

Selecting aggressiveness to improve biological control agents efficiency

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Abstract

In agroecosystems, omnivorous predators are recognized as potential biological control agents because of the numerous species 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 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 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 five generations, we had efficiently selected aggressive behavior. The realized heritability was 0.16 (± 0.04 S.E.) and 0.27 (± 0.1 S.E.) for aggressiveness and docility in the first population. It was 0.25 (± 0.03) and 0.23 (± 0.08 S.E.) 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 is discussed.

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 was successfully increased after three generations.
- Males were 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; Fantinou 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 (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. The zoophytophagous mirid *Nesidiocoris tenuis* Reuter (Hemiptera: Miridae) is another example that highlights the ambiguous potential of such biological control agent. While this species is considered as an efficient biological control agent (Calvo et al. 2012), its deleterious effect on tomatoes (Arnó et al. 2006) led it to be also classified as a pest (Malézieux et al. 1995). While prey availability have an influence on the diet of omnivorous species (Cottrell and Yeorgan 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 variation

of traits may constitute a strong tool to improve the efficiency of omnivorous species as biological control agents (Lommen et al. 2008; Tabone et al. 2010; Lommen et al. 2017; Dumont et al. 2017, 2018; Chinchilla-Ramírez et al. 2020).

Improving the efficiency of an omnivorous species for biological control mostly relies upon their diet preferences and level of zoophagy (Dumont et al. 2018; Chinchilla-Ramírez 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 antagonistic 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 seems 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, which would increase their pest's control efficiency (Maupin and Riechert 2000). Such behavior is valuable for biological control because it has the potential increase the modify the diet preference of zoophytophagous individuals.

Artificial selection is a powerful tool to favor relevant phenotypic expression of traits (Lommen et al. 2008; Tabone et al. 2010; Lommen et al. 2017; Dumont et al. 2017, 2018; Chinchilla-Ramírez et al. 2020). Even though aggressiveness can be context-dependent (Maupin and Riechert 2000; Riechert and Hall 2000; Réale et al. 2007) it has also a genetic basis (Fairbanks et al. 2004; Edwards et al. 2006, Turner et al. 2006; Kralj-Fišer and Schneider 2012; Ariyomo et al. 2013; Araya-Ajoy et al. 2017). 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 differ between species. A heritability of aggressiveness ranging from 0.01 to 0.36 has already been calculated for monkeys (Fairbanks et al. 2004), drosophila (Edwards et al. 2006), spiders (Kralj-Fišer and Schneider 2012), birds (Araya-Ajoy et al. 2017), fishes (Ariyomo et al. 2013), mice (Van Oortmerssen and Bakker 1981) and pigs (Turner et al. 2006). 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 focusses on an omnivorous predatory bug, *Nabis americana* 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 americana* 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. americana* 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. americana* 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. americana* and its impact on biological control.

Materials And Methods

Population and rearing conditions

Two colonies of *N. americana* 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 cm - 40 cm - 40 cm) containing six eggplant plants, *Solanum melongena*, as oviposition support. They were fed with eggs of the flour moth, *Ephesia kuehniella*, Zeller (Lepidoptera : Pyralidae). To maximize their survival and growth, 3rd instar of *N. americana* were placed until adulthood into small, squared boxes (15 cm - 10 cm - 10 cm) containing a salad leaf and *E. kuehniella* eggs. Every individual was maintained in 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 in the first year and 357 for the second year.

To estimate the degree of aggressiveness of *N. americana*, an ethogram comprising five observable behaviors was previously established (Table I). 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. americana* (male to test males and female to test females). The corpse was 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 cm - 15 cm - 15 cm). The stimulus was induced by slowly approaching the head of the organic lure toward the individual. Its behavioral response was recorded according to the ethogram (Table I). Then, the lure was removed for 5 seconds to allow time for the tested individual to calm down.

The stimulus was repeated three times. The aggressiveness degree was calculated by adding up the scores assigned to each response resulting in a score between -6 and 6. With a score close or equal to 6, the individual was considered highly aggressive, conversely, with a score close to -6, the individual was considered docile. The score obtained is defined as the phenotypic value of the individual. For each line, 10 females and 10 males with the highest (aggressive line) or lowest (docile lines) level of aggressiveness were retained to produce the first generation. This process was repeated every two generations to let grow the number of individuals. For the non-selected line, 10 male and 10 female were randomly chosen after every individual was tested.

Table I. Ethogram of values attributed to various responses of *N. americanoferus* adults during an encounter with an organic lure.

Response	Value	Description
Flee	-2	The individual rapidly ran away 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 towards 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.

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):

$$R = h^2 \times S$$

R defines the response to selection and corresponds to the difference between the average of the phenotypic value (i.e., the measured aggressiveness index) 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 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):

$$h^2 = V_a / V_p$$

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 linear model using a quasibinomial distribution. 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 from 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 populations (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 $-2.53 (\pm 0.19$ s.e.) whereas it was $-1.39 (\pm$ s.e.) for the second year.

In the first year (2020), both lines of the first generation (G_1) still had the same mean aggressiveness degree ($LRT_1 = 0.08$; $p = 0.76$) (Figure 1.A.). 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 $0.75 (\pm 0.77$ s.e.) and despite the absence of selection, it kept rising until the fourth generation to reach $1.04 (\pm 0.48$ s.e.). For the docile line, its aggressiveness degree went below the one of the initial population at G_2 and never exceeded it again (Figure 1.A.). In this generation, its aggressiveness degree was $-2.86 (\pm 0.86$ s.e.). Then, despite the absence of selection, its aggressiveness degree kept decreasing until G_4 to reach $-3.25 (\pm 0.31$ s.e.). When all generations are considered, the aggressive and docile lines display a strong statistical difference ($LTR_1 = 13.44$; $p = 0.0002$).

At G_1 of the second year (2021), both the aggressive and docile lines diverged (Figure 1.B) 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-value < 0.0001). In this generation, the aggressive line had a mean aggressive degree of $0.08 (\pm 0.32$ s.e.) whereas the docile had a value of $-2.5 (\pm 0.47$ s.e.). At the last generation (G_5), line were even more different ($LTR_2 = 71.369$; p-value < 0.0001). If the aggressiveness degree of the aggressive line remains stable with a value of $0.05 (\pm \pm 0.3$ s.e.), the docile line reached a value of $-4.62 (\pm 0.21$ s.e.). Concerning the non-selected line, even though its mean aggressiveness degree decrease at the first two generations (Figure 1.B), at G_5 there was no statistical differences between its mean aggressiveness value and the one of the initial populations ($LTR_2 = 0.40$; p-value = 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 95% [-2.04; -3.22]) for female (Figure 2.) There was no statistical difference between sex for the initial population ($LTR_1 = 2.38$; $p = 0.12$) nor there was for the first year experiment ($LTR_1 = 2.31$; $p = 0.12$). The only statistical difference was found at G_1 ($LTR_1 = 5.94$; p -value = 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 ($LTR_1 = 71.59$ p -value < 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]) (Figure 2.). During the selection process, there was a statistical difference between males and females ($LTR_1 = 6.92$; p -value = 0.009) where males had a higher mean aggressiveness degree than females. Statistical differences were also found at G_2 ($LTR_1 = 9.88$; p -value = 0.0016) and G_5 ($LTR_1 = 13.20$; p -value = 0.0002). 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 (Figure 2.A). Instead, the aggressiveness degree of males from the docile line went below the initial mean value of females (Figure 2.B).

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 s.e.). 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 s.e.) The realized heritability of docility the value obtained was 0.23 (± 0.08 s.e.). The phenotypic variation (V_p) for the second year is 8.17. The additive genetic variance (V_a) was 1.63 for both aggressiveness and docility.

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 it was the opposite 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 the 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 where relaxing artificial selection result in a lower selection response (Baer and Travis 2000; Hine et al. 2011).

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 generations. Individuals collected at the end of the summer could be ready to be used for the next year and the colony could be maintained at high aggressiveness through the year with limited effort.

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. Unpublished data of Dumont & al. pointed out a drastic variation of density population of *L. lineolaris* between 2019 and 2020. As many individuals of *N. americanoferus* were recovered at the end of the summer 2019 and 2020 from the region where the survey of Dumont & al. was made, it is possible that it could have influenced the aggressiveness degree of these populations. The year 2019 had high prey density, which would not necessarily favor aggressiveness over docility. As a result, individuals collected at the end of the summer had a low aggressiveness degree. Instead, the year 2020 had a low prey density, which probably favored aggressive individuals which could partially explain why we observed a higher aggressiveness degree from individuals collected in 2021.

Moreover, for this 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 individuals 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 selection process on the diet, Dumont et al. (2017) observed that zoophagous lines of the mullein bug also displayed higher a cannibalism rate. Additionally, the question of intraguild predation is to be evaluated since pest's biological control also relies on the activity of the guild members (Lucas 2012). Furthermore, 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 lower a aggressiveness degree. Therefore, it is important to understand how long the aggressiveness degree of individuals released in fields will remain at a high level. The response to this question will modulate the way they will be used.

Declarations

Aknowledgement

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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.

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Competing Interests

Authors declare no conflict of interest or competing interests.

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.

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Figures

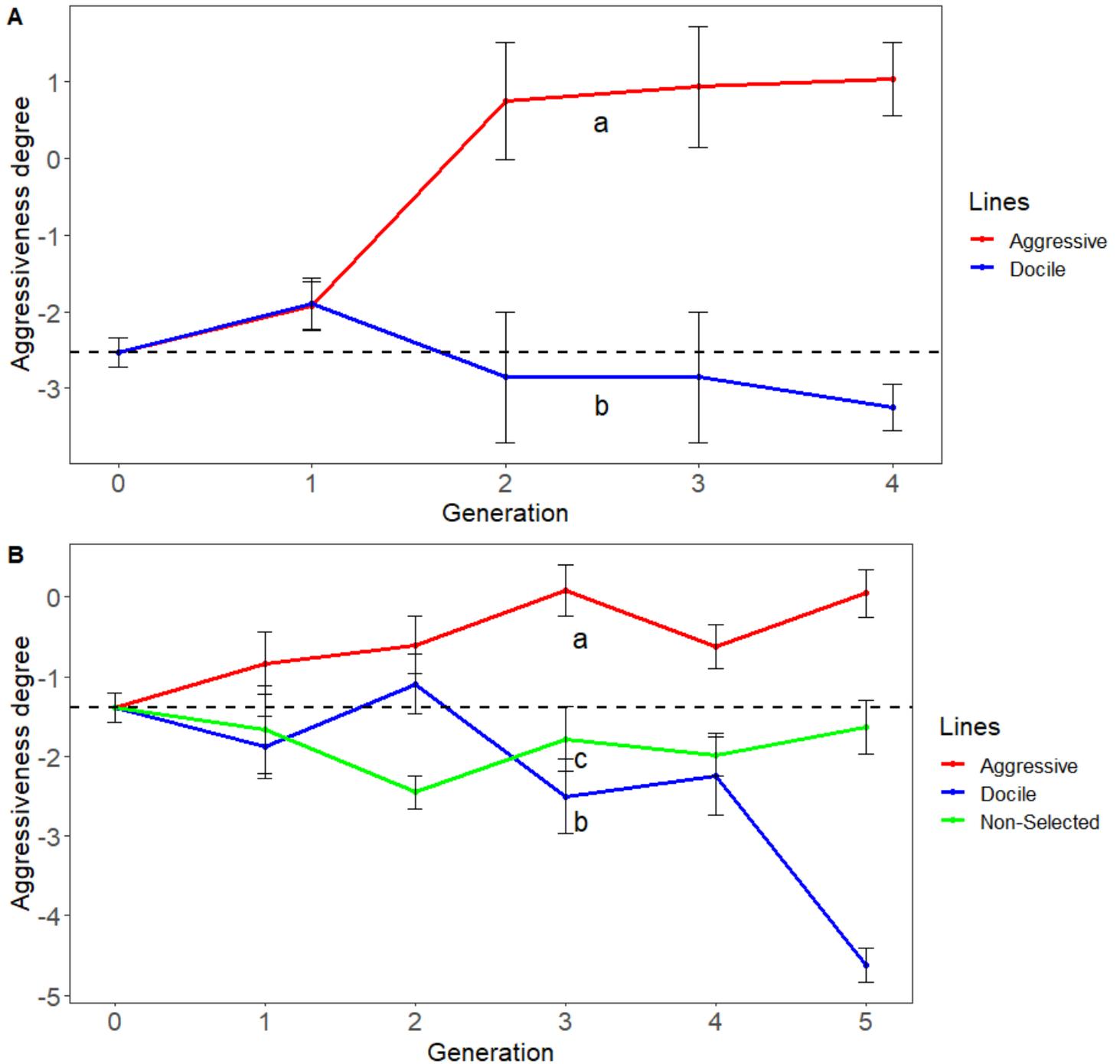


Figure 1

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. Graphic A corresponds to the results of the first year and graphic B to the second year. The black dashed line corresponds to the mean aggressiveness value of the initial population.

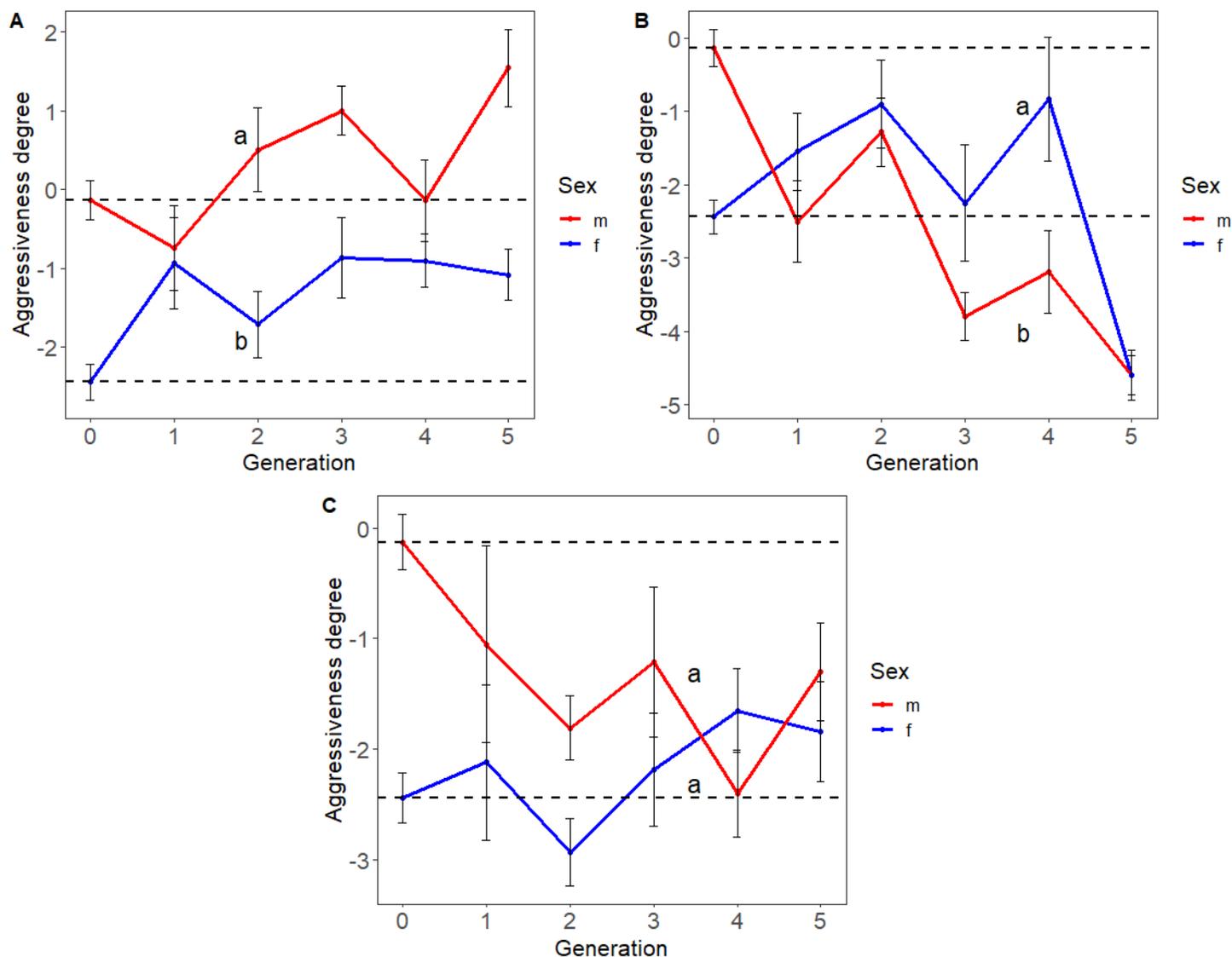


Figure 2

Phenotypic response to the artificial selection of aggressiveness for males and females of the second year. Figures A, B and C correspond to the aggressive line, the docile line and the non-selected line respectively. Red lines refer to males and blue to females. Dashed lines refer to the mean phenotypic value of males and females of the initial population.