



Selecting aggressiveness to improve biological control agents efficiency

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Received: 13 April 2022 / Revised: 26 July 2022 / Accepted: 29 July 2022

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Abstract

In agroecosystems, omnivorous predators are recognized as potential biological control agents because of the numerous pest species they prey on. Nonetheless, it could be possible to enhance their efficiency through artificial selection on traits of economical or ecological relevance. Aggressiveness, which defines the readiness of an individual to display agonistic actions toward other individuals, is expected to be related to zoophagy, diet preferences and to a higher attack rate. The study aimed to assess the aggressiveness degree of the damsel bug, *Nabis americanoferus*, and to estimate its heritability. We hypothesized that a high aggressiveness degree can be selected, and that males are more aggressive than females. Using artificial selection, we reared two separate populations, each composed of nine genetically isolated lines characterized by their different aggressiveness degree (aggressive, docile and non-selected). After three generations, we had efficiently selected aggressive behavior. The realized heritability was 0.16 and 0.27 for aggressiveness and docility in the first population. It was 0.25 and 0.23 for the second population. Males were more aggressive than females only for the second population. The potential of these individuals as biological control agents and the ecological consequences of aggressiveness are discussed.

Keywords *Nabis americanoferus* · Aggressiveness · Artificial selection · Intraspecific variation · Realized heritability · Animal personality

Key message

- Aggressiveness could be a valuable trait to increase the attack rate of omnivorous predators.
- Artificial selection was used to increase the aggressiveness of an omnivorous predator.
- The aggressiveness degree was successfully increased after three generations.
- The second year, males were always more aggressive than females.

Introduction

As generalist predators, omnivorous individuals consume multiple pest species which may offer a broader control (McGregor et al. 1999; Symondson et al. 2002; Fantin et al. 2009; Calvo et al. 2012; Zappala et al. 2013). Moreover, their ability to switch from animal to plant resources when prey density is low allows them to survive and remain in the environment (Lalonde et al. 1999; Naranjo and Gibson 1996; Stilmant et al. 2008). Nonetheless, the latter characteristic might also represent an economic risk according to potential crop damage from more phytophagous individuals (Arnó et al. 2006; Calvo et al. 2009; Castañe et al. 2011). For instance, Dumont et al. (2017) show that diet specialization exists within the omnivorous mullein bug, *Campylomma verbasci* Meyer (Hemiptera: Miridae). Some individuals are more zoophagous, whereas others have a diet mainly based on plant materials. While prey availability has an influence on the diet of omnivorous species (Cottrell and Yeargan 1998; Arnó et al. 2006; Leon-Beck and Coll 2007), a genetic basis has also been identified (Dumont et al. 2016, 2017; Chinchilla-Ramírez et al. 2020). Such intraspecific genetic

Communicated by Alberto Urbaneja .

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variation of traits may constitute a strong tool to improve the efficiency of omnivorous species as biological control agents (Lommen et al. 2017; Dumont et al. 2017, 2018; Lirakis and Magalhães 2019; Bielza et al. 2020; Leung et al. 2020).

Improving the efficiency of omnivorous species for biological control may depend on many characteristics such as their diet preferences and level of zoophagy (Dumont et al. 2018; Bielza et al. 2020; Chinchilla-Ramírez et al. 2020; Leung et al. 2020). For that purpose, Dumont et al. (2018) suggested that selecting individuals for their high aggressiveness degree would be pertinent. Aggressiveness is a social behavior that is expressed through agonistic actions toward other individuals (Réale et al. 2007). Aggressive individuals are less selective concerning preys (Symondson et al. 2002), have a greater foraging rate (Pintor et al. 2009) and seem to have a higher attack rate (Riechert and Hedrick 1993; Michalko et al. 2021). These characteristics provide to aggressive individuals a wider trophic niche than docile individuals (Michalko et al. 2021) and make them more competitive than non-aggressive individuals for food acquisition (Bolnick et al. 2002, 2011; Sih et al. 2012). Aggressiveness is also positively correlated to boldness (propensity to take risks), curiosity and exploration (Réale et al. 2007; Kortet et al. 2014). Additionally, it has been shown that aggressive individuals can also display wasteful killing (Maupin and Riechert 2000). The latter behavior is valuable for biological control because the killing of pests would not be limited to a number equivalent to the satiety state of the predators.

Artificial selection is a powerful tool to favor relevant phenotypic expression of traits (Lommen et al. 2017; Dumont et al. 2016, 2018; Lirakis and Magalhães 2019; Bielza et al. 2020; Leung et al. 2020). Even though aggressiveness can be context-dependent (e.g., food-limited environment, stressful interaction with other individuals) (Maupin and Riechert 2000; Riechert and Hall 2000; Réale et al. 2007) it has also a genetic basis (Edwards et al. 2006; Kralj-Fišer and Schneider 2012). Moreover, the aggressiveness degree is not a fixed phenotypic expression as it exists along a continuum ranging from low to high phenotypic expression of aggressiveness (Réale et al. 2007). These differences also have a genetic basis that can be selected. For instance, Edwards et al. (2006) conducted an artificial selection for 28 generations on *Drosophila melanogaster* Meigen (Diptera: Drosophilidae) and found a lower heritability for a low aggressiveness degree. However, both high and low aggressiveness degrees were successfully selected. Aggressiveness is a trait that is possible to select, but its heritability differs between species. For instance, a heritability of aggressiveness ranging from 0.01 to 0.38 has already been calculated for drosophila (Edwards et al. 2006) and spiders (Kralj-Fišer and Schneider 2012). The lower the heritability is, the bigger the number of generations required for the trait to evolve will be. Furthermore, the heritability of

aggressiveness is not only different within species, but also differ within sex (Brown et al. 2006; Bubak et al. 2014). For instance, (Kralj-Fišer et al. 2019) show that the heritability of aggressiveness is higher for males of the spider *Nuctenea umbratica* Clerck (Araneae: Araneidae). In the nightingales, *Luscinia megarhynchos*, aggressive males have higher pairing success which results in aggressive behavior persisting within their population (Kunc et al. 2006).

Our study focuses on an omnivorous predatory bug, *Nabis americanoferus* Carayon (Hemiptera: Nabidae). It is a potential biological control agent preying upon on the tarnished plant bug, *Lygus lineolaris* Palisot de Beauvois (Hemiptera: Miridae), a notable phytozoophagous pest native to North America. *Nabis americanoferus* is an ambush predator with a « sit and wait » strategy (LaFlair 2022). Since aggressiveness is correlated to both impulsivity (Fairbanks et al. 2004) and a lesser prey selectivity (Symondson et al. 2002), it is likely that aggressive *N. americanoferus* would attack more frequently than docile ones. An increase in the attack rate may be beneficial for biological control because of a broader pest control. The present study aims (1) to artificially select the aggressiveness degree of *N. americanoferus* for generating more aggressive and more docile lines, (2) to estimate the heritability of the trait, (3) to compare the difference between males and females. This study is the first step to better understanding the role of aggressiveness in the ecology of *N. americanoferus* and its impact on biological control.

Materials and methods

Population and rearing conditions

Two colonies of *N. americanoferus* were reared in 2020 and 2021. Individuals used to establish the colonies were recovered from various regions of Quebec and Ontario (Canada). Adults were raised in rectangular boxes (70–40–40 cm) containing six eggplant plants, *Solanum melongena*, as oviposition support. They were fed with eggs of the flour moth, *Ephestia kuehniella*, Zeller (Lepidoptera: Pyralidae). To minimize cannibalism and maximize growth rate (i.e., food acquisition), 3rd instar of *N. americanoferus* were placed until adulthood into small, squared boxes (15 cm–10 cm–10 cm) containing a salad leaf and *E. kuehniella* eggs (four individuals per box). Every individual was maintained under standard abiotic conditions (25 °C, 70% humidity, 16:8 light/dark). Livestock maintenance was carried out once a week.

Experimental design and data collection

Nine genetically different lines were produced per year. Three of them were characterized by their high degree of aggressiveness (aggressive line), three others were selected

for their low degree of aggressiveness (docile line) and finally, three lines were also produced without any selection process. To establish colonies, the aggressiveness degree of 219 individuals was evaluated the first year and 357 the second year.

To estimate the aggressiveness degree of *N. americanus*, an ethogram comprising five observable behaviors related to aggressiveness was previously established (Table 1). Each behavior had a score ranging from -2 to 2 . Every individual was confronted with an organic lure. The lure consisted of a wooden handle of about ten cm, an entomological needle, and a fresh corpse of *N. americanus* (male to test males and female to test females). To get a fresh *N. americanus* corpse, individuals were euthanized by being put in a freezer at -18 °C for 20 min. After this period, the corpse was immediately stung on the needle by the posterior area of the abdomen so that we could effectively direct the head of the lure toward the target. Then, the tested individual was put into a circular-based plastic cup (10–15–15 cm). The stimulus was induced by slowly approaching the head of the organic lure toward the head of the tested individual. The lure was always approached at constant speed (i.e., without jerky movement), in front of the individual and until it touched the head of the tested individual (unless a behavioral response was observed before touching its head). Once a behavioral response was produced, it was recorded according to the ethogram (Table 1). Then, the lure was removed for 5 s to allow time for the tested individual to calm down. The stimulus was repeated three times. The same observer performed and recorded all stimuli for both years. The aggressiveness degree was calculated by adding up the scores assigned to each response resulting in a score between -6 and 6 . This allowed to create a continuum where the closer individuals are to 6 , the more they are considered aggressive and conversely. The score obtained is defined as the phenotypic value of the individual. For each line, 10 males and 10 females with the highest (aggressive line) or lowest (docile lines) level of aggressiveness were retained to produce the first generation. For the non-selected line, 10 males and 10 females were randomly chosen after every individual was tested. Individuals of the non-selected line were chosen before individuals of the aggressive and docile lines. This was done to avoid a selection bias consisting of

choosing individuals from a batch where very aggressive and very docile individuals were already removed. The first year, this selection process was made for the initial population and first generation. The second, third and fourth generation did not undergo selection due to the COVID pandemic consequences (see explanation at the end of Materials and Methods section). For the second year, it has been decided to proceed to the artificial selection at every two generations to let grow the number of individuals per lines. Thus, the selection process was made for the initial population, the second and fourth generation.

Statistical analysis

The realized heritability (h^2) of each selected line was calculated from the cumulative response to the selection (R) on the cumulative value of the differential selection (S) (Brakefield 2003):

$$R = h \times S$$

R defines the response to selection and corresponds to the difference between the average of the phenotypic value (i.e., the measured aggressiveness degree) of the offspring and that of the entire population before selection. It is a value that shows how much the mean of the phenotypic value has changed after the selection. S corresponds to the differential selection, i.e., the difference between the average phenotypic value of the trait in the pre-selection population and the average among selected genitors (Falconer and Mackay 1996). Regarding, h^2 , it is the realized heritability. It is a ratio of the additive genetic variance (V_a) on the phenotypic variance (V_p) such as (Brakefield 2003):

$$h = V_a/V_p$$

The phenotypic variance (V_p) was obtained by calculating the variance of the aggressiveness degree between every individual collected in the environment (i.e., the initial population G_0). The additive genetic variance (V_a) was then obtained by multiplying h^2 with V_p .

Statistical analysis was conducted with R software (version 4.0) (R Core Team 2020). Differences between the mean phenotypic value of lines were compared with a generalized

Table 1 Ethogram and values attributed to various responses of *N. americanus* adults during an encounter with an organic lure

Response	Value	Description
Flee	-2	The individual quickly flees from the lure
Ignorance	-1	The individual is not responding to the lure. It can be immobile or walk slowly in the area
Assessment	0	The individual faces the lure, touches it with its antennae or wave them toward the lure
Threat	$+1$	The individual takes an aggressive posture, exhibiting its front legs and standing on its rear legs
Attack	$+2$	The individual bites or grabs the lure with its front legs

linear model using a quasibinomial distribution following by a Chi square test. Likelihood Ratio Test (LRT_{ν}) is used to show the scaled deviance as well as the degree of freedom (see the subscript number of LRT). Comparisons were made for the entire selection process as a whole, between every generation and between males and females.

Consequences of the COVID-19 restrictions

In the first year, the colony suffered the consequences of the global pandemic of COVID-19 and collapsed in the second generation. To continue our study, we had to merge the aggressive lines together and the docile lines together. For the non-selected lines, the rearing crashed. However, the evaluation of the aggressiveness degree has been recorded for every generation and we were able to calculate a realized heritability for both the aggressive and docile lines.

Results

Phenotypic response to artificial selection

The initial population (G_0) of both years had a statistically different mean aggressiveness degree from each other ($LRT_1 = 17.815$; $p < 0.0001$). The first year, the mean aggressiveness degree of -2.53 (± 0.19 SE), whereas it was -1.39 (\pm SE) for the second year.

In the first year (2020), both lines of the first generation (G_1) still had the same mean aggressiveness degree ($LRT_1 = 0.08$; $p = 0.76$) (Fig. 1). However, at G_2 , the aggressive and docile lines diverged and became statistically different ($LRT_1 = 7.47$; $p = 0.006$). In this generation, the

aggressive degree of the aggressive line was 0.75 (± 0.77 SE) and despite the absence of selection, it kept rising until the fourth generation to reach 1.04 (± 0.48 SE). For the docile line, its aggressiveness degree went below the one of the initial population at G_2 and never exceeded it again (Fig. 1). In this generation, its aggressiveness degree was -2.86 (± 0.86 SE). Then, despite the absence of selection, its aggressiveness degree kept decreasing until G_4 to reach -3.25 (± 0.31 SE). When all generations are considered, the aggressive and docile lines display a strong statistical difference ($LRT_1 = 13.44$; $p = 0.0002$).

At G_1 of the second year (2021), both the aggressive and docile lines diverged (Fig. 2) but had not yet a phenotypical value that was statistically different from each other ($LRT_2 = 2.74$; $p = 0.25$). Statistical differences between these lines appeared at G_3 ($LRT_2 = 24.55$; $p < 0.0001$). In this generation, the aggressive line had a mean aggressiveness degree of 0.08 (± 0.32 SE), whereas the docile had a value of -2.5 (± 0.47 SE). At the last generation (G_5), line was even more different ($LRT_2 = 71.369$; $p < 0.0001$). If the aggressiveness degree of the aggressive line remains stable with a value of 0.05 (± 0.3 SE), the docile line reached a value of -4.62 (± 0.21 SE). Concerning the non-selected line, even though its mean aggressiveness degree decreased at the first two generations (Fig. 2), at G_5 there was no statistical differences between its mean aggressiveness value and the one of the initial populations ($LRT_2 = 0.40$; $p = 0.52$).

Phenotypic variation between males and females

The first year, the initial population was composed of 121 males and 98 females. The mean aggressiveness degree of males was -2.44 (CI 95% $[-1.95; -2.93]$) and -2.63 (CI

Fig. 1 First-year phenotypic response to the artificial selection of aggressiveness. The red line corresponds to the aggressive line and the blue line to the docile line. The black-dashed line corresponds to the mean aggressiveness value of the initial population. Vertical lines correspond to standard error. Letter a and b refer to the moment where statistical differences appeared between the lines. Artificial selection was conducted at the generation 0 and 1

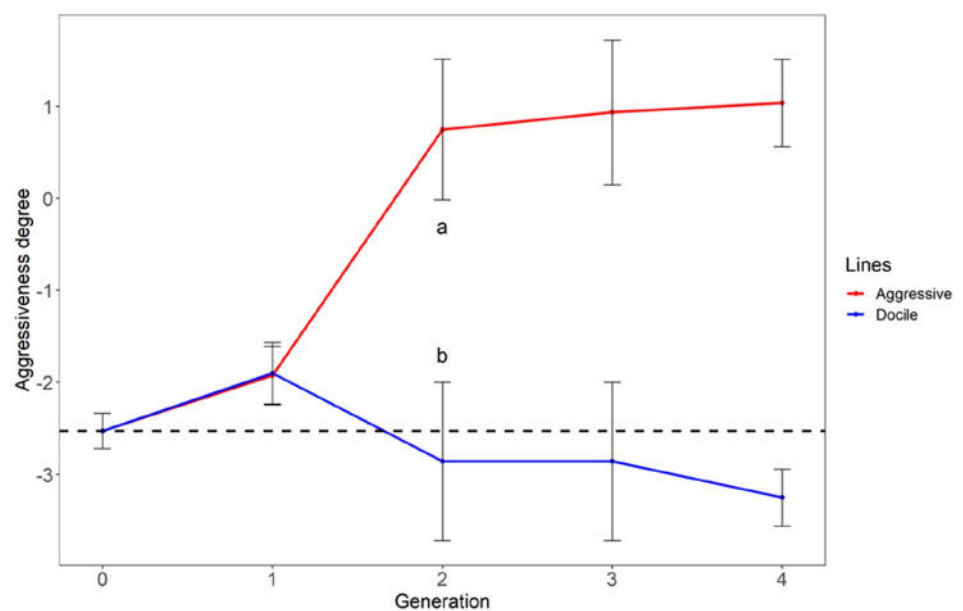
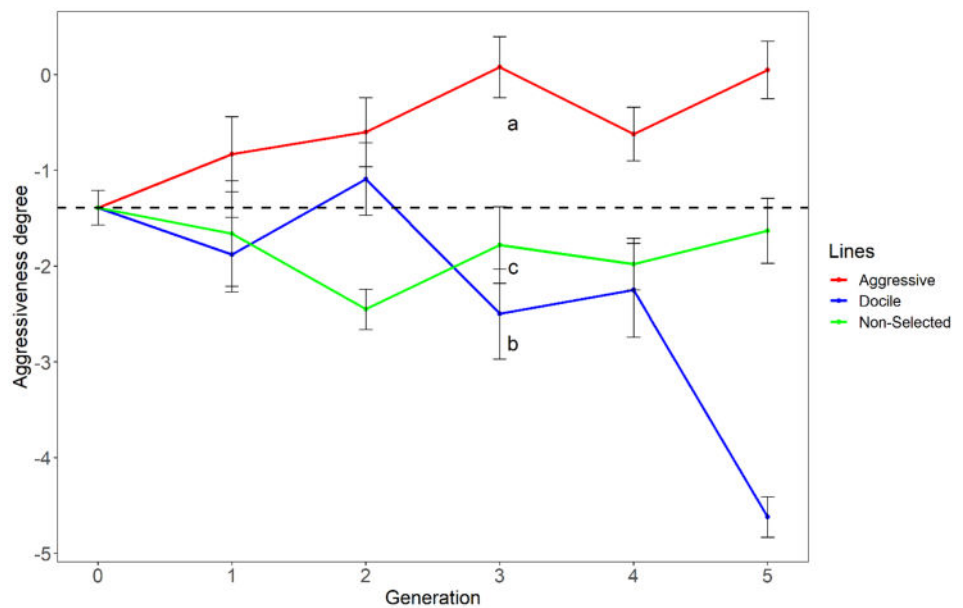


Fig. 2 Second-year phenotypic response to the artificial selection of aggressiveness. The red line corresponds to the aggressive line, the blue line to the docile line, and the green to the non-selected line. The black dashed line corresponds to the mean aggressiveness value of the initial population. Vertical lines correspond to standard error. Letter a, b and c refer to the moment where statistical differences appeared between the lines. Artificial selection was conducted at the generation 0, 2 and 4



95% [-2.04; -3.22]) for female. There was no statistical differences between sex for the initial population ($LRT_1 = 2.38$; $p = 0.12$) nor there was for the first year experiment ($LRT_1 = 2.31$; $p = 0.12$). The only statistical difference was found at G_1 ($LRT_1 = 5.94$; $p = 0.0147$) where males had a higher aggressiveness degree.

For the second year, the initial population was composed of 165 males and 192 females. Males from the initial population had a statistically higher mean aggressiveness value than females ($LRT_1 = 71.59$ $p < 0.0001$). While males had a mean aggressiveness value of -0.13 (CI 95%: [0.36; -0.63]), the mean score of female was -2.44 (CI 95%: [-1.99 ; -2.89]). During the selection process, there was a statistical difference between males and females ($LRT_1 = 6.92$; $p = 0.009$) where males had a higher mean aggressiveness degree than females. Statistical differences were also found at G_2 ($LRT_1 = 9.88$; $p = 0.0016$) and G_5 ($LRT_1 = 13.20$; $p = 0.0002$). For the aggressive line, every time a statistical difference was found, males always had a higher mean aggressiveness degree. The aggressiveness degree of females from the aggressive line never went above the initial mean value of males. Instead, the aggressiveness degree of males from the docile line went below the initial mean value of females.

Realized heritability

For the first year, the realized heritability (h^2) has only been calculated for the first generation. The realized heritability of aggressiveness is 0.16 (± 0.04 s.s.). For docile lines, the realized heritability of docility was 0.27 (± 0.10 SE). The phenotypic variation (V_p) of the first year has been calculated with the scores of the initial population which make

$V_p = 7.96$. The additive genetic variance (V_a) was 1.27 and 2.15 for aggressiveness and docility, respectively.

For the second year, the realized heritability of aggressiveness was 0.25 (± 0.03 SE). The realized heritability of docility the value obtained was 0.23 (± 0.08 SE). The phenotypic variation (V_p) for the second year is 8.17. The additive genetic variance (V_a) was 2.04 and 1.87 for aggressiveness and docility, respectively.

Discussion

Our results show that it was possible to efficiently select both high and low aggressiveness degrees in *N. americanus*. Moreover, we observed significant differences in aggressiveness between males and females in the second year, whereas not for the first year. Finally, we found a different pattern of realized heritability for both years. For the first year, the realized heritability was higher for docility, while the realized heritability of aggressiveness and docility was substantially the same for the second year.

For the first year, despite the absence of selection between the second and fourth generation, the aggressiveness degree increased and decrease for the corresponding lines. It is possibly due to a bottleneck effect that reduced the intraspecific gene variation (James 1970; Bryant et al. 1986). Induced-bottleneck effect experiments have been conducted on the housefly, *Musca domestica* L. (Diptera: Muscidae) and the heritability of the studied traits increased, allowing a quicker selection of traits (Bryant et al. 1986). If alleles favoring aggressiveness and docility remained in a small population at high frequencies, it is possible for these traits to be enhanced without artificial selection (James 1970; Bryant

et al. 1986). For the second year, individuals were selected at the initial population, at the second generation and at the fourth. When the selection pressure was relaxed (i.e., generation one and three), the selection response was lower and the aggressiveness degree of these lines tends to return to the one of the initial population. These results corroborate with other studies by Baer and Travis (2000) and Hine et al. (2011) where relaxing artificial selection result in a lower selection response.

The aggressiveness degree of the non-selected line remains statistically similar to the initial population. These observations are important for biological control: first, the rearing conditions provided to *N. americanoferus* did not influence the intraspecific variation of traits. It is valuable since the colony could be maintained for a long period of time before being released into the environment as a biological control agent. And second, the phenotypic response to artificial selection on aggressiveness was effective within two and three generations for the first- and second-year experiment, respectively. Individuals collected at the end of the summer could be ready to be used for the next year.

Populations of *N. americanoferus* collected in the field differed between the first and second years. In the first year, the aggressiveness degree was lower compared to the second year and there was no difference between males and females. However, males of the initial population of the second year had a higher aggressiveness degree than females. Intraspecific variation in a behavioral trait like aggressiveness can be explained by the spatiotemporal variation of selecting pressures (Sih et al. 2015; Wolf and Weissing 2010) and sexual selection (Brown et al. 2006; Bubak et al. 2014). Aggressiveness is an important component for competitiveness (Riechert and Hall 2000; Bolnick et al. 2002, 2011; Sih et al. 2012), variation of prey density might favor varying aggressiveness degrees accordingly. Such characteristics allow aggressive individuals to cope with environmental variations and get a better fitness. For instance, individuals of the desert spider *Agelenopsis aperta* Gertsch (Aranea: Agelenidae) differ in their aggressiveness depending on their habitat (Riechert and Hall 2000). Namely, individuals were more aggressive in an environment with low resources. In a context where preys are scarce, aggressiveness seems valuable for survival. For *N. americanoferus*, the persistence of an intraspecific variation in aggressiveness might be an evolutionary advantage because it allows populations to thrive when environmental conditions are not optimal. Moreover, for the second year, we also observed inter sex differences in aggressiveness and the selection process worked better for males. Most insect species are under strong sexual selection on traits like aggressiveness because it allows males to win encounters against conspecific (Wcislo and Eberhard 1989; Bubak et al. 2014). Moreover, aggressive individuals tend to have a higher attack rate and to explore more their

environment than less aggressive one (Riechert and Hedrick 1993; Réale et al. 2007; Michalko et al. 2021). It is likely that more aggressive individuals also have greater opportunity to encounter mates which could favor alleles responsible for it in natural populations.

Using aggressive agents for biological control could provide higher efficiency since aggressive individuals tend to have a higher attack rate than non-aggressive ones (Riechert and Hedrick 1993; Michalko et al. 2021). However, predation intensity would probably also include intraspecific predation (i.e., cannibalism) and intraguild predation (IGP), this is toward beneficial organisms (Lucas 2012; Michalko et al. 2021). For instance, in their artificial selection process on the diet, Dumont et al. (2017) observed that zoophagous lines of the mullein bug also displayed a higher cannibalism rate. Whether aggressive predators display higher cannibalism rate raises concerns about potential mass rearing. Although we were able to maintain low cannibalism rate in our rearing, the *N. americanoferus* density was low. Moreover, if aggressive biological control agent are used for field experiments, the question of intraguild predation is also to be evaluated since pest's natural control also relies on the activity of the guild members (Lucas 2012). The question of intraguild predation has already been addressed in laboratory conditions with an experiment where aggressive and docile individuals from this selection experiment were used. Although this experiment is still unpublished, we were able to show that aggressive individuals were more aggressive than docile ones and that they also displayed more IGP. Furthermore, two last points need to be addressed: first, how long the aggressiveness degree of individuals released in fields will remain at a high level. The rearing condition provides food ad libitum, limits the intraspecific competition and constrains individuals to reproduce with mates with a similar aggressiveness degree. In an agroecosystem, individuals will compete with others for food, will potentially emigrate and reproduce with individuals with a lower aggressiveness degree. In these conditions, their aggressiveness degree might decrease after a few generation. And second, is it possible to breed an aggressive line in mass rearing for a long term without having to repeat the selection process for the entire rearing. Unpublished data from another experiment we have conducted using the aggressive line provides interesting insights to answer this concern. After 5 months without artificial selection, the aggressiveness degree of the aggressive line was still statistically similar to what it was before relaxing the selection pressure. Inbreeding could have preserved, or at least slowed down the loss of gains obtained by artificial selection. Moreover, despite aggressiveness has a low heritability, the aggressiveness degree of the aggressive lines rose in a few generation. Therefore, maintaining a high aggressiveness rate in colonies seems possible. Either way, the answers to these questions will shape the rearing

logistics of aggressive biological control agents as well as how they will be used.

Acknowledgements We would like to thank Chiara Chelo and Laurence Bélanger for their support during the rearing. We also thank the editor and anonymous reviewers for their constructive comments on the manuscript.

Author contribution PR, FD and EL conceived and designed research. PR conducted experiments. PR and FD analyzed data. PR wrote the manuscript. All authors read, provided feedback and approved the manuscript.

Funding Funding for this project has been provided in part through the AgriScience program-cluster on behalf of Agriculture and Agri-food Canada.

Data availability Data are available on demand to the corresponding author.

Declarations

Competing interests The authors declare no competing interests.

Conflict of interest Authors declare no conflict of interest or competing interests.

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.

Consent to participate Not applicable.

Consent to publish Not applicable.

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