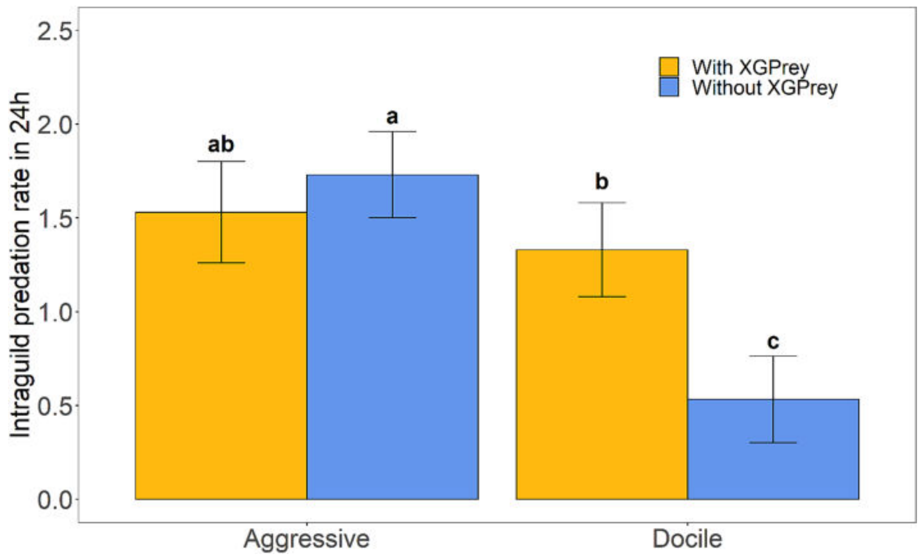

Fig. 2. Intraguild predation rate (number of *O. insidiosus* killed per day) by the docile and the aggressive lines of *N. americoferus* in 24 h and depending on the presence (orange) or absence (blue) of an extraguild prey (*L. lineolaris*). Letters represent statistically significant differences between the four treatments.

line did not demonstrate a high IGP rate when XGPrey were absent, the high IGP rate of the aggressive line in the presence of XGPrey can not be explained by the low dangerousness of *O. insidiosus*. Although one could hypothesize that the IGP propensity of aggressive predators is not dependent on XGPrey availability, it might not be true. Indeed, among the different responses of IGP rates when considering the XGPrey availability (Rosenheim et al., 1995; Lucas et al., 1998; Brodeur and Rosenheim, 2000; Nóia et al., 2008; Lucas and Rosenheim, 2011), one scenario is that the IGP rate decreases only at high XGPrey density (Lucas et al., 1998). Therefore, further investigation needs to be conducted to statute on this hypothesis.

On the other hand, the results of the docile lines suggest that their IGP rate could be dependent on XGPrey availability and also emphasize a higher propensity to behavioral adjustment than the aggressive line. Several hypotheses may justify IGP occurrence: to suppress a competitor, to defend territories, to consume an IGPrey that provides higher energetic value than the XGPrey or because no alternative XGPrey are available (Polis et al., 1989; Lucas et al., 1998; Lucas, 2005). But whereas IGP is generally mitigated or maintained with the introduction of XGPrey (Rosenheim et al., 1995; Lucas et al., 1998; Brodeur and Rosenheim, 2000; Nóia et al., 2008; Lucas and Rosenheim, 2011), the IGP rate of the docile line was 2.5 times higher in the presence of XGPrey and was also similar to the aggressive line. Although this scenario was theorized by Lucas and Rosenheim (2011) due to a recruiting effect of predators from increased prey availability, it has not been reported within laboratory conditions. According to our results, we can formulate an aggressive-exacerbation hypothesis, stating that the environmental conditions imposed on docile individuals when XGPrey were introduced exacerbated their aggressiveness and their tendency to IGP.

Commonly, such behavioral adjustments happens when individuals suffer from stress-inducing conditions (Ninkovic et al., 2013; Ahmad et al., 2015; Michalko and Řežucha, 2018; Zhang et al., 2019). In the animal kingdom, aggressiveness is not a static state, it can be increased or decreased following various causality links like starvation or fear (Réale et al., 2007; Ahmad et al., 2015). For instance, larvae and adults of *Drosophila melanogaster* Meigen (Diptera: Drosophilidae) that are classified as phytophagous organisms, can become cannibalist when they are starving (Ahmad et al., 2015). The hypothesis of a behavioral adjustment towards aggressiveness is also supported by the observation of the XGPrey and IGPrey corpses observations. Similarly to the aggressive line (both with and without XGPrey), all XGPrey and IGPrey corpses were not consumed or were partially consumed (for the docile with XGPrey only), which suggests the occurrence of wasteful killing (Samu and Biro, 1993; Maupin and Riechert, 2001; Lang and Gsödl, 2003; Fantinou et al., 2008).

Since IGP is positively correlated to aggressiveness, it could negatively impact the IGPrey population by direct and also indirect effects. While direct effects are represented by lethal interactions, indirect effects could be the migration of IGPrey to other sites (Briggs and Borer, 2005) or the avoidance by IGPrey of sites already colonized by aggressive predators (Janssen et al., 1997; Ruzicka, 1998). By reducing the local predation pressure, this scenario could be beneficial to the pest population (Rosenheim et al., 1993). As a result, it could reduce the natural control of pests which would increase the herbivory pressure and constrain the primary productivity of agricultural environments (Finke and Denno, 2005, 2006). In a biocontrol perspective, such negative top-down trophic cascades are to be avoided and should be studied prior to any release of aggressive generalist predators. Regarding docile individuals, although they have demonstraded high IGP rate in the presence of XGPrey, they also displayed a low IGP rate when XGPrey were absent. In an agroecosystem, where the complexity of the environment is high compared to our experimental setup and alternative prey abundant, it is likely that their IGP propensity and aggressiveness would remain low. Moreover, in the presence of XGPrey, they killed an average number of individual similar to the aggressive line which suggests that the ability to kill is not related to aggressiveness. From a biocontrol perspective, it is still difficult to ascertain which behavioral type (i.e. aggressive or docile) would provide the moost beneficial trade-off between efficiently controlling pests populations and not having too many detrimental impacts on the local guild composition, dynamic and spatial distribution. Both lines were confronted in a very asymmetric intraguild setup and facing more threatening predators could result in différents IGP outcomes.

To conclude, aggressiveness and IGP are cleraly linked, but not in a simplistic maner. IGP during XGPrey scarcity should be much higher with agressive individuals than with docile ones. However, during XGPrey outbreaks the docile ones may be involved in IGP interactions like the aggressive ones. The singular response of the docile line to XGPrey presence has not been previously described.

Ethic declaration

No approval of research ethics committees was required to accomplish the goals of this study because experimental work was conducted with an unregulated invertebrate species.

Authors' contributions.

Pierre Royer, François Dumont, Kent Marcial Catubis and Eric Lucas conceived the ideas and designed methodology. Pierre Royer conducted experiments and collected the data. Pierre Royer and François Dumont analysed the data. Pierre Royer wrote the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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