



Original Article

Temporally fluctuating selection on a personality trait in a wild rodent population

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Over the past decade, it has been recognized that in many animal species, individuals present consistent behavioral differences across time and/or contexts, thus defining personality traits. A general relationship seems to exist between personality and fitness in wild populations, which raises the question as to how variation in personality is maintained in the presence of selection. Fluctuating selection associated with a heterogeneous environment could contribute to maintaining personality variation, but its presence in wild populations has rarely been tested. In this 6-year study, we investigated the relationship between individual personality differences and 1 component of fitness, annual reproductive success (ARS), in a population of Siberian chipmunk *Tamias sibiricus* that experiences considerable annual variations in food availability. We estimated trappability—the propensity of chipmunks to enter traps—using capture–mark–recapture data, and we showed that it was repeatable over a 1-year interval. Genetic data were used to estimate parentage and thus ARS. Assuming that trappability is an indicator of boldness, we found that bolder chipmunks had higher ARS in years with low food availability, whereas lower ARS in years with high food availability. Temporally fluctuating selection therefore probably contributes to maintaining variation in boldness in the study population.

Key words: boldness, capture–mark–recapture, fluctuating selection, personality evolution, *Tamias sibiricus*, trappability.

INTRODUCTION

Over the past decade, it has been recognized that in many animal species, individuals of the same sex, age, and size present consistent behavioral differences across time and/or contexts, thus defining personality traits (Wolf and Weissing 2010). Personality traits have been described using many terms, although Réale et al. (2007) divided them into 5 categories: activity, shyness-boldness (response to potentially risky situations), exploration (response to novel situations), aggressiveness, and sociability. This framework has since been widely adopted within animal personality studies (Carter et al. 2013). Personality variation has been shown in many species to have an additive genetic basis, that is, to be heritable (reviewed by Réale et al. 2007). Furthermore, a general relationship seems to exist between personality and fitness in wild populations (reviewed by Smith and Blumstein 2008). In this context, selection for the most advantageous trait value would be expected to remove

personality variation. One of the main questions currently being asked by behavioral ecologists regarding animal personality is thus how variation in personality is maintained in wild populations (Carter et al. 2013).

As with other animal characteristics, like for example morphology, 2 types of non-mutually exclusive mechanisms could explain the maintenance of variation in the presence of selection. A first possibility is mutation-selection balance (Zhang and Hill 2005). If, when averaged across environments, there is an optimal value of a personality trait, then selection will tend to eliminate alleles that do not predispose to this optimum, thus decreasing genetic variation. However, new mutations constantly arise in the population, in turn restoring variation. In this case, personality variation is the result of the equilibrium between selection and mutation, and it is not adaptive: personality trait values that differ from the optimum are selected against. The second possibility is that personality variation is adaptive, meaning that selection actively maintains rather than diminishes variation, that is, some form of balancing selection is acting. Various mechanisms may be involved here. Variation in personality trait values can be maintained by selection that 1) favors rarer trait values (i.e., negative frequency-dependent selection),

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2) involves trade-offs among different components of fitness, 3) is balanced by opposing indirect selection on a correlated trait (correlated selection), and 4) fluctuates over time or space (fluctuating selection) (e.g., Verweij et al. 2012).

To date, studies on the evolution of animal personality have focussed on the latter explanation, adaptive personality differences. A recent synthetic analysis of phenotypic selection in wild populations (Kingsolver et al. 2012) showed little evidence of trade-offs among different components of fitness or for correlated selection (except for size), but instead suggested that fluctuating selection is relatively common (but see Morrissey and Hadfield 2012). So far, only a handful of studies have tested the occurrence of temporally or spatially heterogeneous selective pressures in the wild (Dingemanse et al. 2004; Quinn et al. 2009; Bergeron et al. 2013).

In this study, we investigated the link between individual personality differences in boldness and 1 component of fitness, reproductive success, in a population of Siberian chipmunk *Tamias sibiricus barberi*, introduced into a suburban forest near Paris, France (the relationship between boldness and survival was not examined in this study). This population provides an interesting model to test the presence of temporally fluctuating selection because 1) personality variation in exploration-activity and boldness was documented in a previous study (Boyer et al. 2010), and 2) the animals under study experience large yearly fluctuations in one of their main food sources, namely acorns from 2 dominant oak species, *Quercus petraea* and *Q. robur* (e.g., Crawley and Long 1995), present on our study site. In this 6-year study, we used capture–mark–recapture data to estimate the propensity of chipmunks to enter traps (i.e., trappability), often taken as an index of boldness in chipmunks (Boyer et al. 2010; Montiglio et al. 2012), with its repeatability being verified between years. We used genetic data to estimate annual reproductive success (ARS), and tested whether the relationship between trappability and ARS varied between years according to the level of acorn availability.

MATERIALS AND METHODS

Study species and site

The Siberian chipmunk is a diurnal ground squirrel native to Eurasia with solitary and sedentary habits (Oboleskaya et al. 2009). Adults weigh approximately 100 g (no sexual dimorphism). They use burrows to hibernate and reproduce (Chapuis et al. 2011). From an age of 8 months, female chipmunks can enter estrus once per year in Japan (late April–early May; Kawamichi and Kawamichi 1993) or twice per year in France

(in March and in June; Chapuis et al. 2011). The period of estrus lasts 1–2 day(s) during which a female utters distinctive estrous calls (Blake 1992). Several males aggregate near the female and pursue her; the female will then mate with 1 or several males (Kawamichi et al. 1987). Juveniles are born after a gestation period of about 1 month and remain in the nest at least another month (Chapuis et al. 2011). Young begin their dispersal shortly after their emergence from the nest (Marmet et al. 2009).

In France, animals imported from South Korea (Pisanu et al. 2013) have been sold in pet shops since the 1960s (Chapuis et al. 2011). Siberian chipmunk populations were observed a decade later in several suburban forests and urban parks (Chapuis et al. 2011). Our study site was a 14-ha area located in the Forest of Sénart (3200-ha; 48°39'N, 02°29'E), situated 22 km southeast of Paris, where the largest known French population of Siberian chipmunks is found (Pisanu et al. 2013). Two main types of habitat are found within the study site: a semi-open oak grove (6.0 ha; herbaceous layer: 90%, shrubby layer: 5%, arboreal layer: 60% dominated by *Q. robur* and *Q. petraea*) and a closed oak-hornbeam grove (6.5 ha; herbaceous layer: 10%, shrubby layer: 30%, arborescent layer: 90% dominated by *Q. robur*, *Q. petraea*, and *Carpinus betulus*), with grassland and buildings representing an additional 1.5 ha (Marmet et al. 2009, 2012).

Acorn availability is known to be mainly relevant for chipmunk reproduction just after hibernation (Kawamichi 1980). From 2008 to 2012, spring acorn availability was estimated between late February and early March by counting the acorns on random sample surfaces under about 30 oaks across the study site. Two acorn availability levels were defined: “low” or “high,” respectively, correspond to less or more than the average acorn spring biomass of 402.2 g acorn/m² (Table 1; Supplementary Material I). Because acorn availability was not estimated in 2006 at the study site, we used Office National des Forêts (ONF) data on acorn production in nearby forests (Conche J, ONF, unpublished data) to determine acorn availability in 2006 (Supplementary Material I).

Live trapping, habitat, and periphery indices

The chipmunk population has been monitored since 2005 using the capture–mark–recapture technique with 104 geolocalized Sherman live traps distributed on a grid throughout the study site (Marmet et al. 2009, 2012). Five traps placed in highly anthropized areas (lawn and buildings) were excluded from the present analysis. Among the remaining traps, 47 were placed in the semi-open oak grove and 52 in the closed oak-hornbeam grove.

Table 1

Annual spring biomass of acorns, number of young included in parentage analyses, mean trappability, and mean ARS of adult Siberian chipmunks in La Faisanderie, Forest of Sénart, between 2006 and 2012

Year	Acorn availability	Chipmunks			
	Spring biomass (low/high)	Young Number analysed	Adult <i>n</i>	Trappability	ARS
2006	Low	106	29	12.2 ± 1.8	1.7 ± 0.4
2008	High	143	14	3.3 ± 0.5	2.1 ± 0.4
2009	Low	50	9	5.0 ± 1.0	1.8 ± 0.4
2010	High	138	9	2.8 ± 0.6	5.6 ± 0.8
2011	Low	76	26	5.3 ± 0.7	2.2 ± 0.5
2012	High	72	17	5.9 ± 0.8	1.6 ± 0.3

Between 2005 and 2012, monthly trapping sessions of 5 consecutive days were set during the chipmunk active period from March to October. Traps were opened and baited (sunflower seeds and peanut butter) in the morning, checked and provisioned as necessary 3–4 times per day, and then closed at the end of the afternoon. At first capture, chipmunks were sexed and tagged (PIT-tag and numbered ear ring; Marmet et al. 2009). The trap locations were recorded with each trapping event, as were chipmunk identity, sex, and age (adult or juvenile, based on the date of capture and body mass; see Marmet et al. 2009, 2012). After being handled, chipmunks were released at their capture point.

For each chipmunk, a quantitative periphery index was calculated as the percentage of captures in the outermost traps of the trapping grid. The individuals for which more than 25% of the trapping events occurred in the peripheral line of traps were not included in the analyses. For each chipmunk, we also defined a habitat index. As the vast majority of animals were captured in only a semi-open or closed habitat, this habitat index was coded as a qualitative variable with 2 categories: semi-open or closed.

Trappability

Boldness is most commonly defined as an individual's response to a risky situation (Réale et al. 2007). Trappability—the propensity to enter baited traps—reflects individual differences in the willingness to accept the risk associated with trapping in order to obtain a food reward; it may therefore be considered as an index of boldness (e.g., Montiglio et al. 2012). Trappability was calculated as the total number of trapping events that occurred during the three 5-day sessions in April, May, and June, a 3-month period during which all individuals are out of hibernation. We only calculated the trappability of animals known to be alive during the entire 3-month period, that is, the animals that were recaptured at least once after this period. Because lactating females usually spend more time in their burrow during the month of May, the reproductive status of the females (but not those of the males) might affect their trappability estimate. However, the fact that we did not detect any sex differences in trappability nor a significant interaction between sex and trappability on ARS (see Results) suggests that this potential confounding effect is probably small in our study population.

Genetic methods, parentage analyses, and ARS index

Parentage inferences based on 10 polymorphic microsatellite loci were used to estimate the ARS (defined as the genetically detected number of offspring of an individual) of 63 adults in the population in 2006 (Marmet et al. 2012). An identical procedure was used to estimate the ARS of adults in the population between 2007 and 2012, although the microsatellite set was partially changed (see below).

In short, since 2006, a hair sample was taken from each newly trapped chipmunk, and stored in 95% ethanol. DNA was extracted from approximately 20 hairs per individual using a NucleoSpin® Tissue Kit (Machery-Nagel) following the manufacturer's protocol. We then amplified 10 microsatellites labelled with fluorescent dyes in polymerase chain reactions (PCR) in standard conditions (see Supplementary Material II). We kept the 6 most polymorphic loci from the study of Marmet et al. (2012) and added 4 loci chosen for their high level of polymorphism (Schulte-Hostedde et al. 2000; Anderson et al. 2007; Peters et al. 2007; see Supplementary Material II). PCR products were

analysed using an ABI 3700 capillary DNA sequencer (Applied Biosystems) at the Plateforme Gentyane (UMR INRA 1095). The size of the microsatellite alleles was calculated using Genemapper software (Applied Biosystems).

Following the procedure described in Marmet et al. (2012), we used the program CERVUS (Kalinowski et al. 2007) to identify parent-offspring trios where possible. Briefly, CERVUS uses a likelihood-based approach to assign parentage, combined with the simulation of parentage analysis to determine the confidence of parentage assignments (see Supplementary Material III for details). Using this approach, parent-pair assignment analyses were conducted for all juveniles of the population using strict (95%) and relaxed (80%) levels of statistical confidence. When a parent pair could not be assigned with at least the confidence level of 80%, we assigned maternity or paternity alone using the same method. We then used the parentage inferences to estimate the ARS of all adults, defined as their genetically detected number of offspring in a given year.

Data analysis

Consistency of individual trappability (Réale et al. 2007) was estimated from a set of 46 individuals for which we could ascertain the number of capture events from April to June (see “Trappability” above) in at least 2 consecutive years between 2005 and 2012 ($n = 101$ observations). We estimated the repeatability of an individual's number of trapping events using a linear mixed model (Dingemanse and Dochtermann 2013) based on the log-transformed response variable (Nakagawa and Schielzeth 2010). The dataset used to perform the analysis and the R function used to calculate the mean-adjusted repeatability and obtain bootstrapped confidence intervals (CIs) are shown in Supplementary Material IV. The periphery index was included as a fixed covariate in the model in order to take into account the reduced number of capture events for individuals living at the edge of the trapping grid (Boyer et al. 2010). Availability in food may influence the space use behavior of rodents according to sex (e.g., Stradiotto et al. 2009; Tioli et al. 2009), hence their capture probability. Therefore, sex, habitat, and years with high or low levels of acorn in spring were added as fixed effects in the model. The repeatability of individual trapping events was estimated by adding the identity of chipmunks as a random intercept in the model (Boyer et al. 2010). We also added year as a random intercept to capture any extra-variation of trappability due to temporally related factors.

The relationships among ARS, acorn availability, and trappability were investigated on a set of 95 individuals ($n = 104$ observations; Table 1) marked between 2006 and 2012 for which we could estimate both trappability and ARS. Owing to a DNA conservation problem, we were not able to estimate ARS in 2007. The dataset thus covers the years 2006 and 2008–2012. The relationships among ARS and habitat, sex, acorn availability, and trappability along with all 2-way interactions were investigated using a Poisson-log generalized linear mixed model (Bolker et al. 2009), which included the identity of chipmunks as a random effect. We also added acorn availability in spring as random intercept to capture any extra-variation of ARS due to temporally related factors associated with these years. The periphery index was also included in this analysis. We performed a model selection using a dredging procedure selecting and averaging all models that are within 2 AICc units of the most parsimonious model (i.e., the lowest AICc). The dataset used to perform the analysis is shown in Supplementary Material V.

Mixed models were run using the package “lme4” v.1.1-7 (Bates et al. 2014) and the correctness of the error variance was graphically checked (Zuur et al. 2010). The continuous explanatory variables were scaled prior to analyses (Schielzeth 2010). Evidence threshold was set at the 98% level for CIs following Johnson (2013). Parameter estimates and their CIs were calculated from 3000 parametric bootstrap simulations. All analyses were performed in R 3.1.2 (R Core Team 2014).

To test whether the strength and direction of selection on trappability varied according to acorn availability level, we calculated linear selection gradients (Lande and Arnold 1983) by regressing the relative ARS on the standardized trappability, for low and high acorn availability years. Estimates and standard errors were generated using a “delete-one” jackknifing technique from simple regressions (Crawley 2007). The method is inspired from the Jackknifed linear regression function described in the Supplementary Material of Marmet et al. (2012), which was here adapted to a linear mixed model that incorporates a random intercept for chipmunks’ identity while also controlling for random year intercept. We used the variable specification described in McGlothlin et al. (2010), relative fitness (here ARSi/mean [ARS]) correlated to standardized trait values (i.e., centered to zero mean and unit variance). The R-code for the Jackknife procedure used to calculate the standardized linear selection gradient is shown in Supplementary Material VI.

RESULTS

Trappability

Based on the 46 adults for which we could ascertain the number of capture events from April to June in at least 2 consecutive years (30 ♀ and 16 ♂ trapped on average 2.1 ± 0.1 and 2.3 ± 0.1 consecutive years, respectively; $n = 101$ observations; Supplementary Material IV. All results are presented as “mean \pm mean standard error”), we found that trappability did not significantly differ between males and females (Table 2). The average trappability was 9 ± 1 ($n = 67$) and 7 ± 1 ($n = 34$) for ♀ and ♂, respectively. The average trappability was not significantly different between low acorn availability years (9 ± 1 ; $n = 46$) and high acorn availability years (8 ± 1 ; $n = 55$; Table 2). Trappability was negatively influenced by periphery. We found that the trappability of chipmunks was repeatable between years (mean estimated adjusted repeatability = 30%, 98% CI = 2–53%; Table 2).

Table 2
Parameter estimates of the linear mixed model investigating the repeatability of chipmunks trappability

Sources of variation	Estimates (98% CI)
Random effects	
σ_{α} (individual level)	0.56 [0.36; 0.78]
σ_{ϵ} (Year)	0.37 [0.05; 0.75]
$\sigma_{\epsilon'}$ (Residual)	0.50 [0.38; 0.62]
Repeatability [$\sigma_{\alpha}^2 / (\sigma_{\alpha}^2 + \sigma_{\epsilon}^2 + \sigma_{\epsilon'}^2)$]	0.30 [0.02; 0.53]
Fixed effects	
Intercept	1.64 [1.01; 2.82]
Periphery	-0.22 [-0.43; -0.01]
Sex _[Male]	-0.29 [-0.77; 0.20]
Acorn _[High]	-0.31 [-1.02; 0.39]
Habitat _[Open]	0.48 [0.00; 0.96]

Significant effects in bold.

Relationships between ARS, acorn availability, trappability, and selection gradients

A total of 585 young could be assigned to a parent, allowing us to obtain a set of adults for which both ARS and trappability were estimated ($n = 104$ observations for 95 adults; Table 1). The average ARS was 1.9 ± 0.3 ($n = 57$) for ♀ and 2.6 ± 0.4 ($n = 47$) for ♂ when averaged across the 6 years of the study.

ARS was not influenced by the chipmunks’ degree of periphery, habitat, sex, or trappability (Table 3). Among the 2-ways interactions, only the interaction of trappability and acorn availability had a significant effect on ARS. In the years with low acorn availability, chipmunks with higher trappability had a higher ARS, whereas the opposite was true in the years with high acorn availability (Table 3; Figure 1). Additionally, from selection gradients analysis, we found significant positive directional selection on trappability in the years with low acorn availability ($\beta_{\text{low}} = +0.27 \pm 0.01$; $P < 0.001$); whereas in the years with high acorn availability we found significant negative directional selection ($\beta_{\text{high}} = -0.30 \pm 0.04$; $P < 0.001$).

DISCUSSION

We found that the adult Siberian chipmunks of the study population differed consistently in their propensity to enter traps, often taken as an index of boldness (Boyer et al. 2010; Patterson and Schulte-Hostedde 2011; Montiglio et al. 2012). We also showed that the variation in trappability was associated with a variation in 1 component of fitness, ARS, but that the direction of this association fluctuated between years according to food availability. We shall now discuss the use of trappability as an index of boldness, the relationship between trappability and ARS, and finally, the implication of fluctuating selection on trappability.

Trappability as an index of boldness

Presently, in behavioral ecology studies on wild rodents, personality traits are estimated in 2 ways: individual patterns of behavior are recorded either in response to standardized experimental stimuli or in the natural environment of the animals (Carter et al. 2013). For wild chipmunks, previous studies have used open-field or bag tests as standardised environments to estimate exploration/activity and docility, respectively (Patterson and Schulte-Hostedde 2011; Montiglio et al. 2012; Bergeron et al. 2013). Behavioral recording in the natural environment often relies on trapping data, with trappability being taken as an index of boldness and trap diversity as an index of space use (Boyer et al. 2010; Patterson and Schulte-Hostedde 2011; Montiglio et al. 2012). Both types of methods have advantages and drawbacks. An experimental setting usually allows for quicker, easier, and more standardized measurements, but probably produces indices with less ecological validity (Réale et al. 2007); the reverse is true for behavioral recordings in the natural environment. A recent study by Dammhahn and Almeling (2012) showed that in a population of wild lemurs, boldness measured in an experimental context (novel object test) was correlated with risk-taking in a foraging task in nature, suggesting that both types of methods can be reliably used to estimate personality traits in wild animals.

We confirmed that trappability—the propensity to enter baited traps—is substantially repeatable between years in Siberian chipmunks, and hence it can be considered a personality trait (Boyer et al. 2010). As the average lifespan for adult chipmunks in this population is about 1–2 years (Le Coeur C, unpublished data), the

Table 3

Details of the model selection and parameter estimates of the generalized linear mixed model investigating the variation in ARS of Siberian chipmunks in Sénart

Model's sources of variation	Selection				Parameter
	<i>K</i>	<i>-LL</i>	<i>AICc</i>	<i>w_i</i>	Estimates (98% CI)
Full model					
Periphery + (acorn + habitat + trappability + sex) ²	14	198.4	429.52	—	
Selected and averaged models					
Acorn + trappability + sex + acorn:trappability + sex:trappability	8	200.1	417.61	0.53	
Acorn + trappability + sex + habitat + acorn:trappability + sex:trappability	9	199.6	419.17	0.24	
Acorn + habitat + trappability + sex + acorn:trappability + sex:trappability + acorn:habitat	10	198.5	419.33	0.23	
Random effects					
σ _{ID}					0.64 [0.44; 0.95]
σ _{ACORN}					<0.01 [-0.06; 0.04]
Fixed effects					
Intercept					0.10 [-0.37; 0.56]
Acorn _(High)					0.03 [-0.67; 0.75]
Trappability					-0.04 [-0.40; 0.37]
Sex _(Male)					0.42 [-0.06; 0.89]
Habitat _(Open)					-0.07 [-0.71; 0.57]
Acorn _(Good) :trappability					-0.84 [-1.73; -0.02]
Sex _(Male) :trappability					0.43 [-0.05; 0.89]
Acorn _(Good) :habitat _(Open)					0.56 [-0.32; 1.41]

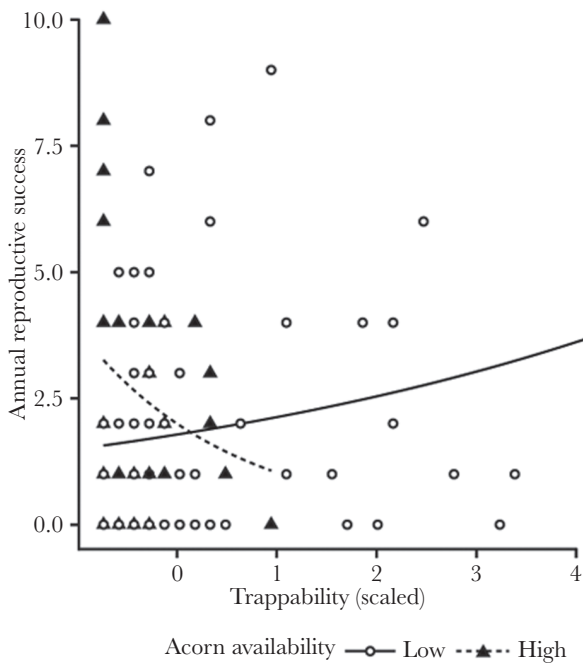


Figure 1
Relationship between the ARS of adult Siberian chipmunks and their trappability according to the level of acorn availability.

fact that trappability is repeatable after 1 year means that it is stable over most of the chipmunks' lifetime. Such long-term stability of a personality trait has already been demonstrated in a closely related species: eastern chipmunks show a tendency toward exploration that is repeatable after 1 year (Montiglio et al. 2012).

Relationship between boldness, food availability, and ARS

We found that boldness significantly influenced ARS in our study population. Such a relationship between a personality trait and

fitness component has already been described on several occasions in wild populations (see Smith and Blumstein 2008, for a review). In the eastern chipmunk, Patterson and Schulte-Hostedde (2011) showed that bolder males had more offspring when controlling for endoparasite load. In the same species, Bergeron et al. (2013) recently found a strong disruptive viability selection on adult exploration behavior. Individuals with low or high exploration scores were almost twice as likely to survive over a 6-month period compared with individuals with intermediate scores. Personality traits therefore seem to be strongly correlated with fitness in chipmunks.

In years with low acorn availability, we found that chipmunks with higher trappability tended to have a higher ARS. Several explanations, not mutually exclusive, can be proposed to explain this pattern. First, as described in several fish and mammal species (Biro and Stamps 2008), bolder chipmunks can be more efficient in acquiring resources. A higher food intake could then translate into better body condition and subsequently higher reproductive success. Additionally, bolder males may be more dominant or use a larger home range, thus increasing their access to females and consequently their reproductive success (Marmet et al. 2012). If this was the case, and because this effect does not apply to females, we would have expected to detect a significant interaction between trappability and sex in terms of ARS. This, however, was not the case (Table 3), although it is possible that we did not detect such an interaction because of our relatively limited sample size.

On the contrary, in years with high acorn availability, chipmunks with higher trappability had lower ARS. This may suggest that being bolder is costly for animals and that when this cost is not offset by a benefit—for example higher resource acquisition during low acorn availability years—then bold animals are worse off than shyer ones. At the study site, during the high resource years, acorn density is so high that food is probably available almost without restriction to all animals when they come out of hibernation, meaning that the better ability to acquire food is probably not advantageous in these circumstances. There are at least 2 hypotheses, again not mutually exclusive, that may explain why boldness could be costly in chipmunks. First, bolder

chipmunks seem to have a higher parasite load (Patterson and Schulte-Hostedde 2011), perhaps due to more frequent encounters with parasites or to the immunosuppressive effects of endocrine-related factors (e.g., Pisanu et al. 2010). Second, in several species, boldness is associated with a higher basal metabolic rate (Biro and Stamps 2010, which could translate into higher basic costs of living for bolder animals.

Fluctuating selection on boldness

One of the main questions currently being asked by behavioral ecologists regarding animal personality is how variation in personality can be retained in wild populations in the presence of selection (Carter et al. 2013). If personality variation is adaptive, it can be maintained by fluctuating selection, negative frequency-dependent selection, trade-offs among different components of fitness, and correlated selection. Of course, these mechanisms are not mutually exclusive, and several can simultaneously occur in a given population.

In our study, bolder chipmunks had a higher ARS in years with low resource availability, whereas the reverse was true in years with high resource availability. If we suppose that boldness mostly influence resource acquisition abilities (Van Noordwijk and de Jong 1986), that is, if bold animal are able to acquire more resource than shy ones when resource are scarce (Biro and Stamps 2008), then in low resource years, bold animals should in average be in better condition and have both higher ARS and survival than shy one. In such a case, selection on boldness would be temporally fluctuating in our study population. Note however that survival data, which are currently not available in our study population, would be needed to confirm this hypothesis.

Surprisingly, Bergeron et al. (2013) recently studied a population of eastern chipmunks subjected to similarly strong variations in food availability, but they found no evidence of temporally fluctuating viability selection on adult exploration behavior. Instead, they found strong disruptive viability selection on this behavior, possibly caused by negative frequency dependent selection, though independent of seasonal variations. The discrepancy with our study could be due to the fact that boldness and exploration may not usually be subjected to the same selective regime. Smith and Blumstein (2008) conducted a meta-analysis of published studies reporting fitness consequences on personality to identify general trends across species. They observed that whereas bolder individuals usually had a markedly increased reproductive success, particularly in males (but incurred a survival cost), there was no relationship between exploration and reproductive success, and only a small, positive effect of exploration on survival, suggesting that different mechanisms may be responsible for the maintenance of variation in different personality traits.

To our knowledge, temporally fluctuating selection on a personality trait has only been described to date for exploration in the great tit, *Parus major*. Dingemanse et al. (2004) showed that in a Dutch population, exploration behavior was related to annual adult survival, but with opposite effects for males and females, and reversed between years. Quinn et al. (2009) showed that in a population from the United Kingdom, the same personality trait was related to lifetime reproductive success, but not survival, through temporally and spatially heterogeneous selection. Our study adds a second example, suggesting that fluctuating selection could commonly contribute to maintain personality variation in wild populations, although further studies would evidently be needed to confirm this hypothesis.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.behco.oxfordjournals.org/>.

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