LEONARDO MORAIS TURCHEN

BIDIRECTIONAL SELECTION OF WALKING VELOCITY, ASSOCIATED BEHAVIORAL SYNDROME AND FITNESS CONSEQUENCES IN THE MAIZE WEEVIL *Sitophilus zeamais*

Dissertação apresentada à Universidade Federal de Viçosa, como parte das exigências do Programa de Pós-Graduação em Entomologia para a obtenção do título de *Magister Scientiae*.

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Raul Narciso Carvalho Guedes
(Orientador)

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SUMÁRIO

ABSTRACT

TURCHEN, Leonardo Morais, M.Sc., Universidade Federal de Viçosa, July, 2017. **Bidirectional selection of walking velocity, associated behavioral syndrome and fitness consequences in the maize weevil *Sitophilus zeamais***. Advisor: Raul Narciso Carvalho Guedes.

The individual behavioral types (i.e., personality traits) and their inter-correlations (i.e., behavioral syndrome) are recognized in the arthropods and reveal ecological and evolutionary importance. The issue is also important for applied entomology, where distinct personality types have differ with consequence for the insect fitness. Here, we attempted to understand how within-population variation in personality traits are maintained. Therefore, we focus on selection of a behavioral trait (i.e., walking velocity) to check whether it is inherited and inter-correlated with other personality traits configuring a behavioral syndrome, and their fitness consequences. The maize weevil (*Sitophilus zeamais*) was used as experimental model to test the above mentioned hypothesis. We detected that walking velocity is inherited and maintained among generations of maize weevil. Furthermore, the selection procedure exhibited impact on the behavioral types allowing us to recognize different behavioral patterns among strains. The multidimensional behavioral constructs of maize weevil personality indicate divergence among personality types within and between strains with stronger contribution of the activity dimension. Lastly, we assessed the inter-relations between walking velocity and the other behavior traits, and behavioral traits with reproductive output. The former indicated the existence of behavioral syndrome in the maize weevil, particularly within the activity dimension. The second indicated that this behavioral dimension, and particularly walking velocity, does affect the reproductive output of maize weevil.

RESUMO

TURCHEN, Leonardo Morais, M.Sc., Universidade Federal de Viçosa, julho de 2017. **Seleção bidirecional da velocidade de caminhamento, síndrome comportamental associada, e consequências sobre o fitness de caruncho-do-milho *Sitophilus zeamais***. Orientador: Raul Narciso Carvalho Guedes.

Os tipos individuais de comportamento (traços de personalidade) e suas inter-correlações (síndrome comportamental) são reconhecidos para artrópodes e revelam importância ecológica e evolutiva. Esta importância também se estende à entomologia aplicada, onde tipos distintos de personalidade mostram consequências distintas no valor adaptativo de insetos. Aqui, nós procuramos entender como é mantida a variação da personalidade dentro da população através da seleção de um traço comportamental (no caso, velocidade de caminhamento) a fim de investigar se este é herdado e se inter-correlaciona outros traços de personalidade, configurando uma síndrome comportamental. Além disto, nós avaliamos se a seleção feita teve consequência sobre a capacidade reprodutiva dos indivíduos selecionados. Para testar tal hipótese, nós utilizamos o caruncho-do-milho (*Sitophilus zeamais*) como modelo experimental. Nós observamos que a velocidade de caminhamento é uma característica que pode ser herdada e mantida entre gerações de caruncho-do-milho. O procedimento de seleção também teve impacto sobre os tipos comportamentais, o que nos permitiu reconhecer diferentes padrões comportamentais nas linhas de seleção. Os desenhos das construções comportamentais multidimensionais para a personalidade confirmaram uma divergência consistente entre os tipos de personalidade e dentro das linhagens selecionadas, com maior contribuição da dimensão atividade. Verificamos ainda a existência de inter-correlações entre velocidade de caminhamento com outros traços de comportamento, particularmente na dimensão atividade, indicando a existência de síndrome comportamental no caruncho-do-milho. As características comportamentais também mostraram relação com a capacidade reprodutiva dos insetos, com destaque para o impacto da velocidade de caminhamento sobre a reprodução do caruncho-do-milho.

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Bidirectional selection of walking velocity, associated behavioral syndrome and fitness consequences in the maize weevil *Sitophilus zeamais*

Leonardo M. Turchen[a], Lírio Cosme Jr.[a], Raul Narciso C. Guedes[a]

[a] Department of Entomology, Universidade Federal de Viçosa, Viçosa, MG 36570-000, Brazil

Correspondence to:

Raul Narciso Carvalho Guedes
Department of Entomology
Universidade Federal de Viçosa
Viçosa, MG 36570-000
Brazil
E-mail: guedes@ufv.br

Abstract

The individual behavioral types (i.e., personality traits) and their inter-relations (i.e., behavioral syndrome) are recognized in the arthropods and reveal ecological and evolutionary importance. These subject is also important for applied entomology, as distinct personality types may exhibit different fitness consequences. Here, we attempted to understand how within-population variation in personality is maintained. The focus of attention was in the selection of a quantifiable behavioral trait (i.e., walking velocity) to learn whether it is inherited and if it is inter-related with other personality traits, and how these traits are related to reproductive output. The maize weevil (*Sitophilus zeamais*) was used as experimental model to test these hypotheses. We detected that walking velocity is inherited and maintained across successive generations of the maize weevil. Furthermore, selection for walking velocity exhibited impact on behavioral types, which allowed us to recognize different behavioral patterns among strains. The generated multidimensional behavioral constructs of personality indicates consistent divergence among personality types within and between strains with stronger contribution of the activity dimension. Lastly, we assessed the inter-relations between walking velocity and other behavior traits, and also between behavioral traits and reproductive output. The former indicated the existence of behavioral syndrome in the maize weevil, particularly within the activity dimension. The second indicated that this behavioral dimension, and particularly walking velocity, does affect the reproductive output of maize weevil.

Key word: Personality traits; Stored grain pest; Behavioral types; Insect behavior;

Introduction

Conspecifics differ in morphology, physiology and behavior, which is known as intraspecific variation (Darwin 1859). These variations, especially of behavior, are related to mechanical and/or physiological processes integrated to environmental stimulus in individual organisms and extended to populations. However, some behavioral traits exhibit individual consistence and are frequently referred to as individuality and/or personality traits (Bergmüller 2010; Dingemanse and Réale 2005; Mather 2012; Réale et al. 2007; Sih et al. 2004)

Personality traits are evident in humans, where some individuals are more sociable, bold and/or aggressive than others, and these differences are genetically based leading to a range of consequences for the health, social relations and sexual behavior of individuals (Carere and Eens 2005). Similarly, other animals (i.e., arthropods) exhibit inter-correlated personality traits, or behavioral syndromes, that may be heritable and/or exhibit fitness consequences (Réale et al. 2007; Sih et al. 2004; van Oers and Mueller 2010).

Studies with arthropods (i.e., insect) have increased considerably and provided information on the biological, ecological, and evolutionary importance of different personality types (Gosling 2001; Kralj-Fiser and Schuett 2014; Pruitt 2014; Schuett et al. 2015; Sih et al. 2004; Sih et al. 2012; van Oers and Mueller 2010; Wolf and Weissing 2012). Furthermore, ongoing studies with arthropods recognized the potential importance of personality and behavioral syndromes for managing pest populations (Malia et al. 2016; Morales et al. 2013; Schuett et al. 2015). For instance, three personality dimensions (activity, bold/shy and exploration/avoidance) were characterized in the maize weevil *Sitophilus zeamais* Motschulsky (Coleoptera: Curculionidae), a key worldwide pest of stored cereals, in which the activity dimension (particularly walking velocity) was an important divergence trait among individual weevils and populations. Furthermore, this personality dimension affected the susceptibility to insecticides and to a physical control agent (i.e., diatomaceous earth) with impact on insect survival (Malia et al. 2016; Morales et al. 2013).

A curiously fundamental question with serious management consequences for arthropod pest species remains unanswered nonetheless - how within-population variation in personality is maintained in the face of selection for optimal behavioral phenotypes. Such possibility implies the maintenance of individuals exhibiting suboptimal behavior within a population that may better withstand environmental changes, including the introduction of management tactics aimed at arthropod pest species. Therefore, here we aimed at investigating whether a behavioral trait, walking velocity, representative of a behavioral dimension, is inherited and inter-related with other personality traits, potentially exhibiting fitness consequences, when the insects are submitted to selection for such a trait.

The hypothesis stated above was tested by selecting strains of the maize weevil for high and low walking velocity and assessing their behavioral traits encompassing three personality dimensions (i.e., activity, bold/shy and exploration/avoidance). We assessed whether the weevils under selection exhibited correlated changes in other behavioral traits (thus, inheritable behavioral correlation) with consequences for their reproductive output. We expected velocity to be an inheritable trait since walking velocity confers adaptive value for maize weevils (i.e., favoring survival) (Malia et al. 2016; Morales et al. 2013). Other behavioral traits within the same personality dimension (e.g., resting time) are expected to be correlated, but we were uncertain of the impact from selection on behavioral traits of other personality dimensions and the consequences of our selection in the weevil reproductive output.

Material and Methods

Maize weevil populations

Ten populations of the maize weevil were used to establish a mixed colony with a broad gene pool for the intended selection. These ten populations are derived from laboratory colonies maintained in high numbers to minimize loss of genetic diversity and they were all established from field-collected insects within the past eight years, except for the populations from Sete Lagoas (Brazil), which were collected in the late 1980s. Besides the eight maize weevil populations from Brazil (Curitiba, State of Paraná; Piracicaba, State of São Paulo; Anápolis, State of Goiás; Rio Branco, State of Acre; and Sete Lagoas, Unaí, Juiz de Fora and Viçosa, State of Minas Gerais), one population is from Amambay in Paraguay and another is from Maputo in Mozambique.

Fifty unsexed adult insects from each population were placed together in 1.5 L glass jar establishing a mixed colony and reared on maize kernels, free of insecticide residues. Three jars containing the mixed population and about 500 adult weevils per jar were maintained as stoke culture. The insects were maintained in a rearing room with controlled environmental conditions of 27 ± 2 ºC temperature, 70 ± 10 % relative humidity, and a 12 h photoperiod. The selections for high and low walking velocity started after allowing the insects to interbreed and natural selection take place for two generations.

General selection procedure

The behavioral trait under selection was walking velocity (low and high), which was chosen because it allowed greater contribution for the behavioral divergence recorded among populations of the maize weevil, as reported by Morales et al. (2013) and Malia et al. (2016). This trait was also recognized as important for the efficacy of both insecticides and diatomaceous earth, a physical control agent important in stored product protection (Malia et al. 2016; Morales et al. 2013). Maize weevil adults (< 3 days old) obtained from the stock colonies containing the mixed populations were used for the selection procedure. The insects were sexed using their pattern of rostrum length, texture and punctuation (Halstead 1965; Tolpo and Morrison 1965), and subsequently submitted to the behavioral bioassays to recognize the behavioral patterns in the parental (mixed) population. The same general procedure was used at each generation of selection for low and high walking velocity.

The average and standard deviation (SD) of the walking velocity of the parental population were considered as parameters for the intended selection allowing the simultaneous maintenance and assessment of three strains: strain 1 (unselected); strain 2 (selected for low velocity), whose individuals selected exhibited walking velocity below the average of the parental population (- 1 SD); and strain 3 (selected for higher velocity), whose individuals selected exhibited walking velocity above the average of the parental population (+ 1 SD). All strains were maintained isolated and reared as the stock colony, as previously described. Four generations and four cycles of selection were carried out and the behavioral traits and reproductive output (number of individuals produced per female) were assessed at each one.

Behavioral bioassays

Three personality dimensions of the five proposed by Réale et al. (2007) were assessed in the behavioral bioassays; they were: activity, bold/shy, and exploration/avoidance. The behavioral bioassays were performed as described elsewhere (Carvalho et al. 2014; Malia et al. 2016; Morales et al. 2013), where activity was assessed with a walking bioassay, a free-fall (flight) bioassay, and a body-righting bioassay. Bold/shy was assessed with a death-feigning bioassay, and exploration/avoidance was assessed with intraspecific interaction bioassays. All the bioassays were performed with 30 couples/per strain and are briefly described below.

Activity dimension - walking bioassay: Walking activity was recorded for 10 min in Petri dish arenas (9 cm diameter) whose inner walls were coated with Teflon PTFE (DuPont, Wilmington, DE, USA) to prevent insect escape, as described elsewhere (Braga et al. 2011; Malia et al. 2016; Morales et al. 2013). Briefly, a single insect was released in the center of the arena, and its movement was recorded and digitally transferred to a computer using an automated video tracking system equipped with a charge coupled device (CCD) camera (ViewPoint Life Sciences, Montreal, Canada). The following characteristics (or traits) were recorded: distance walked (cm), walking velocity (cm/s), number of stop (no.), and resting time (s).

Activity dimension - free-fall (flight) bioassay: A wooden framed tower (88 cm high) covered with organza was used, and from the top, an individual adult was released from a central hole. The landing distance from the center bottom surface after the start of wing fluttering was recorded based in a scale (i.e., 0, 3, 6 and 9 score) of concentric circles 3 cm apart from one another, following Carvalho et al. (2014). The bioassay was replicated three times for each individual insect, and the mean score was used as the measure of flying activity.

Activity dimension - body-righting bioassay: Each individual was placed on the dorsum in an arena and prodded with a fine hairbrush, and the time for the beetle to recover the normal ventral posture was recorded. The procedure was replicated three times for each individual weevil, and the mean score was used as the measure of body-righting activity (Malia et al. 2016; Morales et al. 2013).

Bold/shy dimension - death-feigning bioassay: Death-feigning (or thanatosis) was induced by prodding the adult dorsum with a fine hairbrush, and the time to start moving again was recorded. The procedure was replicated three times for each adult insect, and the mean score was used as the duration of the death-feigning (Malia et al. 2016; Morales et al. 2013).

Exploration/avoidance dimension - intraspecific interaction bioassay: A Petri dish arena (18 cm diameter) was used to assess the exploration/avoidance behaviors. The inner walls of the arena were coated with Teflon to prevent insect escape. A maize kernel infested with a conspecific adult was placed in the center of the arena. The other individual under investigation was placed at the edge of the arena, and the weevil movement was recorded for 15 min to determine the time required for interaction (or not) with infested kernel (Malia et al. 2016; Morales et al. 2013).

Reproductive output

The reproductive output of the different strains was assessed at each one of four generations. Thirty pairs of weevils were used from each strain and generation, which were removed 28 days later. The removal of the parental pairs allowed the unbiased recording of the offspring in each generation. The number of individuals produced per female (i.e., fertility) was assessed until no more progeny emerged some 100 days after the start of the experiment, like as previous described for this species (Carvalho et al. 2014; Fragoso et al. 2005).

Statistical analysis

The assumptions of normality and homoscedasticity were checked using Shapiro-Wilk and Bartlett tests, respectively. The relationship among walking velocity through generations for each strain (i.e., heritability) was tested by linear regression analysis with walking velocity as the response variable (y-axis) and the number of generations as the explicative variable (x-axis). Behavioral consistency was assessed using Spearman's correlation to check the association between results of test and retest of the same individuals for each behavioral trait recorded. Multivariate analysis of variance was used to recognize strain differences at the end of the four cycles of selection, which was eventually complemented with univariate analyses of variance and contrasts, when required ($P < 0.05$). The strain divergence in behavioral traits with selection was tested using canonical variate analysis (CVA), with the strains as the independent variable and the behavioral traits as the dependent (response) variables. The behavioral divergence among individuals was subjected to principal R-factor analysis with orthogonal rotation (Varimax) to reduce the potential bias towards the first factor. The sampling adequacy was estimated using Kaiser's measure, which should exceed 0.50 when the generated correlation matrix is suitable. In addition, (partial) canonical correlation analyses were used to test the association between walking velocity and the other behavioral traits, and also between behavioral traits (including walking velocity) and the reproductive output. The fertility among strains was contrasted by paired t-test ($P > 0.05$). All analyze were performed using the R-software version. 3.1.3, with the packages stats, psych and CCA (R Development Core Team 2016).

Results

Selection results

The heritability and consequent gain in the selection for walking velocity was confirmed in the weevil strains, as the relationship between generations of selections was significant (Fig 1). The unselected (Fig 1a - white points) and the high-velocity strain (Fig 1b) exhibited a significant increase in the walking velocity with selection, albeit with a higher slope in the latter (Figs. 1a and 1b). In contrast, the low-velocity strain exhibited a significant decrease on walking velocity across generations (Fig. 1b).

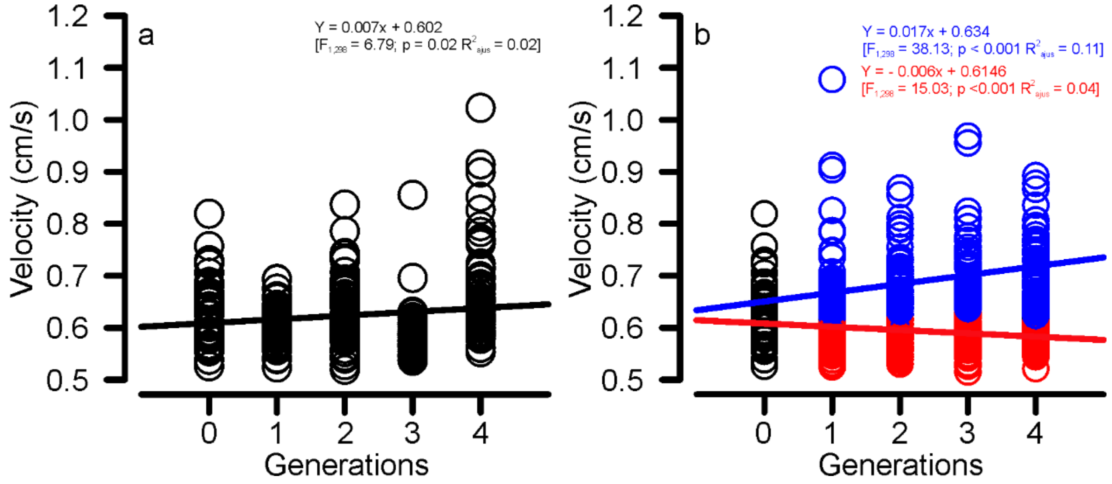

Figure 1. Walking velocity (cm/s) of strains of *Sitophilus zeamais* unselected (a) and selected for higher walking velocity (blue circles) and low walking velocity (red circles) (b).

Personality and behavioral types

Behavioral consistency was observed with test and retest of the behavioral traits in the same individuals (n = 900, r > 0.33, $P < 0.05$), confirming the existing behavioral consistence in maize weevils. The multivariate analysis of variance used to recognize whether there is significant difference in the (overall) behavioral types among strains indicates that this is the case after four cycles of selection (Wilks′ lambda = 0.49, $F_{24/2230} = 25.53$, $P < 0.001$). This results is consistent with the results from analyses of variance (univariate) performed for each behavioral trait, which indicated significant differences among strains for all of the three dimensions tested, namely activity (i.e., walked distance, resting time and number of stops), bold/shy (i.e., duration death-feigning) and exploration/avoidance dimensions (i.e., latency to conspecific interaction), which allowed us to recognize the different behavioral patterns of each strain (Table 1). Furthermore, both strain and individual behavioral divergence were also recorded using canonical variate analysis (CVA) and R-factor analysis, respectively.

Table 1. Behavioral traits (±SE) of the maize weevil *Sitophilus zeamais* from three strains: unselected, selected for low velocity and selected for higher velocity after end of the four cycles of selection

Population/ Strain	**Personality dimensions**							
	Activity						**Bold/shy**	**Exploration/ avoidance**
	Free fall (flight) (cm)	Body-righting (s)	Distance walked (cm)	Resting time (s)	Velocity (cm/s)	Stops (no.)	Death-feigning (s)	Conspecific interaction (min)
Parental	3.65±0.25	3.52±0.29	234.39±7.16b	208.66±8.98b	0.63±0.008b	870.15±18.42c	7.07±0.45c	8.40±0.47a
Unselected	4.02±0.12	3.93±0.09	241.27±3.65b	199.47±4.14b	0.62±0.004b	934.05±11.37b	10.28±0.12b	7.24±0.29b
Low velocity	3.71±0.12	3.85±0.13	217.73±2.59c	221.80±3.86a	0.58±0.002c	1005.33±8.02a	10.94±0.18a	6.45±0.28b
High velocity	3.76±0.11	3.89±0.09	288.89±4.62a	151.70±3.82c	0.69±0.004a	747.42±11.33d	10.94±0.20a	7.13±0.25b
$F_{3,776}$	1.54	0.94	65.09	55.20	150.34	112.39	36.46	3.81
P	0.202	0.418	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.01

The CVA ordination generated two significant axes (*P* > 0.01), with the 1st axis explaining 80% of the variance, where the walking velocity and number of stops were responsible for the greater canonical loads and, therefore, contributed the most for strain divergence. The death-feigning also provided high loadings but for the 2nd axis (Table 2). The CVA ordination diagram depicts the significant divergence among all three strains with significant distance (D^2) between them (Fig. 2a).

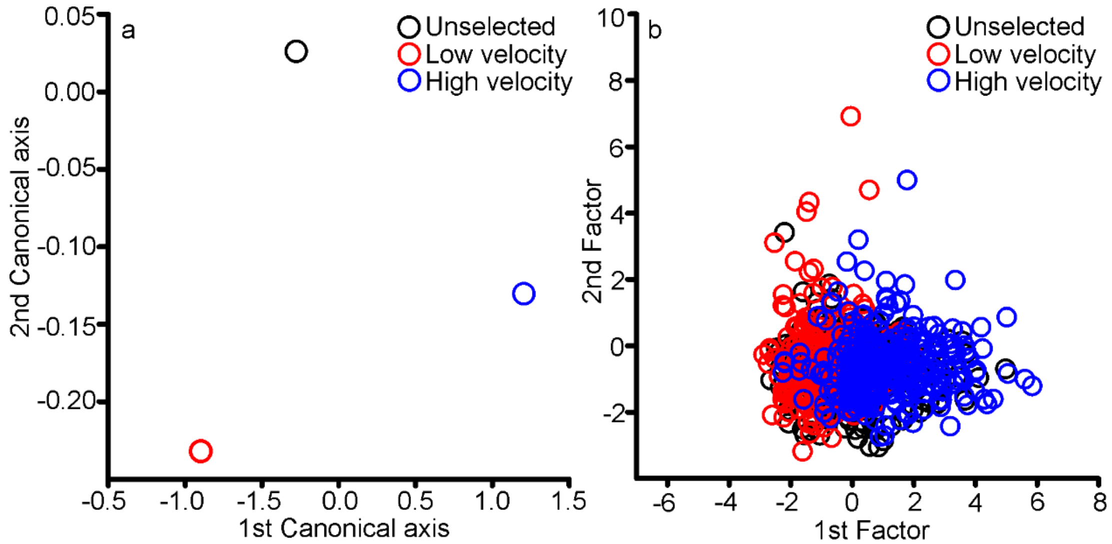

Figure 2. CVA (a) and principal R-factor (b) ordination diagrams showing the behavioral divergence among strains and individuals of the maize weevil (*Sitophilus zeamais*) (see Table 2). The symbols in (a) are mean canonical variates from each strain, and differ by the approximated F test ($P < 0.05$), based on the Mahalanobis (D^2) distance between class means in the CVA ordination. The symbols in (b) represent individuals from each strain in the R-factor ordination.

The inter-individual divergence in personality tested using R-factor analysis, provided results consistent with the population-based CVA analysis. The R-factor analysis was suitable based on the Kaiser measure, which was 0.62 and therefore exceeded the threshold value of 0.50. The analysis procedure generated three factors explaining 100% of the variation, with the 1st and 2nd factor explaining 77% of the variation. The activity dimension, in particular walking activity (i.e., distance walked, resting time, velocity and number of stop) were the main contributors of the 1st axis, whereas the body-righting and the free-fall (flight) were the main contributors of the 2nd and 3rd axes, respectively (Table 2).

Table 2. Factor loadings from CVA and principal R-factor analysis of the main axes of the behavioral traits of the maize weevil *Sitophilus zeamais* after end of the four cycles of selection

Personality dimensions	Behavior traits	Canonical axes			Principal main factors		
		1	**2**	**3**	**1**	**2**	**3**
Activity	Free fall (flight) (cm)	0.01	0.08	-0.35	0.05	0.08	**0.83**
	Body-righting (s)	0.004	0.08	-0.35	0.03	**0.86**	0.12
	Distance walked (cm)	0.21	-0.02	-0.07	**-0.83**	-0.01	-0.03
	Resting time (s)	-0.10	0.12	0.26	**0.82**	0.01	0.06
	Velocity (cm/s)	**0.53**	-0.07	-0.21	**-0.86**	0.02	0.10
	Stops (no.)	**-0.44**	-0.22	-0.51	**0.73**	-0.02	-0.12
Bold/shy	Death-feigning (s)	0.05	**-0.96**	0.10	-0.06	0.66	-0.39
Exploration/ Avoidance	Conspecific interaction	-0.02	0.22	-0.32	-0.11	-0.13	0.48
Eigenvalue		0.72	0.16	0.01	2.65	1.30	1.00
Proportion of variance explained		0.80	0.18	0.02	0.53	0.24	0.22
Sampling adequacy (Kaiser)		-	-	-	0.62		
F_{appr}		25.53	9.15	1.44	-	-	-
P		>0.01	>0.01	0.19	-	-	-

Bold numbers indicate the primary contributors of each axis.

The ordination diagram obtained with the R-factor analysis indicated a similar pattern to that observed for strain divergence using CVA, although with greater overlap among individuals from the unselected and each of the selected strains. This pattern allows the recognition of the distinct behavioral types between individuals from the low-velocity and the high-velocity, but not from the unselected since it overlaps with the two selected strains (Fig. 1b). In summary, the activity dimension (i.e., distance walked, resting time, walking velocity and number of stop) exhibits greater contribution for the divergence among strains and individuals, as expected. Other dimensions like bold/shy and exploration/avoidance seem to provide little contribution for divergence at both strain and individual levels.

Behavioral syndrome and reproductive output

Walking velocity exhibited significant (partial) canonical correlation with the other recorded behavioral traits across individual weevils from all strains (r = 0.79; $F_{7, 772}$ = 183.56; P < 0.001). The behaviors from the activity dimension were particularly important for such correlation exhibiting robust and significant correlation coefficients with walking velocity (Table 3). No significant correlation was detected between walking velocity and the other behavioral dimensions (i.e., bold/shy and exploration/avoidance) indicating lack of radiation in the behavior syndrome (Table3).

Table 3 – Partial canonical correlations (r) and canonical loadings (ca) between velocity or reproduction and behavioral traits of individual maize weevils from all three strains.

Personality dimensions	Behavioral traits	Velocity		Reproduction	
		r	ca	r	ca
Activity	Free fall (flight) (cm)	0.002	-0.004	-0.060	0.291
	Body-righting (s)	0.011	0.026	-0.053	0.024
	Distance walked (cm)	**0.609**	**0.603**	0.086	-0.074
	Resting time (s)	**-0.501**	0.089	-0.074	-0.112
	Velocity (cm/s)	-	-	**0.175**	-0.174
	Stops (no.)	**-0.675**	**-0.686**	**-0.213**	**0.575**
Bold/shy	Death-feigning (s)	0.006	-0.015	**-0.208**	**0.683**
Exploration/Avoidance	Conspecific interaction	0.098	-0.043	0.057	-0.081
Statistic	R	0.79		0.32	
	F	183.56		10.75	
	$df_{num/den}$	7/772		8/771	
	P	< 0.001		< 0.001	

Bold indicates main contributors of each axis (P < 0.05)

Likewise, when the association between the behavioral traits and the reproductive output were tested using (partial) canonical correlation, a significant correlation was obtained (r = 0.32; $F_{8, 771}$ = 10.75; P < 0.001) (Table 3). Again the activity dimension, including number of stop (r = - 0.213, added by death-feigning (r = - 0.208)) and walking velocity (r = 0.175), provided the highest contributions. (Table

3). Indeed, the selection procedure led to an increase in the number of insects produced by females when the strain selected for high walking velocity (18.94 ± 0.53 insects/female) is compared with the strain selected for low walking velocity (16.93 ± 0.66 insects/female) ($t = 2.36$, $P < 0.001$) and the unselected strain (12.95 ± 0.51 insects/female) ($t = 8.11$, $P < 0.001$).

Discussion

The bidirectional selection procedure revealed that the behavioral trait selected walking velocity was inherited (Fig. 1). This is so because there was gain by selection across generations for each strain (low and high velocity). These results were expected because previous population-based studies with maize weevils indicated that some populations are noticeably more active than others (Braga et al. 2011; Guedes et al. 2009). Furthermore, walking velocity was also reported as a diverging trait among individual weevils and populations, and exhibits adaptive value (Malia et al. 2016; Morales et al. 2013).

In animal personality studies, the personality traits are categorized in up to five dimensions (i.e., activity, bold/shy and exploration/avoidance, sociability and aggressiveness), as previously proposed by Réale et al. (2007). Three of these dimensions (i.e., activity, bold/shy and exploration/avoidance) are measurable to *S. zeamais* and have implication for weevil management (Carvalho et al. 2014; Malia et al. 2016; Morales et al. 2013). Consistency in response is an important characteristic in the recognition of animal personality (Bell et al. 2009; Uher 2011), reason for their testing in the maize weevil (Carvalho et al. 2014; Malia et al. 2016; Morales et al. 2013). Significant correlations ($r > 0.33$; $P < 0.005$) were observed in our study consistent with previous determinations with the same species (Carvalho et al. 2014; Malia et al. 2016; Morales et al. 2013), indicating that these traits are stable with moderate reliability ($r > 0.30$ and < 0.50). However, the range of correlation coefficients observed is within the range expected for animal behavior (Bell et al. 2009; Uher 2011), including weevils (Malia et al. 2016; Morales et al. 2013).

The bidirectional selection had impact on (overall) behavioral types, after four cycles of selection. Likewise, the behavioral traits exhibited by individuals from each strain indicated differences among strains for all of the three dimensions tested, which allowed us to recognize the different behavioral patterns of each strain (Table 1), as expected by earlier studies with the species (Braga et al. 2011; Guedes et al. 2009; Morales et al. 2013). Based on these behavioral patterns individual and strain divergence were recognized and relatively consistent, although the population types were greatly simplified not detecting the greater individual diversity in the unselected strain. This is also expected since selection is likely to reduce individual diversity, particularly when associated activity traits played crucial whole for the detected divergence.

The inter-relation between walking velocity and the other behavior traits was perceived across individual weevils from all strains, which confirms the existence of behavioral syndrome in the maize weevil. The behavioral syndrome was predominantly within the activity dimension (i.e., distance walked, resting time and number of stop) and not radiated to other dimensions (i.e., bold/shy and exploration/avoidance). This result was expected since these activity variables are inter-dependent and thus directly related with walking velocity. Walking velocity (low and high velocity) is a behavioral trait with curious practical consequences because less active weevils minimized their exposure to agents control, while the most active weevils are able to quickly escape treated surfaces also minimizing exposure, which enhances survival of maize weevils in both cases (Malia et al. 2016; Morales et al.

2013). Thus, the activity dimension in maize weevils seem to have implications for this species management deserving attention when designing pest management programs.

This activity-based behavioral syndrome exhibited significant correlation with reproductive fitness among individual maize weevils. This result is interesting because selection for one trait within the syndrome spectrum will impact individual fitness favoring reproductive output of a pest species. Furthermore, the activity dimension and particularly walking of maize weevils impacted their exposure and survival to control agents (i.e. insecticides, inert dust) (Malia et al. 2016; Morales et al. 2013). Other weakly correlated traits may also indirectly affect the maize weevil fitness, which is consistent with the concept of behavioral syndrome (Bergmüller 2010; Jandt et al. 2014; Monceau et al. 2015; Sih et al. 2004; Sih et al. 2012; Smith and Blumstein 2007). In our case, we detected some weak irradiation to the bold/shy dimension (i.e., via death-feigning), which suggests a potential contribution of this dimension with the reproductive output of maize weevils, in addition to the activity dimension. Interestingly, studies have reported negative phenotypic correlations between death feigning and activity, and suggest trade-offs between survivorship and mating success (Nakayama and Miyatake 2010), which are in accordance to our findings, although this deserves future attention in the maize weevil.

In summary, we verified that walking velocity is inherited and maintained across generations of the maize weevil with impact on their behavioral types. This allowed the recognition of divergent behavioral types among maize weevil strains and existing behavioral syndrome centered on the activity dimension. Finally, we verified the impact of this dimension on the reproductive output of the maize, which also favors survival against chemical and physical control agents emphasizing the relevance of this personality trait for managing purposes.

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