



# Unraveling behavioral and pace-of-life syndromes in a reduced parasite and predation pressure context: personality and survival of the Barbary ground squirrel

Julien C. Piquet<sup>1</sup> · Marta López-Darias<sup>1</sup> · Annemarie van der Marel<sup>2</sup> · Manuel Nogales<sup>1</sup> · Jane Waterman<sup>2</sup>

Received: 1 March 2018 / Revised: 7 July 2018 / Accepted: 18 July 2018  
© Springer-Verlag GmbH Germany, part of Springer Nature 2018

## Abstract

Personality traits overlap in behavioral syndromes that are assumed to be related to physiology and life history traits, shaping pace-of-life syndromes. Boldness and explorative behavior are frequently associated with higher parasite loads, increased resource acquisition, less efficient antipredator behavior, and reduced survival (e.g., through predation). We explored how personality is related to these biological traits using an invasive species—*Atlantoxerus getulus* in Fuerteventura island—as a model system with reduced parasitism and low predation pressure. We used breath rate during handling, open field tests, and escape trials to test for the existence of interindividual differences in boldness, explorative behavior, and escape speed, respectively. We also tested whether the personality traits were related and formed behavioral syndromes in *A. getulus*. At the same time, we explored how personality is related to ectoparasite load, body condition, and survival in the species. We found strong between-individual differences in breath rate, readiness to get in the open field arena, and escape speed. We found a behavioral syndrome, linking open field entrance and escape speed, in *A. getulus*. However, personality was not related to parasite load or body condition and survival was higher for bolder individuals. As a whole, our results suggest reduced parasites and predator pressures on Fuerteventura may have potentially neutralized the typical drawbacks of a fast pace-of-life in the introduced population of *A. getulus*.

## Significance statement

Research on the interactions of animal personality with other ecological and evolutionary factors, such as parasitism and selection gradients, has yielded some intriguing perspectives about many ecological and evolutionary processes. However, our understanding of the eco-evolutionary consequences of animal personality and how it interacts with other relevant biological processes is still limited. Invasive species often experience specific ecological conditions that can allow testing of the general assumptions related to animal personality. The present contribution explores if and how personality traits are related to key ecological and evolutionary factors, such as parasitism and survival, in the context of an invasive population subjected to reduced parasite and predation pressure. Unlike other studies conducted under different ecological contexts, our results suggest Barbary ground squirrels from the assessed population with fast pace-of-life syndromes have higher survival chances than their counterparts.

---

Communicated by A. I. Schulte-Hostedde

---

**Electronic supplementary material** The online version of this article (<https://doi.org/10.1007/s00265-018-2549-8>) contains supplementary material, which is available to authorized users.

---

✉ Julien C. Piquet  
jchрпи@gmail.com

<sup>1</sup> Island Ecology and Evolution Research Group, Instituto de Productos Naturales y Agrobiología (IPNA-CSIC), Astrofísico Francisco Sánchez no. 3, 38206 La Laguna, Tenerife, Canary Islands, Spain

<sup>2</sup> Department of Biological Sciences, University of Manitoba, Winnipeg, MB R3T 2N2, Canada

**Keywords** Animal personality · *Atlantoxerus getulus* · Behavioral syndrome · Fitness · Invasive species · Parasite load

## Introduction

The existence of behavioral differences among individuals within species and populations, consistent over time and across contexts, has led to the concept of animal personality or animal temperament (Réale et al. 2007). Personality traits are correlated in behavioral syndromes (Sih et al. 2004a; Sih and Bell 2008), which are in return integrated in complex pace-of-life syndromes, linking animal personality to life-history productivity and physiology (Réale et al. 2010). For instance, personality has been linked to immune function and parasitism (Barber and Dingemanse 2010; Kortet et al. 2010; Ezenwa et al. 2016; Monceau et al. 2017), along with metabolic rate and feeding behavior (Stamps 2007; Careau et al. 2008; Le Coeur et al. 2015). Evidence from small mammals suggest individuals with a faster pace-of-life, i.e., more explorative, aggressive, and bolder individuals (defined in Réale et al. 2007), are more parasitized (Boyer et al. 2010; Zohdy et al. 2017), potentially leading to severe energetic and fitness costs (Khokhlova et al. 2002; Lemaître et al. 2009; Hillegass et al. 2010; Patterson et al. 2013). However, explorative behavior, along with boldness, can also improve individual resource acquisition capacity (Dingemanse et al. 2004; van Oers et al. 2004; Biro and Stamps 2008; Le Coeur et al. 2015), enhancing body condition and fitness in explorative and bold individuals (Le Coeur et al. 2015). In return, the increment in feeding rate incurs higher predation risk, so that fast pace-of-life personality types are associated with reduced antipredator behavior efficiency (Carter et al. 2010; Jones and Godin 2010; Rodríguez-Prieto et al. 2011). Personality variation is thus assumed to be connected to the trade-off between feeding and the strategies used to reduce predation risk (i.e., antipredator strategies; Houston et al. 1993; Macleod et al. 2005), although few empirical studies have directly assessed such relationships (Quinn and Cresswell 2005; Boon et al. 2008; Rodríguez-Prieto et al. 2011).

Pace-of-life syndrome hypothesis suggests the relationship between behavioral traits, physiology, and life history is due to correlational selection (Réale et al. 2010). In this context, personality traits incur different fitness costs and benefits for individuals (Smith and Blumstein 2007; Stamps 2007; Wolf et al. 2007; Biro and Stamps 2008; Boon et al. 2008; Réale et al. 2010; Kight et al. 2013). However, fitness penalizations (e.g., reduced survival) for personality traits are heavily context dependent (Sih et al. 2012; Le Coeur et al. 2015), and differing patterns of selection are frequently detected in personality research (Dingemanse et al. 2004; Boon et al. 2008; Bergeron et

al. 2013; Rödel et al. 2014). Despite such an entangled relationship, an increasing number of studies have supported the idea that personality and life history are intertwined, and these studies have attracted the attention of other research fields, such as invasive species biology. For instance, in early stages of the invasion process, bolder and explorative individuals are hypothesized to perform better than shy and less explorative ones (Chapple et al. 2012). Yet, despite the interesting and specific ecological conditions associated with biological invasions (e.g., changing environmental conditions, variable ecological constraints, and natural enemy release; Torchin et al. 2003; Blackburn et al. 2011), few empirical studies have attempted to directly evaluate how personality traits are related to fitness in invasive species (Chapple et al. 2012). Research has mainly focused on the relationship between personality and dispersal (Cote et al. 2010; Phillips and Suarez 2012; Thorlacius et al. 2015; Malange et al. 2016; Mutascio et al. 2017), although information on how personality is related to other biological traits is almost absent for established invasions (but see Blight et al. 2017).

The present paper is focused on the Barbary ground squirrel (*Atlantoxerus getulus*), a native rodent from Morocco and Algeria that was deliberately introduced in Fuerteventura in 1965, when two individuals (male and female) were released into the island (Machado 1979; Machado and Domínguez 1982). The species is now present and abundant all throughout the island (population density attains 296 squirrels/ha) (López-Darías 2007). Previous research on *A. getulus* found that individuals from Fuerteventura are less parasitized and have fewer predators than individuals in the native range (López-Darías 2007). Such ecological release offers an interesting scenario to study the relationship of personality with other key ecological and evolutionary mechanisms such as parasitism or selection gradients.

Our objective was to test for the existence of personality traits and a behavioral syndrome in *A. getulus* and their relationship to ectoparasite load, body condition, and survival. Our main hypothesis is that the species shows both personality traits and a behavioral syndrome that links boldness, explorative, and antipredator behavior (i.e., escape speed). Explorative and bold individuals are expected to have reduced escape speed, higher parasite loads, and better body condition, compared to less explorative and shy individuals. Finally, the occurrence of fast pace-of-life traits may not reduce a squirrel's survival chances due to their reduced parasitism and predation pressure.

## Material and methods

### Study area

The island of Fuerteventura, situated approximately 100 km from the African continent, belongs to the Canary Islands, a group of volcanic islands located between 27 and 29° N off the Atlantic coast of NW Africa. Fuerteventura has a warm desert climate (Marzol-Jaén 1988), which is characterized by high temperatures (~20 °C), low rainfall (53.5–253.5 mm per year), high insolation, and intense, as well as frequent, trade winds (Marzol-Jaén 1988). Such climatic conditions have shaped the semidesert habitats that occupy most of the island (del Arco et al. 2010). The study area was located near the protected area of “Montaña de Tindaya” (28° 35′ 56, 18″ N–13° 59′ 43, 37″ W), in the northern municipality of La Oliva, where previous behavioral studies were conducted for three consecutive years (2013–2015). Three sampling sites were selected in the area where squirrels were locally abundant (site 1, 28° 35′ 58, 10″ N–13° 59′ 49, 15″ W; site 2, 28° 35′ 36, 81″ N–13° 59′ 48, 71″ W; site 3, 28° 35′ 38, 51″ N–14° 00′ 01, 41″ W). All of the sites were covered by stony plains and xerophytic scrubland (mainly composed by *Launaea arborescens*, *Lycium intricatum*, and *Salsola vermiculata*) interspersed with areas that were formerly cultivated. For this study, all data were collected between September 2015 and November 2015, during the nonreproductive period of *A. getulus*.

### Trapping method, ectoparasite quantification, and body condition

We trapped *A. getulus* individuals in live traps (Tomahawk Live Trap Co., Tomahawk, Wisconsin, 40.64 × 12.7 × 12.7 cm), baited with peanut butter. We trapped each site twice every 6 days, from 9:00 to 18:00 (period of squirrel activity). We only used individuals older than 1 year in this study (age of each individual was known as animals at the sites had been trapped and marked from 2014 onward). To minimize confinement stress, we checked traps every 40–60 min. Furthermore, we placed traps in shaded areas, and covered them with cardboard sections to provide extra shade. Every time an individual was caught in a trap, we transferred it to a handling bag (Koprowski 2002), where it was identified by reading already implanted passive integrated transponders tags (PIT tags, AVID, USA). After other parameters were noted down (see below), we quantified ectoparasites by counting the number of *Neohaematopinus pectinifer* lice (see Machado and Domínguez 1982) in a 2-cm diameter circle on the abdomen, the base of the tail, and the central dorsal region of each squirrel. As all squirrels in this study had lice, we did not include prevalence (proportion of animals with infections) in the analysis. We recorded lice intensity (number of lice per infected animal; Bush et al. 1997; Rózsa

et al. 2000) for the entire sample population. We discarded other ectoparasites known for *A. getulus* (Machado and Domínguez 1982) because of their very low rates of infection. Afterwards, we measured mass (g) using a spring scale ( $\pm 5$  g; Pesola AG, Baar, Switzerland), and hind-foot length (mm) using a digital caliper (Mitutoyo Corp., Japan) to calculate an individual's body condition through a scaled mass index (hereafter body condition), according to Peig and Green (2009).

### Behavioral tests: “shyness-boldness”, “exploration-avoidance”, and “escape speed”

We evaluated the squirrel's behavioral phenotype using three different trials: breath rate, open field test, and escape trial; corresponding to shyness-boldness, exploration-avoidance, and escape speed behavioral categories, respectively. As personality is expected to be consistent and repeatable (Dingemanse and Dochtermann 2013), we repeatedly assessed individuals for each behavioral trait to calculate repeatability (open field tests and escape trials were repeated up to a maximum of three and four times, respectively). To minimize habituation to the open field test or the escape trial (Stamps and Groothuis 2010), we never exposed a single individual to the same experiment within 3 days of the former trial. Since our study involved focal animals in the field, it was not possible to record data blind. We performed all behavioral tests in each site at the same location to minimize variation in conditions among trials.

We measured breath rate (number of breast moves during 10 s) 1 min after transferring squirrels from traps to a handling bag and just before the assessment of any other trait, to avoid bias due to handling. Certain discrepancy exists in the literature regarding the use of this trait; while a large proportion of studies on animal personality refers to breath rate as a proxy of behavior (Boon et al. 2007; Brommer and Kluen 2012; Kluen et al. 2014; Hall et al. 2015; Class and Brommer 2016; Corti et al. 2017; Haigh et al. 2017b), other authors have considered breath rate as a physiological trait-reflecting stress response (David et al. 2012; Ferrari et al. 2013; Krams et al. 2014; Dubuc-Messier et al. 2017; Šimková et al. 2017). In this study, we used breath rate as an indicator of individual behavioral reaction towards handling stress (i.e., boldness as defined in Réale et al. 2007), following previous research on mammals suggesting handling stress response, and particularly breath rate (Boon et al. 2007; Haigh et al. 2017b), is tightly linked to individuals' personality (see Montiglio et al. 2012). Once breath rate, ectoparasite load, and morphology were obtained for each individual, we started the open field test to measure a squirrel's exploration-avoidance (e.g., Réale et al. 2007; Bijleveld et al. 2014). We performed this test by using a 73 × 53 × 30 cm plastic box (open field arena) with one entrance (10 × 15 cm), covered on top with metallic mesh. To do

so, we connected the handling bag to the arena for a 5-min habituation period, with the entrance blocked to prevent the squirrel entering the arena. Once the habituation period elapsed, we opened the entrance to the arena and filmed the squirrel's behavior for 10 min using a video camera (Canon Inc., ON, Canada, Model VIXIA HFM41) mounted on a tripod above the arena. Recent empirical evidence suggests reluctance to enter a novel space is related to the shyness-boldness axis, rather than exploration-avoidance (Perals et al. 2017). Thus, we first examined the individual's readiness to enter in the open field arena as follows: (1) we assessed in each trial whether the individual entered the open field arena or not (thereafter called open field entrance), (2) we calculated for each squirrel the percentage of open field trials in which it entered the open field (hereafter percentage entrances). Additionally, we recorded the time spent in the open field arena (thereafter exploration time) and used it as a measure of exploration-avoidance. We calculated exploration time using solely trials in which the squirrels entered the open field. To avoid any confounding effects on squirrel behavior, we removed the scent from any previous squirrel in the open field arena with a solution of water and vinegar (1:1) (Phillips and Waterman 2014).

Finally, we used escape trials to assess escape speed, which is commonly referred to as a performance trait (Blumstein et al. 2010, 2015). However for the purpose of the present study, we did not stimulate squirrels to attain their maximum running speed, so that escape speed reflected individual's reaction to predation risk (i.e., antipredator behavior) instead of a performance trait. To avoid obstacles interfering with a squirrel's flight, we performed escape trials in open plain areas with similar substrate and scarce or no vegetation. To standardize the starting point of the flight, we started escape trials immediately after the open field trial, when animals were released from the open field arena. Because rock walls are intensively used by the species as shelters (López-Darias and Lobo 2008), the finish line of the escape trial was a rock wall located 10 m away. To start the test, we encouraged squirrels to exit the arena by passing a hand over the mesh on the top of the open field arena from the back to the exit. To ensure animals fled the arena, we chased individuals at a consistent speed (~ 2 m/s) for 3 m. We performed all trials so that the flight was orientated towards the home range of the squirrel and filmed with a video camera (Canon Inc., ON, Canada, Model VIXIA HFM41) mounted on a tripod. We quantified escape speed by analyzing the videotapes with Solomon Coder (Solomon Coder, version 15.03.15, András Péter, <http://solomoncoder.com>). For each trial, we calculated escape speed (m/s) as the time from the beginning of the flight to the moment when the squirrel reached the rock wall or stopped the flight. The observer signaled the end of each escape trial on the camera, and the delay between escape ending (e.g., squirrel paused or entered

rock wall) and observer's reaction was calculated if the escape stopped within camera range. For those escapes that finished out of the camera range, we subtracted the delay in the observer's reaction from the calculated time of flight. A single observer (JCP) performed all escape trials to standardize measurements. We corrected the distances of escape with a measuring tape for any of the following situations: (1) if a squirrel paused before reaching the rock wall, (2) if a squirrel deviated greatly from a straight trajectory, and (3) if a flight continued through the open field and not towards the wall (the observer signaled trial end on the camera). As some squirrels were not always able to find suitable holes while fleeing, we considered any approach within 0.5 m of the rock wall as reaching it.

## Survival

In November 2016, 12 months after we performed the last behavioral trial, we trapped the study sites to determine the survival of individuals. As the same population had been thoroughly studied for several consecutive years, we knew that the dispersal of individuals above 1 year of age was extremely rare (especially females). Thus, for the purpose of our survival calculation, we considered all those individuals above 1 year of age, who were not trapped in 2016, were dead. For the survival analysis, we did not include adult individuals that were first captured during 2015 fieldwork, as they could potentially be visiting from neighboring populations. We calculated the average lifespan for the studied population for 32 adult and subadult individuals (squirrels over 6 months old, that did not become reproductive during their first breeding season) of known age. Furthermore, we classified squirrels used in personality trials into three age classes, according to the year of birth (AvdM et al. unpublished data): 1 (born in 2014), 2 (born in 2013), and 3 (born before 2013).

## Statistical analyses

We performed all statistical tests with R 3.4.1 (R Core Team 2017). Results are presented as means  $\pm$  SD.

### Behavioral tests: "shyness-boldness", "exploration-avoidance", and "escape speed"

We calculated adjusted repeatability (Nakagawa and Schielzeth 2010; Dingemanse and Dochtermann 2013) of behavioral traits following Nakagawa and Schielzeth (2010); we employed linear mixed models (LMMs) to obtain breath rate and escape speed adjusted repeatability, and general linear mixed models (GLMMs) with logit-link function for open field entrance. Both LMMs and GLMMs for repeatability calculation included sex and test repetition as fixed factors, and time of day (in decimal format) and squirrels identity



(henceforth ID) as covariate and random factor, respectively. Adjusted repeatability was not calculated for exploration time because of the small number of individuals repeatedly entering in the open field arena. We extracted significant fixed factors and covariates for further analyses. We square-root-transformed breath rate and escape speed in order to meet normality assumptions and increase model fitting. We performed LMMs and GLMMs using the *lme4* package (Bates et al. 2015), and repeatability calculation with *rptR* package (Stoffel et al. 2017).

### Behavioral syndrome and pace-of-life syndrome

We tested the existence of a behavioral syndrome (i.e., between-individual covariance for personality traits) and a pace-of-life syndrome in a multivariate generalized mixed model using Monte Carlo Markov Chain (MCMC-GLMM) with breath rate, open field entrance, escape speed, lice intensity, and body condition, as dependent variables. As individual consistency for exploration time was not verified, we did not include it in the behavioral syndrome analysis. To set lice intensity, body condition, breath rate, and escape speed on a similar scale and meet normality assumptions, we square root-ed, mean centered, and standardized to units of one standard deviation all these dependent variables. Variable distribution for lice intensity, body condition, breath rate, and escape speed was set as Gaussian, whereas open field entrance was included as a categorical variable (Hadfield 2010). We included random intercepts for ID and all significant factors and covariates extracted from the univariate LMMs for personality traits as fixed factors. We estimated the within-individual covariance by setting an unstructured R-matrix in the model (Dingemanse and Dochterman 2013). We used an inverse-gamma prior distribution in the model specification after we tested the model prior robustness (see Text S1 for prior specifications), and generated a sample size of 2500 iterations by sampling 1 from every 2000 iterations after the first 50,000 iterations. We ran the MCMC-GLMM three times to assess chain convergence of posterior distribution through Gelman Rubin diagnostic (Gelman and Rubin 1992). We implemented MCMC-GLMM using the *MCMCglmm* package (Hadfield 2010).

### Survival

Finally, we calculated relative survival (i.e., survival probability, 0 and 1, divided by survival mean's value) in order to estimate selection gradients for ectoparasite load (lice intensity), body condition, and personality (i.e., repeatable behavioral traits) (Lande and Arnold 1983). We calculated an individual's average for personality traits, lice intensity, and body condition, and employed them, along with percentage of entrances and squirrel age, as covariates in a linear regression with relative survival as dependent variable. Sex was used as a

fixed factor. We mean centered and standardized to units of one standard deviation all independent variables except sex.

### Data availability

The datasets analyzed during the current study are available from the corresponding author on reasonable request.

## Results

### Trapping, ectoparasite load quantification, and body condition

We captured a total of 24 male and 25 female squirrels across the three study sites. *Neohaematopinus pectinifer* mean intensity per individual was  $16.64 \pm 9.68$ , whereas mean body condition was  $241.58 \pm 21.12$ .

### Behavioral tests: “shyness-boldness”, “exploration-avoidance” and “escape speed”

Breath rate, open field entrance, and escape speed were all repeatable; i.e., a great proportion of all variables' variation was related to consistent differences among individuals (LMMs and GLMMs for repeatability: breath rate,  $17.44 \pm 3.57$  breaths/10s,  $r_{adj} = 0.35$ ,  $CI = 0.17-0.56$ ,  $p < 0.001$ ; open field entrance,  $r_{adj} = 0.35$ ,  $CI = 0.02-0.97$ ,  $p = 0.007$ ; escape speed,  $3.46 \pm 0.84$  m/s,  $r_{adj} = 0.51$ ,  $CI = 0.32-0.69$ ,  $p < 0.001$ ) (See Table 1 for numbers of individuals assessed for each behavioral trait). Breath rate was influenced by sex (females had a higher breath rate than males; Table 2) whereas both individual's open field entrance and escape speed were independent from all predictors included in the model (Table 2). A total of 31 squirrels never entered the open field arena, whereas 18 squirrels entered at least once.

**Table 1** Number of individuals of each sex of *A. getulus* used in each behavioral test ( $N_1$ ), and by trial repetition ( $N_2$ ,  $N_3$ ,  $N_4$ ,  $N_5$ )

Behavioral tests	Sex	$N_1$	$N_2$	$N_3$	$N_4$	$N_5$
Breath rate	Males	24	15	11	5	1
	Females	25	21	18	9	2
Open field tests	Males	24	16	11	—	—
	Females	25	22	18	—	—
Escape trials	Males	23	12	9	5	—
	Females	25	20	18	6	—

**Table 2** Estimates ( $\beta$ ) of predictors with 95% confidence intervals (95% CI) of fixed factors and covariates included in linear mixed models for breath rate and escape speed, and generalized mixed models for open field entrance and exploration time for *A. getulus*

Fixed factors/covariates	Breath rate		Open field entrance		Escape speed	
	$\beta$	(95% CI)	$\beta$	(95% CI)	$\beta$	(95% CI)
Intercept	3.62	(3.06, 4.18)	-2.21	(-6.97, 2.54)	1.94	(1.66, 2.22)
Sex (females)	0.27	(0.07, 0.45)	0.11	(-1.39, 1.61)	-0.07	(-0.18, 0.04)
Time of the day	0.03	(-0.01, 0.06)	0.02	(-0.29, 0.32)	< -0.01	(-0.02, 0.01)
Trial repetition (2)	0.07	(-0.07, 0.22)	-0.23	(-1.59, 1.13)	< -0.01	(-0.08, 0.07)
Trial repetition (3)	-0.05	(-0.21, 0.11)	0.76	(-0.03, 2.95)	0.05	(-0.02, 0.13)
Trial repetition (4)	< -0.01	(-0.22, 0.21)	-	-	< 0.01	(-0.11, 0.11)
Trial repetition (5)	-0.03	(-0.46, 0.39)	-	-	-	-

Significant results are indicated in *italics*

### Behavioral syndrome and pace-of-life syndrome

We found open field entrance and escape speed were negatively correlated at the between-individual level (Table 3), and breath rate was positively correlated to body condition at the within-individual level (Table 3). No between-individual covariance was found between personality traits and lice intensity or body condition (Table 3). Breath rate was higher for females than males (Table 4), whereas open field entrance,

escape speed, lice intensity, and body condition were unaffected by sex (Table 4).

### Survival

Average lifespan of the population was  $1.40 \pm 0.55$  years. After 82 fieldwork days and 524.38 h of trap effort, 12 males (57.14%) and 14 females (56.00%) were seen alive between November 2016 and March 2017. We discarded in our

**Table 3** Between-individual and within-individual covariance in *A. getulus* in lice intensity, body condition, breath rate, open field entrance, and escape speed extracted from a generalized linear mixed model with Monte Carlo Markov Chain (MCMC-GLMM). Estimated means (covariance) are shown in each case, along with 95% confidence intervals (95% CI)

Trait 1	Trait 2	Covariance	(95% CI)
Between-individual covariance			
Breath rate	Open field entrance	0.11	(-0.294, 0.587)
	Escape speed	-0.04	(-0.412, 0.361)
	Lice intensity	-0.02	(-0.418, 0.362)
	Body condition	0.11	(-0.262, 0.486)
Open field entrance	Escape speed	-0.44	(-0.808, -0.075)
	Lice intensity	0.17	(-0.215, 0.601)
	Body condition	-0.17	(-0.571, 0.276)
Escape speed	Lice intensity	-0.07	(-0.425, 0.336)
	Body condition	-0.09	(-0.438, 0.266)
Lice intensity	Body condition	-0.10	(-0.492, 0.246)
Within-individual covariance			
Breath rate	Open field entrance	0.05	(-0.429, 0.505)
	Escape speed	-0.22	(-0.445, 0.019)
	Lice intensity	0.03	(-0.175, 0.238)
	Body condition	0.24	(0.039, 0.416)
Open field entrance	Escape speed	0.03	(-0.421, 0.454)
	Lice intensity	-0.21	(-0.631, 0.233)
	Body condition	0.03	(-0.402, 0.477)
Escape speed	Lice intensity	-0.03	(-0.235, 0.182)
	Body condition	-0.15	(-0.379, 0.080)
Lice intensity	Body condition	0.08	(-0.098, 0.258)

Significant results are indicated in *italics*

**Table 4** Effects of fixed factors employed in generalized linear mixed model with Monte Carlo Markov Chain (MCMC-GLMM) on the breath rate, open field entrance, escape speed, lice intensity, and body condition of individual *A. getulus*. Posterior estimated effects ( $\beta$ ) are shown as well as 95% confidence intervals (95% CI) and estimated *p* values (*p*)

Traits	Fixed factors/covariates	$\beta$	(95% CI)	<i>p</i>
Breath rate	Intercept	− 0.29	(− 0.690, 0.058)	0.121
	Sex (females)	<i>0.56</i>	(0.069, 1.056)	<i>0.023</i>
Open field entrance	Intercept	− 2.08	(− 3.671, − 0.483)	<i>0.001</i>
	Sex (females)	− 0.30	(− 2.207, 1.698)	0.754
Escape speed	Intercept	0.12	(− 0.265, 0.542)	0.558
	Sex (females)	− 0.24	(− 0.805, 0.302)	0.393
Lice intensity	Intercept	0.15	(− 0.180, 0.515)	0.414
	Sex (females)	− 0.28	(− 0.806, 0.181)	0.238
Body condition	Intercept	0.09	(− 0.312, 0.501)	0.654
	Sex (females)	− 0.21	(− 0.732, 0.371)	0.458

Significant results are indicated in italics

analysis two additional males captured in 2015 as they potentially came from neighboring populations. We found relative survival was unaffected by breath rate, escape speed, body condition, lice intensity, sex, and age (Table 5). However, we found a significant and positive selection gradient on percentage entrances (Table 5); relative survival was higher for individuals with higher percentage of entrances.

## Discussion

### Consistency of behavioral differences among individuals

Consistency over time and across contexts is a central concept in animal personality (Sih et al. 2004a, b, 2012). We detected consistent interindividual differences in three out of the four behavioral traits measured (breath rate, escape speed, and

open field entrance), thus providing the first evidence of personality in *A. getulus*. Breath rate during handling is commonly used as a boldness proxy and thus consistent interindividual variability for this trait has already been described in many species (Boon et al. 2007; Klueen et al. 2014; Hall et al. 2015). Yet, previous studies in other species have explicitly questioned the use of breath rate as a behavioral trait reflecting individuals' boldness, suggesting its evaluation during handling may reveal individuals' physiology instead of a behavioral reaction to risk (David et al. 2012). Although we initially decided to use breath rate as a behavioral trait, we found females had higher breath rate than males. Considering breath rate is tightly coupled with metabolic rate and oxygen consumption (Mortola and Lanthier 2005; David et al. 2012; Haigh et al. 2017b), both of which have been reported to be higher for females in other rodent species (Perez et al. 1980), we suggest, in a similar way to David et al. (2012) for birds, that breath rate reflects more appropriately physiological variation among individuals in mammal species too (Ferrari et al. 2013). Consistent individual differences were also found for open field entrance, suggesting an individual's willingness to expose itself to risk was consistent over time (Perals et al. 2017). However, in contrast with previous research using open field tests on other species (Perals et al. 2017), a large proportion of individuals failed to enter the open field arena, precluding us from properly estimating exploration time repeatability. A potential explanation for this result could be capture stress, as squirrels were tested in the open field test shortly after capture. Previous research, allowed individuals to acclimatize for as much as 2 days before submitting them to behavioral trials (Perals et al. 2017). Nonetheless, in our study, all individuals were considerably habituated to trapping and handling, suggesting that a habituation period of 5 min should have been enough to prevent capture stress biasing their behavior. Furthermore, the confinement of the squirrels for an extended period was not feasible in our study without incurring considerable stress and heatstroke risk, due to high

**Table 5** Influence of body condition, lice intensity, and personality on survival of *A. getulus* extracted from a Lande-Arnold's analysis. Body condition, lice intensity, breath rate, and escape speed were all averaged per individual and included as covariate along with percentage entrances and age, whereas sex was employed as fixed factor. Predictor estimates ( $\beta$ ) are shown with standard errors (SE) and *p* values

Predictors	$\beta \pm SE$	<i>p</i>
Intercept	<i>0.97 ± 0.23</i>	<i>&lt; 0.001</i>
Breath rate	0.14 ± 0.17	0.419
Escape speed	0.17 ± 0.15	0.267
Body condition	0.06 ± 0.16	0.686
Lice intensity	− 0.04 ± 0.14	0.793
Percentage entrances	<i>0.30 ± 0.15</i>	<i>0.049</i>
Age	− 0.11 ± 0.16	0.492
Sex (females)	0.02 ± 0.35	0.944

Significant results are indicated in italics

ambient temperatures and the poor thermoregulatory abilities of the species (Machado and Domínguez 1982). Finally, escape speed repeatability indicates that squirrels' behavior across trials was consistent, which is in line with previous research in other species (Oufiero and Garland 2009; Blumstein et al. 2010; Marras et al. 2011; Cabrera et al. 2017). A large part of the variation detected in escape speed in *A. getulus* was caused by consistent interindividual differences, despite the expectation that escape would be under strong selective pressures that should decrease variability (Schulte-Hostedde and Millar 2002; Husak 2006a, b).

### Behavioral syndrome and pace-of-life syndromes

Bolder individuals are assumed to have less efficient antipredator strategies and, thus, suffer from higher predation risk (Biro and Stamps 2008; Carter et al. 2010). In the present study, we found breath rate was unrelated to open field entrance or escape speed at the between-individual level, despite a negative relationship was found between the latter. Breath rate during handling has been repeatedly reported to correlate with personality traits in several species (Carere and van Oers 2004; Šimková et al. 2017), including mammals (Boon et al. 2007; Montiglio et al. 2012; Ferrari et al. 2013). Consequently, breath rate is commonly referred to as a risk-related behavioral trait (Hall et al. 2015; Haigh et al. 2017b). Nonetheless, the use of breath rate during handling as a behavioral trait has been recently disputed in birds (David et al. 2012), and is now frequently used as a predictor of individuals' physiological status, rather than a proxy of boldness (Krams et al. 2014; Dubuc-Messier et al. 2017). Yet, such questioning has not been addressed for other taxonomical groups (e.g., mammals). In the light of such discrepancy, our results (i.e., the above-mentioned intersexual differences in breath rate and the lack of relationship with open field entrance and escape speed), reinforce the interpretation of breath rate as a physiological trait, which can be potentially correlated with behavior. Taking into account that stress induces an increase in metabolic rate (Haigh et al. 2017a, b), potentially detectable as an increase in breath rate, it would be potentially more informative of an individual's boldness to use the differential between breath rate under risk and an individual's basal rate. Our interpretation of breath rate seems even more plausible considering we found a relationship between shyness-boldness and escape speed; escape speed was related to open field entrance at the between-individual level, suggesting the existence of a behavioral syndrome in *A. getulus* (Dingemanse et al. 2012; Dingemanse and Dochterman 2013). As a negative relationship between boldness and antipredator response efficiency is supported in the literature (Biro and Stamps 2008; Jones and Godin 2010; Rodríguez-Prieto et al. 2011; Rödel et al. 2014), our results agree with previous research (Boon et al. 2008; Jones and Godin 2010; Rödel et al. 2014).

We found no relationship between parasite infection, body condition, and personality (i.e., boldness-shyness and escape speed). Parasite loads are known to incur heavy energy requirements and metabolic rate increases for hosts (Khokhlova et al. 2002; Careau et al. 2010), and parasites are actually considered a strong selective force-shaping animal personality (Boon et al. 2008; Barber and Dingemanse 2010; Ezenwa et al. 2016). Yet, invasive species are frequently released from their parasites in terms of diversity and prevalence (Torchin et al. 2003). Previous research on *A. getulus* found that individuals from Fuerteventura are less parasitized compared to individuals from the native range (López-Darias 2007; López-Darias et al. 2008). Consequently, the lack of association between parasite infection, body condition, and personality traits in this species may be due to the reduced energy allocation required by a low parasite load. Thus, one major cost of a fast pace-of-life syndrome may be lacking in the introduced population of *A. getulus*. Nonetheless, we performed our study over a relatively short period of the year. We measured *N. pectinifer* intensity during the nonbreeding season, when individuals were sleeping together in communal burrows. Social species such as *A. getulus* are able to control ectoparasite loads through grooming and allogrooming (Altizer et al. 2003; Hillegass et al. 2008), especially at the time of this study. Moreover, patterns of infection within a population are known to vary over time because of fluctuations in androgen concentrations and differences in spatial and burrowing behavior among individuals (Krasnov et al. 2005; Careau et al. 2010; Kiffner et al. 2013).

Individuals with fast pace-of-life (i.e., more explorative and bolder individuals) are expected to perform better than less explorative and shyer individuals when resources are scarce (Dingemanse et al. 2004; Le Coeur et al. 2015). Yet, we did not find any relationship between body condition and any of the behavioral traits considered in this study at between-individual level, although body condition was positively related to breath rate at within-individual level. Considering that with the exception of survival, we conducted our research right after summer, when some of the resources used by this species are at their lowest on Fuerteventura (López-Darias and Nogales 2008), the absence of a relationship between personality and body condition is an unexpected result. Nonetheless, the study area contained both natural and introduced plant species, including *Opuntia* species, which provide nutritional resources (e.g., fruits) when natural conditions on the island are impoverished (López-Darias and Nogales 2008). In addition, *A. getulus* is an omnivorous species able to exploit multiple nutritional resources, including native mollusks (Machado and Domínguez 1982; López-Darias 2007; López-Darias and Nogales 2008). Consequently, strong differences in body condition between individuals with different pace-of-life may be masked or nonexistent due to the continuous food supply provided by native and alien species. On the



other hand, the positive relationship we found between body condition and breath rate is in line with previous research in other species, relating breath rate to physiology instead of behavior (David et al. 2012). Thus, this result provides further support to our interpretation on the inappropriateness of breath rate to assess an individual's boldness (see above).

### Survival chances and behavior

Survival was unrelated to lice intensity, body condition, breath rate, or escape speed. However, unexpectedly, we found a positive selection gradient for percentage entrances, i.e., the likelihood of survival was higher for bolder individuals. This result is particularly interesting as boldness was negatively related to antipredator behavior (i.e., escape speed), which is known to incur survival costs in other terrestrial species (Husak 2006a, b). Personality traits associated with fast pace-of-life (i.e., activity, boldness, and explorative behavior) are assumed to incur reduced survival chances for individuals (Smith and Blumstein 2007; Boon et al. 2008; Réale et al. 2010). However, the relationship between fitness and personality is complex (Smith and Blumstein 2007; Bijleveld et al. 2014) and highly context dependent (Dingemanse et al. 2004; Réale et al. 2010; Le Coeur et al. 2015). Such a surprising result may be related to the invasive species status and specific ecological conditions of this species. Although no empirical study has attempted to compare predation pressure in *A. getulus* in their native and introduced ranges, the number of species preying on the squirrels is much higher in its native range compared to its introduced habitat (López-Darias 2007). This reduction in the number of predators has most likely reduced predation pressure and may have led to a major ecological release for bolder individuals.

### Concluding remarks and future avenues

Our study suggests a behavioral syndrome exists in *A. getulus* that links boldness and antipredator behavior (i.e., escape speed). However, no relationship seems to exist between personality and parasite loads, probably due to lower parasite diversity and abundance in the invasive population. The resulting reduction in energy necessary to deal with infection, together with a broad generalist diet that can exploit year-round resources, may have led to diminished interindividual differences in body condition. The release from major ecological constraints has potentially allowed individuals with a fast pace-of-life to perform better than their relatives with a slow pace-of-life. Our study provides the first evidence in our knowledge, of how personality is related to parasitism and survival in an established invasive species, suggesting that the positive relationship between fitness and personality traits associated with a fast pace-of-life are not only present in early stages of biological invasions but may also persist in post-

establishment phases of biological invasions. Yet, it is important to point out that little is known about the biology of *A. getulus*, particularly the ecological and behavioral biology of native populations. Previous research has pointed out pace-of-life syndromes may also be absent in noninvasive species (Le Galliard et al. 2015; Závorka et al. 2015). Consequently, research on the relationship between parasites, body condition, personality, and fitness in the native populations of *A. getulus* would clarify if the absence of a pace-of-life syndrome is inherent to the species or just in the invasive population. The specific ecological conditions related to the success of an invasive species have rarely been used to test assumptions about animal personality. Our study poses an intriguing scenario for evolutionary research based on animal personality. Indeed, the fitness consequences of personality traits are a central idea of evolutionary theories of animal personality (Kight et al. 2013). Yet, despite the tremendous interest devoted to animal personality, our understanding of the causes underlying phenotypic differences is still limited. A combination of invasive species biology and animal personality research may help to solve some of the mysteries surrounding animal personality while increasing our understanding of a major conservation concern.

**Acknowledgments** We would like to thank E. Koole and T. Dorta Morales for their help during fieldwork. We acknowledge all constructive comments regarding data analyses from R. Dorta. We are thankful to A. Martín, M. Molina Borja, and J. María Fernández-Palacios, as their comments during the master thesis of JCP have been incorporated into this manuscript. Special thanks to the Cabildo de Fuerteventura for the kindness of its staff and for providing allocation and facilities on Fuerteventura that greatly contributed to this work. Particular thanks as well to Instituto de Productos Naturales y Agrobiología (Consejo Superior de Investigaciones Científicas) and its previous director (Dr. Cosme García), by providing a vehicle to accomplish the fieldwork. The excellent reviews by two anonymous reviewers from BES contributed significantly to the improvement of the final version of this manuscript.

**Funding** This study was also supported by the National Research Council of Canada, the Canadian Foundation for Innovation, and a university research grant from the University of Manitoba to JMW. AvdM was also supported by the University of Manitoba, Faculty of Science graduate studentships and the Faculty of Graduate Studies Graduate Enhancement of the Tri-Council Stipend. JCP was supported with a student grant from Ministerio de Educación, Cultura y Deporte while doing his master's thesis. ML-D was funded by the Program Agustín de Betancourt, under the identification mark "Tenerife 2030" (P. INNOVA 2016–2021).

### Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

**Ethical approval** All applicable international, national, and institutional guidelines for the care and use of animals were followed. All procedures were made in accordance with the American Mammal Association guidelines (Sikes et al. 2011), and were approved by the University of Manitoba's Animal Care and Use Committee (#F14–032).

## References

- Altizer S, Nunn CL, Thrall PH, Gittleman JL, Antonovics J, Cunningham AA, Dobson AP, Ezenwa V, Jones KE, Pedersen AB, Poss M, Pulliam JRC (2003) Social organization and parasite risk in mammals: integrating theory and empirical studies. *Annu Rev Ecol Evol* 34:517–547
- Barber I, Dingemanse NJ (2010) Parasitism and the evolutionary ecology of animal personality. *Phil Trans R Soc B* 365:4077–4088
- Bates D, Maechler M, Bolker B, Walker S (2015) Fitting linear mixed-effect models using lme4. *J Stat Softw* 67:1–48
- Bergeron P, Montiglio P-O, Réale D, Humphries MM, Gimenez O, Garant D (2013) Disruptive viability selection on adult exploratory behaviour in eastern chipmunks. *J Evol Biol* 26:766–774
- Bijleveld AI, Massourakis G, van der Marel A, Dekinga A, Spaans B, van Gils JA, Piersma T (2014) Personality drives physiological adjustments and is not related to survival. *Proc R Soc B* 281:20133135
- Biro PA, Stamps JA (2008) Are animal personality traits linked to life-history productivity? *Trends Ecol Evol* 23:361–368
- Blackburn TM, Pyšek P, Bacher S, Carlton JT, Duncan RP, Jarošík V, Wilson JR, Richardson DM (2011) A proposed unified framework for biological invasions. *Trends Ecol Evol* 26:333–339
- Blight O, Josens R, Bertelsmeier C, Abril S, Boulay R, Cerdá X (2017) Differences in behavioural traits among native and introduced colonies of an invasive ant. *Biol Invasions* 19:1389–1398
- Blumstein DT, Flores G, Munoz NE (2015) Does locomotor ability influence flight initiation distance in yellow-bellied marmots? *Ethology* 120:1–8
- Blumstein DT, Lea AJ, Olson LE, Martin JGA (2010) Heritability of anti-predatory traits: vigilance and locomotor performance in marmots. *J Evol Biol* 23:879–887
- Boon AK, Réale D, Boutin S (2007) The interaction between personality, offspring fitness and food abundance in North American red squirrels. *Ecol Lett* 10:1094–1104
- Boon AK, Réale D, Boutin S (2008) Personality, habitat use, and their consequences for survival in North American red squirrels *Tamiasciurus hudsonicus*. *Oikos* 117:1321–1328
- Boyer N, Réale D, Marmet J, Pisanu B, Chapuis J-L (2010) Personality, space use and tick load in an introduced population of Siberian chipmunks *Tamias sibiricus*. *J Anim Ecol* 79:538–547
- Brommer JE, Klun E (2012) Exploring the genetics of nestling personality traits in a wild passerine bird: testing the phenotypic gambit. *Ecol Evol* 2:3032–3044
- Bush AO, Lafferty KD, Lotz JM, Shostak AW (1997) Parasitology meets ecology on its own terms. Margolis et al. revisited. *J Parasitol* 83: 575–583
- Cabrera D, Andres D, McLoughlin PD, Debeffe L, Medill SA, Wilson AJ, Poissant J (2017) Island tameness and the repeatability of flight initiation distance in a large herbivore. *Can J Zool* 95:771–778
- Careau V, Thomas D, Humphries MM, Réale D (2008) Energy metabolism and animal personality. *Oikos* 117:641–653
- Careau V, Thomas DW, Humphries MM (2010) Energetic cost of bot fly parasitism in free-ranging eastern chipmunks. *Oecologia* 162:303–312
- Carere C, van Oers K (2004) Shy and bold great tits (*Parus major*): body temperature and breath rate in response to handling stress. *Physiol Behav* 82:905–912
- Carter AJ, Goldizen AW, Tromp SA (2010) Agamas exhibit behavioral syndromes: bolder males bask and feed more but may suffer higher predation. *Behav Ecol* 21:655–661
- Chapple DG, Simmonds SM, Wong BBM (2012) Can behavioral and personality traits influence the success of unintentional species introductions? *Trends Ecol Evol* 27:57–64
- Class B, Brommer JE (2016) Senescence of personality in a wild bird. *Behav Ecol Sociobiol* 70:733–744
- Corti M, Bazzi G, Costanzo A, Podofillini S, Saino N, Rubolini D, Romano A (2017) Behavioural stress response and melanin-based plumage colouration in barn swallow nestlings. *Behaviour* 154:853–874
- Cote J, Clobert J, Brodin T, Fogarty S, Sih A (2010) Personality-dependent dispersal: characterization, ontogeny and consequences for spatially structured populations. *Phil Trans R Soc B* 365:4065–4076
- David M, Auclair Y, Dechaume-Moncharmont F-X, Cézilly F (2012) Handling stress does not reflect personality in female zebra finches (*Taeniopygia guttata*). *J Comp Psychol* 126:10–14
- del Arco Aguilar M-J, González-González R, Garzón-Machado V, Pizarro-Hernández B (2010) Actual and potential natural vegetation on the Canary Islands and its conservation status. *Biodivers Conserv* 19:3089–3140
- Dingemanse NJ, Both C, Drent PJ, Tinbergen JM (2004) Fitness consequences of avian personalities in a fluctuating environment. *Proc R Soc Lond B* 271:847–852
- Dingemanse NJ, Dochtermann NA (2013) Quantifying individual variation in behaviour: mixed-effect modelling approaches. *J Anim Ecol* 82:39–54
- Dingemanse NJ, Dochtermann NA, Nakagawa S (2012) Defining behavioural syndromes and the role of ‘syndrome deviation’ in understanding their evolution. *Behav Ecol Sociobiol* 66:1543–1548
- Dubuc-Messier G, Réale R, Perret P, Charmantier A (2017) Environmental heterogeneity and population differences in blue tits personality. *Behav Ecol* 28:448–459
- Ezenwa VO, Archie EA, Craft ME, Hawley DM, Martin LB, Moore J, White L (2016) Host behaviour-parasite feedback: an essential link between animal behaviour and disease ecology. *Proc R Soc B* 283: 20153078
- Ferrari C, Pasquaretta C, Carere C, Cavallone E, von Hardenberg A, Réale D (2013) Testing for the presence of coping styles in a wild mammal. *Anim Behav* 85:1385–1396
- Gelman A, Rubin DB (1992) Inference from iterative simulation using multiple sequences. *Stat Sci* 7:457–511
- Hadfield JD (2010) MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. *J Stat Softw* 33:1–22
- Haigh A, Butler F, O’Riordan R, Palme R (2017a) Managed parks as a refuge for the threatened red squirrel (*Sciurus vulgaris*) in light of human disturbance. *Biol Conserv* 211:29–36
- Haigh A, O’Riordan R, Butler F (2017b) Variations in aggression and activity levels amongst squirrels inhabiting low and high density areas. *Ecol Res* 32:931–941
- Hall ML, van Asten T, Katsis AC, Dingemanse NJ, Magrath MJL, Mulder RA (2015) Animal personality and pace-of-life syndromes: do fast-exploring fairy-wrens die young? *Front Ecol Evol* 3:28
- Hillegass MA, Waterman JM, Roth JD (2008) The influence of sex and sociality on parasite loads in an African ground squirrel. *Behav Ecol* 19:1006–1011
- Hillegass MA, Waterman JM, Roth JD (2010) Parasite removal increases reproductive success in a social African ground squirrel. *Behav Ecol* 21:696–700
- Houston AI, McNamara JM, Hutchinson JMC (1993) General results concerning the trade-off between gaining energy and avoiding predation. *Phil Trans R Soc B* 341:375–397
- Husak JF (2006a) Does survival depend on how fast you can run or how fast you do run? *Funct Ecol* 20:1080–1086
- Husak JF (2006b) Does speed help you survive? A test with collared lizards of different ages. *Funct Ecol* 20:174–179
- Jones KA, Godin J-GJ (2010) Are fast explorers slow reactors? Linking personality type and anti-predator behaviour. *Proc R Soc Lond B* 277:625–632

- Khokhlova IS, Krasnov BR, Kam M, Burdelova NI, Degen AA (2002) Energy cost of ectoparasitism: the flea *Xenopsylla ramesis* on the desert gerbil *Gerbillus dasyurus*. *J Zool* 258:349–354
- Kiffner C, Stanko M, Morand S, Khokhlova IS, Shenbrot GI, Laudisoit A, Leirs H, Hawlena H, Krasnov BR (2013) Sex-biased parasitism is not universal: evidence from rodent-flea associations from three biomes. *Oecologia* 173:1009–1022
- Right CR, David M, Dall SRX (2013) The evolution of animal personality variation. In: eLS. John Wiley & Sons Ltd., Chichester, <http://www.els.net>
- Kluen E, Siitari H, Brommer JE (2014) Testing for between individual correlations of personality and physiological traits in a wild bird. *Behav Ecol Sociobiol* 68:205–213
- Koprowski JL (2002) Handling tree squirrels with a safe and efficient restraint. *Wildlife Soc Bull* 30:101–103
- Kortet R, Hedrick AV, Vainikka A (2010) Parasitism, predation and the evolution of animal personalities. *Ecol Lett* 13:1449–1458
- Krams IA, Vrublevska J, Sepp J, Abolins-Abols M, Rantala MJ, Mierauskas P, Krama T (2014) Sex-specific associations between nest defence, exploration and breathing rate in breeding pied flycatchers. *Ethology* 120:492–501
- Krasnov BR, Morand S, Hawlena H, Khokhlova IS, Shenbrot GI (2005) Sex-biased parasitism, seasonality and sexual size dimorphism in desert rodents. *Oecologia* 146:209–217
- Lande R, Arnold SJ (1983) The measurement of selection on correlated characters. *Evolution* 37:1210–1226
- Le Coeur C, Thibault M, Pisanu B, Thibault S, Chapuis J-L, Baudry E (2015) Temporally fluctuating selection on a personality trait in a wild rodent population. *Behav Ecol* 26:1285–1291
- Le Galliard J-F, Paquet M, Mugabo M (2015) An experimental test of density-dependent selection on temperament traits of activity, boldness and sociability. *J Evol Biol* 28:1144–1155
- Lemaître J, Fortin D, Montiglio P-O, Darveau M (2009) Bot fly parasitism of the red-backed vole: host survival, infection risk, and population growth. *Oecologia* 159:283–294
- López-Darias M (2007) Ecología de una invasión: el caso de la ardilla moruna (*Atlantoxerus getulus*) en la isla de Fuerteventura (Islas Canarias). University of La Laguna, San Cristóbal de La Laguna
- López-Darias M, Lobo JM (2008) Factors affecting invasive species abundance: the Barbary ground squirrel on Fuerteventura island, Spain. *Zool Stud* 47:268–281
- López-Darias M, Nogales M (2008) Effects of the invasive Barbary ground squirrel (*Atlantoxerus getulus*) on seed dispersal systems of insular xeric environments. *J Arid Environ* 72:926–939
- López-Darias M, Ribas A, Feliú C (2008) Helminth parasites in native and invasive mammal populations: comparative study on the Barbary ground squirrel *Atlantoxerus getulus* L. (Rodentia, Scuriidae) in Morocco and the Canary Islands. *Acta Parasitol* 53:296–301
- Machado A (1979) The introduction of the Getulian squirrel (*Atlantoxerus getulus* L. 1758) in Fuerteventura, Canary Islands. *Egypt J Wildl Nat Res* 2:182–203
- Machado A, Domínguez F (1982) Estudio sobre la presencia de Ardilla Moruna (*Atlantoxerus getulus* L.) en la isla de Fuerteventura; su introducción, su biología y su impacto en el medio. Ministerio de Agricultura, Pesca y Alimentación, Instituto Nacional para la Conservación de la Naturaleza, San Cristóbal de La Laguna
- Macleod R, Barnett P, Clark JA, Cresswell W (2005) Body mass change strategies in blackbirds *Turdus merula*: the starvation-predation risk trade-off. *J Anim Ecol* 74:292–302
- Malange J, Izar P, Japyassú H (2016) Personality and behavioural syndrome in *Necromys lasiurus* (Rodentia: Cricetidae): notes on dispersal and invasion processes. *Acta Ethol* 19:189–195
- Marras S, Killen SS, Claireaux G, Domenici P, McKenzie DJ (2011) Behavioural and kinematic components of the fast-start escape response in fish: individual variation and temporal repeatability. *J Exp Biol* 214:3102–3110
- Marzol-Jaén MV (1988) La Lluvia: un recurso natural para Canarias. Servicio de Publicaciones de la Caja General de Ahorro de Canarias, Santa Cruz de Tenerife
- Monceau K, Dechaume-Montcharmont F-X, Moreau J, Lucas C, Capoduro R, Motreuil S, Moret Y (2017) Personality, immune response and reproductive success: an appraisal of the pace-of-life syndrome hypothesis. *J Anim Ecol* 86:932–942
- Montiglio P-O, Garant D, Pelletier F, Réale D (2012) Personality differences are related to long-term stress reactivity in a population of wild eastern chipmunks, *Tamias striatus*. *Anim Behav* 84:1071–1079
- Mortola JP, Lanthier C (2005) Breathing frequency in ruminants: a comparative analysis with non-ruminant mammals. *Respir Physiol Neurobiol* 145:265–277
- Mutascio HE, Pittman SE, Zollner PA (2017) Investigating movement behavior of invasive Burmese pythons on a shy–bold continuum using individual-based modeling. *Perspect Ecol Conserv* 15:25–31
- Nakagawa S, Schielzeth H (2010) Repeatability for Gaussian and non-Gaussian data: a practical guide for biologists. *Biol Rev* 85:935–956
- Oufiero CE, Garland T (2009) Repeatability and correlation of swimming performances and size over varying time-scales in the guppy (*Poecilia reticulata*). *Funct Ecol* 23:969–978
- Patterson JEH, Neuhaus P, Kutz SJ, Ruckstuhl KE (2013) Parasite removal improves reproductive success of female North American red squirrels (*Tamiasciurus hudsonicus*). *PLoS One* 8:e55779
- Peig J, Green AJ (2009) New perspectives for estimating body condition from mass/length data: the scaled mass index as an alternative method. *Oikos* 118:1883–1891
- Perals D, Grif S, Bartomeus I, Sol D (2017) Revisiting the open-field test: what does it really tell us about animal personality? *Anim Behav* 123:69–79
- Perez VJ, Eatwell JC, Samorajski T (1980) A metabolism chamber for measuring oxygen consumption in the laboratory rat and mouse. *Physiol Behav* 24:1185–1189
- Phillips BL, Suarez AV (2012) The role of behavioural variation in the invasion of new areas. In: Candolin U, Wong BBM (eds) Behavioural responses to a changing world. Oxford University Press, Oxford, pp 190–200.
- Phillips MA, Waterman JM (2014) Anti-snake behaviour in a facultative cooperative breeder, the cape ground squirrel. *Behaviour* 151:1735–1758
- Quinn JL, Cresswell W (2005) Personality, anti-predation behaviour and behavioural plasticity in the chaffinch *Fringilla coelebs*. *Behaviour* 142:1377–1402
- R Development Core Team (2017) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna <http://www.R-project.org>
- Réale D, Garant D, Humphries MM, Bergeron P, Careau V, Montiglio P-O (2010) Personality and the emergence of the pace-of-life syndrome concept at the population level. *Phil Trans R Soc B* 365:4051–4063
- Réale D, Reader SM, Sol D, McDougall PT, Dingemanse NJ (2007) Integrating animal temperament within ecology and evolution. *Biol Rev* 82:291–318
- Rödel HG, Zapka M, Talke S, Kornatz T, Bruchner B, Hedler C (2014) Survival costs of fast exploration during juvenile life in a small mammal. *Behav Ecol Sociobiol* 69:205–217
- Rodríguez-Prieto I, Martín J, Fernández-Juricic E (2011) Individual variation in behavioural plasticity: direct and indirect effects of boldness, exploration and sociability on habituation to predators in lizards. *Proc R Soc Lond B* 278:266–273
- Rózsa L, Reiczig J, Majoros G (2000) Quantifying parasites in samples of hosts. *J Parasitol* 86:228–232

- Schulte-Hostedde AI, Millar JS (2002) Effects of body size and mass on running speed of male yellow-pine chipmunks (*Tamias amoenus*). *Can J Zool* 80:1584–1587
- Sih A, Bell AM (2008) Insights for behavioral ecology from behavioral syndromes. *Adv Stud Behav* 38:227–281
- Sih A, Bell A, Johnson JC (2004a) Behavioral syndromes: an ecological and evolutionary overview. *Trends Ecol Evol* 19:372–378
- Sih A, Bell AM, Johnson JC, Ziemba RE (2004b) Behavioral syndromes: an integrative overview. *Q Rev Biol* 79:241–277
- Sih A, Cote J, Evans M, Fogarty S, Pruitt J (2012) Ecological implications of behavioural syndromes. *Ecol Lett* 15:278–289
- Sikes RS, Gannon WL (2011) Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *J Mammal* 92:235–253
- Šimková O, Frýdlová P, Žampachová B, Frynta D, Landová E (2017) Development of behavioural common boa (*Boa imperator*): repeatable independent traits of personality? *PLoS One* 12:e0177911
- Smith BR, Blumstein DT (2007) Fitness consequences of personality: a meta-analysis. *Behav Ecol* 19:448–455
- Stamps JA (2007) Growth-mortality tradeoffs and “personality traits” in animals. *Ecol Lett* 10:355–363
- Stamps J, Groothuis TGG (2010) The development of animal personality: relevance, concepts and perspectives. *Biol Rev* 85:301–325
- Stoffel MA, Nakagawa S, Schielzeth H (2017) RptR: repeatability estimation and variance decomposition by generalized linear mixed-effect models. *Methods Ecol Evol* (published online, <https://doi.org/10.1111/2041-210X.12797>)
- Thorlacius M, Hellström G, Brodin T (2015) Behavioral dependent dispersal in the invasive round goby *Neogobius melanostomus* depends on population age. *Curr Zool* 61:529–542
- Torchin ME, Lafferty KD, Dobson AP, McKenzie VJ, Kuris AM (2003) Introduced species and their missing parasites. *Nature* 421:628–630
- van Oers K, Drent PJ, de Goede P, van Noordwijk AJ (2004) Realized heritability and repeatability of risk-taking behaviour in relation to avian personalities. *Proc R Soc Lond B* 271:65–73
- Wolf M, van Doorn GS, Leimar O, Weissing FJ (2007) Life-history trade-offs favour the evolution of animal personalities. *Nature* 447:581–584
- Závorka L, Aldvén D, Näslund J, Höjesjö J, Johnsson JI (2015) Linking lab activity with growth and movement in the wild: explaining pace-of-life in a trout stream. *Behav Ecol* 26:877–884
- Zohdy S, Bisanzio D, Tecot S, Wright PC, Jernvall J (2017) Aggression and hormones are associated with heterogeneity in parasitism and parasite dynamics in the brown mouse lemur. *Anim Behav* 132: 109–119