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Disruptive viability selection on adult exploratory behaviour in eastern chipmunks

P. BERGERON*, P.-O. MONTIGLIO†, D. RÉALE†, M. M. HUMPHRIES‡, O. GIMENEZ§ & D. GARANT*

*Département de Biologie, Université de Sherbrooke, Sherbrooke, QC, Canada
†Département des Sciences Biologiques, UQAM, Montreal, QC, Canada
‡Natural Resource Sciences, Macdonald Campus, McGill University, Ste-Anne de Bellevue, QC, Canada
§Centre d'Écologie Fonctionnelle et Évolutive, CNRS Montpellier, Montpellier, France

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Abstract

Heterogeneous forces of selection associated with fluctuating environments are recognized as important factors involved in the maintenance of inter-individual phenotypic variance within populations. Consistent behavioural differences over time and across situations (e.g. personality) are increasingly cited as examples of individual variation observed within populations. However, the suggestion that heterogeneous selective pressures target different animal personalities remains largely untested in the wild. In this 5-year study, we investigated the dynamics of viability selection on a personality trait, exploration, in a population of eastern chipmunks (*Tamias striatus*) experiencing substantial seasonal variations in weather conditions and food availability associated with masting trees. Contrary to our expectations, we found no evidence of fluctuating selection on exploration. Instead, we found strong disruptive viability selection on adult exploration behaviour, independent of seasonal variations. Individuals with either low or high exploration scores were almost twice as likely to survive over a 6-month period compared with individuals with intermediate scores. We found no evidence of viability selection on juvenile exploration. Our results highlight that disruptive selection might play an important role in the maintenance of phenotypic variance of wild populations through its effect on different personality types across temporally varying environmental conditions.

Introduction

Understanding how selection forces are involved in the maintenance of phenotypic variation within a population is a central aim in evolutionary biology. Heterogeneous selective pressures associated with temporally variable environments are recognized as one of the mechanisms involved in the maintenance of inter-individual variation because they usually select for different optimal trait values over time (Brodie *et al.*, 1995; Bell, 2010). A classical example of temporal fluctuating selection resulting in the maintenance of variable phenotypes in the wild is that acting on Darwin finches (*Geospiza* sp.) where optimal beak size depends on seed size, which is itself affected by the highly variable precipitation regime in the Galapagos (Grant & Grant, 2002). In addition to fluctuating selection, nonlinear disruptive selection can also maintain variation within population by simultaneously favouring two distinct phenotypic optima (Smith, 1993; Brodie *et al.*, 1995; Rueffler *et al.*, 2006; Hendry *et al.*, 2009). For example, Calsbeek & Smith (2008) reported divergent viability selection on male limb length of *Anolis* lizards associated with perch size. However, empirical evidence of divergent viability selection remains rare in nature (Hoekstra *et al.*, 2001; Kingsolver *et al.*, 2001), in part because episodes of strong directional or stabilizing selective pressures associated with shifts in environmental conditions may overwhelm disruptive selection (Kingsolver & Diamond, 2011). In the same *Anolis*

Correspondence: Patrick Bergeron, Life Sciences Center, Dartmouth College, Hanover, NH 03755 USA. Tel.: +1 603 646 9916;
e-mail: patrick.bergeron@dartmouth.edu

lizards, Calsbeek *et al.* (2009) found directional selection on limb size during a year characterized by an unusual drought event. Together, these results highlight the importance of long-term studies in understanding the dynamics of phenotypic selection and the maintenance of individual variation in the wild (Siepielski *et al.*, 2009; Bell, 2010).

Consistent behavioural differences over time and across situations, hereafter called personality, are increasingly cited as examples of individual variation observed within populations (Wilson, 1998; Sih *et al.*, 2004; Réale *et al.*, 2007). Several personality traits are known to have a genetic basis (Dingemanse *et al.*, 2002; reviewed in Taylor *et al.*, 2012) and there is increasing evidence that they affect reproductive success and survival (reviewed in Dingemanse & Réale, 2005; Réale *et al.*, 2007; Smith & Blumstein, 2008). Personalities are thought to have coevolved as a suite of adapted behaviours (behavioural syndrome: Sih *et al.*, 2004) along with physiological traits (coping style: Koolhaas *et al.*, 1999; Careau *et al.*, 2008) and life-history traits (pace-of-life: Stamps, 2007; Wolf *et al.*, 2007; Biro & Stamps, 2008; Réale *et al.*, 2010). For example, proactive individuals are usually more active, aggressive, bold and explorative, are expected to have a higher metabolism, but to reproduce and die at younger age than reactive individuals. Personality may thus be a key individual characteristic that can be shaped by selection.

A central component of environmental variation relates to fluctuation in food abundance (Yang *et al.*, 2008). One could expect heterogeneous selective pressures to target different animal personalities adapted to environments with different levels of food availability. Yet, there is only limited evidence from wild populations relating shifts in selective pressures and personality to variable food abundance. For example, Dingemanse *et al.* (2004) found that the strength of viability selection on adult exploration score in great tits (*Parus major*) fluctuated in opposite direction among years in a sex-specific manner, following variations in environmental conditions (masting of beeches). Females with higher exploration scores survived better in years of low food abundance and the pattern was opposite for males. They suggested that variation in population density associated with food abundance may have affected the competitive regime of birds and led to variation in selective pressures. Heterogeneous selection on exploratory behaviour has been found to be related to habitat quality in a different population of the same species (Quinn *et al.*, 2009). In red squirrels (*Tamiasciurus hudsonicus*), Boon *et al.* (2007) reported that more active females had faster growing offspring in years of high food abundance (masting of spruces) and slow-growing offspring in years of low food abundance. However, whether personality traits can be under disruptive selection within the same year or sex remains mostly unknown.

In this 5-year study, we investigated the dynamics of viability selection on a personality trait, exploration, in a population of eastern chipmunks (*Tamias striatus*), a forest dwelling sciurid that lives in a highly variable environment, dominated by masting beech trees (*Fagus grandifolia*), characterized by seasons of very high and low food abundance (Bergeron *et al.*, 2011a). We measured chipmunk exploratory behaviour in a novel environment, the open field, in trials conducted within a wild population (Martin & Réale, 2008; Montiglio *et al.*, 2010). Montiglio *et al.* (2012) have previously shown that these exploration patterns were consistent across time in our study population and were correlated with docility (measured during handling by humans) and with short-term trappability in the field, although all adults in this population have an equal chance of being caught at least once during a given season (Bergeron *et al.*, 2011a). We therefore used capture-mark-recapture analyses to estimate adult survival with respect to exploration and its potential interactions with year and food abundance while controlling for variable recapture rates (Gimenez *et al.*, 2008). We hypothesized that fluctuating selection should favour different personality during seasons of high or low food abundance, based on the assumption that high food abundance promotes competitiveness, while low food abundance promotes inactivity and self-maintenance. Therefore, following Dingemanse *et al.* (2004) and Boon *et al.* (2007), we predicted that highly explorative individuals would have a selective advantage over less explorative individuals during masting periods and that this pattern would be reversed during periods of low food abundance. We tested this hypothesis using analyses of linear and nonlinear viability selection acting on exploratory behaviour in this population. We also performed viability selection analyses on juveniles with respect to their exploration score and seasons.

Materials and methods

We monitored an eastern chipmunk population from 2006 to 2010 on a 25 ha study site located in a deciduous forest of southern Québec, Canada (45°05′ N, 72°26′ W). The entire study area was marked with numbered stakes at 20 m intervals. We designated a fixed trapping grid inside a 250 m radius circle and used every second grid stake as a permanent trap location for a total of 228 locations (Bergeron *et al.*, 2011a). We trapped chipmunks, using Longworth traps checked at intervals of 2 h, daily from 08:00 hours until dusk during their active period, every week from the end of April to October. At each capture, we weighed all individuals to the nearest 1 g using a Pesola balance. Every new animal was aged, sexed and uniquely marked with ear tags and a Trovan® PIT tag. Juveniles were differentiated from adults based on either their mass at emergence (juveniles < 80 g) or the absence of darkened scrotum or developed mammae for individuals > 80 g (as in Careau *et al.*, 2010).

Chipmunks are food hoarders that consume hoarded food during winter hibernation when they remain underground in their burrows. They can reproduce during two distinct reproductive seasons: in spring, summer or both (Bergeron *et al.*, 2011b). Spring mating occurs in March and juveniles emerge from their maternal burrow in May. Summer mating occurs in June and juveniles emerge in August. Juveniles first captured before 1 August were assigned to spring reproduction, whereas juveniles first captured after 1 August were assigned to summer reproduction (Bergeron *et al.*, 2011a). Both juveniles born from spring and summer reproductive seasons were classified as adults the following spring. We previously documented a strong link between the occurrence of chipmunk reproduction and masting patterns in beech trees, the main source of storable food items for chipmunks on our study site (Bergeron *et al.*, 2011a). We monitored beech seed production in autumn using 30 plastic buckets placed under the canopy of 30 beech trees evenly distributed on the grid (Landry-Cuerrier *et al.*, 2008; Munro *et al.*, 2008). During our study, beech mast occurred approximately on a 2-year cycle (gram of seeds/m^2: 2006, 8.2; 2007, 0.0; 2008, 5.1; 2009, 0.15; see Bergeron *et al.*, 2011a for details). Chipmunk summer reproduction (2006, 2008 and 2009) occurred during summers preceding a beech seed mast (although very small in 2009) while spring reproduction (2007 and 2009) occurred in springs following a mast. In summers preceding and springs following no seed production, chipmunks had no reproduction (Bergeron *et al.*, 2011a).

We measured the exploration/activity behaviour of chipmunks from open-field (OF) tests performed on the study site each year between May and October (see Montiglio *et al.*, 2010 for details). The OF is a white rectangular plastic box with a transparent Plexiglas lid. Two OF sizes were used during this study (small: 80 × 40 × 40 cm, large: 80 × 80 × 40, Montiglio *et al.*, 2012). Chipmunks were introduced into this novel environment and recorded during 90 s from above with a video camera mounted on a tripod. The observer remained silent and was not visible during the test. The videos were then analysed using a video editing program to super-impose a digital grid on the footage. We quantified chipmunk exploration/activity level as the number of times a chipmunk crossed lines during the 90 s trial which has previously been shown to be significantly repeatable at 32% in our study population (Montiglio *et al.*, 2010, 2012). Our OF test does not allow to separate activity from exploration. For simplicity, we will refer here to exploration behaviour instead of exploration/activity behaviour. Individual chipmunks vary along a slow-fast exploration gradient: during a novel environment test, slow/thorough explorers generally freeze or show very low level of exploration, but increase exploration level over time, whereas fast/superficial explorers explore actively the novel environment in first instance, after which they rapidly reduce their movement over time (Montiglio *et al.*, 2010). Nevertheless, exploration recorded during the first 30 s of the trial is correlated with the exploration measured during the overall 90 s trial (Montiglio *et al.*, 2012). Line crosses varied between 1 and 466 (mean = 73) during the 90 s trial.

We followed 98 adults (41 males, 57 females) for which OF trials were completed, captured from 2006 to 2010 representing, respectively, 6, 17, 23, 65 and 42 individuals followed each year. We measured on average 1.47 OF per adult. We also followed 175 juveniles (91 males, 84 females): 11 from the cohort of summer 2006, 45 from spring 2007, 92 from summer 2008 and 27 from spring 2009.

Statistical analyses

We analysed juvenile and adult survival separately. To avoid selective disappearance effects, we only considered individuals tested in the OF arena prior to the survival analysis. For the adult survival analysis, we included measures of exploratory behaviour made on individuals before their first spring as adults ($n = 98$). Most individuals were measured more than once in the OF before adulthood. To estimate exploration scores, we included chipmunk identity as a random term in a mixed model with the number of times chipmunks crossed lines during the OF test as the dependent variable. We included sex, cohort, year, age, date and arena size as fixed effects in the model. We predicted the exploration score of each adult chipmunk using Best Linear Unbiased Predictors (BLUP) (see also Montiglio *et al.*, 2010, 2012). To avoid spurious effects of the number of measures on BLUP, that could generate patterns resembling disruptive selection irrespective of the actual shape of selection, we considered a maximum of two OF trials per individual prior to the survival analysis and verified that there was no relationship between the number of trials (one or two) and the BLUP obtained. We justify the use of BLUP in our specific context based on the fact that hierarchical models are difficult to implement given the data available and because potential biases associated with the use of BLUP are limited.

We estimated adult survival and its relationship with exploration based on capture-recapture histories analysed with the program E-SURGE v1.8 (Choquet *et al.*, 2009) following the procedure detailed in Bergeron *et al.* (2011a). Briefly, each year we divided capture histories into two discrete seasons, early (E) and late (L), corresponding to potential juvenile emergence. The first season E spanned from spring emergence in April to May to the end of July, while the second season L started on 1 August and lasted until all chipmunks retreated in their burrow to spend the winter, by the end of October. Such a design allowed us to estimate summer (from E to L, 3 months) and winter survival (from L to E, 9 months). We accounted for the unequal time interval between seasons and report survival estimates on a 6-month basis from the E season of 2006 to the E season of 2010 (nine seasons). Following Bergeron *et al.* (2011a), we first simplified the model structure of recapture probabilities and then held the selected recapture structure constant and simplified the survival probabilities. Once the final survival structure was selected, we checked its robustness to modification in the recapture structure. We modelled recapture probabilities with respect to sex and time and also considered potential linear and quadratic effects of exploratory behaviour. Recapture rates varied across seasons, but there was no effect of exploration score or sex on the recapture rates. We then modelled survival probabilities (phi) as a function of sex (s), age (a), the seasons as either a two level discrete variables (E or L) or as a eight level discrete variables (*t*, where each season is allowed to affect survival independently) and chipmunk exploratory behaviour (linear and quadratic effects). Both additive (+) and interaction terms (×) effects were considered between variables, allowing us to specifically test the form of selection acting on exploration. An interaction between exploration and discrete seasons or *t* would indicate fluctuating selection, while an additive relationship would be indicative of directional or nonlinear viability selection. Model selection was based on the Akaike's Information Criterion corrected for small sample size (AICc), and the model with the lowest AICc value was retained for inferences (Burnham & Anderson, 2002). The adult data set respected the assumptions of the Cormack–Jolly–Seber modelling (Bergeron *et al.*, 2011a). As we studied resident adults only, we used disappearance as a reliable proxy for death of chipmunks (Bergeron *et al.*, 2011a).

We also conducted traditional viability selection analyses of exploration (Lande & Arnold, 1983). As recapture rates are very variable on a seasonal basis, relative survival was assessed on an annual basis as virtually all individuals are caught at least once per year (Bergeron *et al.*, 2011a; see results). The selection differential was obtained using a linear model that included exploration and exploration^2 as explanatory variables (second-order estimate and associated standard error were doubled – see Stinchcombe *et al.*, 2008). Statistical significance was assessed using a generalized linear model with a binomial error structure. We also investigated viability selection gradients in a multivariate analysis to account for potential correlated traits that could cause apparent selection on exploration. In addition to exploration and exploration^2, this analysis included sex, annual body mass, annual body growth and the number of parasites as explanatory variables (details on trait measurements are available in Appendix 1).

The juvenile survival analysis was based on exploration measures taken on individuals from a single OF trial performed during the season of their birth ($n = 175$). Juvenile exploratory behaviour was the standardized number of lines crossed per min after controlling for OF size. We assessed the relationship between juvenile survival to adulthood (discrete variable: 1 or 0) and exploration using a logistic regression with a binomial error structure (Lande & Arnold, 1983). There was no need to account for recapture probabilities as only two individuals that reached adulthood were first recaptured as adults later than the following spring. A quadratic exploration term was included as an explanatory variable in the model, along with sex, season and the interactions exploration × season, exploration × sex and sex × season.

All analyses other than the one performed with E-SURGE were conducted using the statistical software R 2.14.1 (www.r-project.org) and GenStat V15.1 (VSN intl.). We used AIC only in the capture-mark-recapture analyses conducted with E-SURGE. Otherwise, we performed model selection using stepwise backward procedures, sequentially removing the least significant term from the model based on its *P*-value ($\alpha = 0.05$). All means are presented ± SE.

Results

Survival was best described by a model that included a nonlinear quadratic exploration term and an additive effect of season (Table 1); individuals with either low or high exploration scores were almost twice as likely to survive over a 6-month period compared to individuals with intermediate scores (Fig. 1), independent of the season (Beta estimates (logit): exploration^2: 0.52, 95% confidence intervals (CI) = 0.14 to 0.91). Individuals with extreme level of exploration had a probability of survival higher than 90% compared to close to 40% for individuals with average levels of exploration (Fig. 1). The linear estimate of exploration was not significant as 0 was included in the 95% CI (exploration: −0.17, 95% CI = −0.55 to 0.21). Our best model provided about 25 times more support to the data (AICc weight = 0.51) than the same model without exploration behaviour (model 'season', AICc weight = 0.02, Table 1). Despite contrasted environmental contexts between summer and winter intervals and between seasons of mast and no mast years, the model that included an interaction between the season, exploration behaviour and exploration behaviour^2 did not provide more support to the data than the model that included only an additive effect of the season (Table 1). Including age, sex, season as a continuous variable (*t*) or exploration only as a linear term did not improve the fit of the model compared with our best model (Table 1). Our best model also suggests higher survival in winter (between L and E) than in

Table 1 Model selection of adult survival rates of eastern chipmunks during nine seasons between 2006 and 2010 as a function of individual exploration behaviour (linear = exp; quadratic = $\exp^2$) and seasons (survival constrained to vary according to Early or Late seasons) or time (t, survival is allowed to vary independently over time). Recapture rates account for t in all models. Only the best model along with the other models directly associated with our hypotheses testing are presented, sorted in ascending order based on their AICc values ($n = 98$ adults). No other models that included age or sex provided better support to the data than the best fitting model.

Model	Number of parameter	Deviance	AICc	Delta AICc	AICc weight
season + (exp + $\exp^2$)	12	231.617	257.131	0.00	0.51
exp + $\exp^2$	11	235.724	259.000	1.87	0.20
season × (exp + $\exp^2$)	14	230.509	260.568	3.44	0.09
season	10	242.536	263.594	6.46	0.02
t + (exp + $\exp^2$)	18	224.273	263.693	6.56	0.02
season + exp	11	242.073	265.348	8.22	0.01
exp	10	246.333	267.390	10.26	0.00
t + exp	17	233.562	270.607	13.48	0.00
season × exp	12	246.306	271.820	14.69	0.00
t × (exp + $\exp^2$)	25	215.188	271.924	14.79	0.00
t × exp	17	240.301	277.346	20.21	0.00

summer (between E and L) (Tables 1 and 2). Recapture rates were usually high but varied across seasons, especially in the late season of 2007 when no adults were caught (Table 2).

The univariate selection analysis of relative annual survival as a function of exploration behaviour also provided evidence for disruptive selection (exploration: -0.10 ± 0.09, t-value = 0.95, d.f. = 1, P-value = 0.35, exploration^2: 0.46 ± 0.14, t-value = 2.70, d.f. = 1, P-value = 0.008). In the multivariate selection analysis, beside exploration^2, no other trait was significantly affecting survival (Table S1). Also, there was no significant correlation between any of the additional traits considered and exploration^2 (all $r < 0.11$, all P-values > 0.29; see Table S2).

For juvenile survival, we found no effect of exploration score and its quadratic term on survival (exploration behaviour: χ^2-value = 0.011, d.f. = 1, P-value = 0.92; exploration behaviour^2: χ^2-value = 0.493, d.f. = 1, P-value = 0.48). Also, we found no interaction between exploration score and the season of birth on survival to adulthood (exploration behaviour × season: χ^2-value = 0.015, d.f. = 1, P-value = 0.90). Juveniles born in the E season were less likely to reach adulthood the following spring than juveniles born in the L season (season: -0.915 ± 0.353, χ^2-value = 7.121, d.f. = 1, P-value = 0.008; phi juveniles born in the E season = 0.24 ± 0.05, phi juveniles born in the L season = 0.41 ± 0.05). Males were less likely than females to be recaptured the following spring (sex: -0.811 ± 0.336, χ^2-value = 5.983, d.f. = 1, $P = 0.014$; phi males = 0.26 ± 0.05, phi females = 0.42 ± 0.05), independently of the season of birth (sex × season: χ^2-value = 0.874, d.f. = 1, $P = 0.35$).

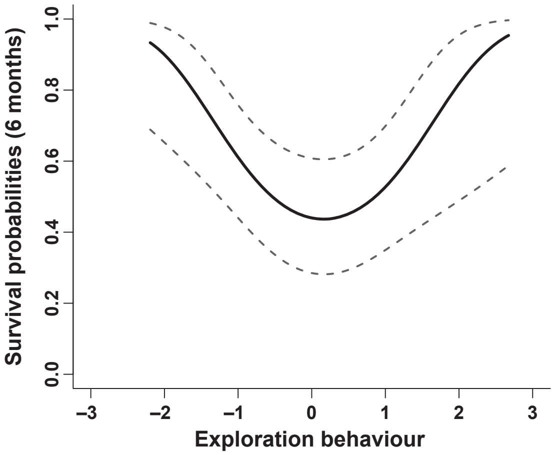

Fig. 1 Relationship between standardized exploration behaviour and 6-month survival probabilities of adult eastern chipmunks ($n = 98$). The black line represents the predicted values of the relationship between exploration and survival obtained from the best fitted model presented in Table 1 which accounts for seasonal effects. Grey lines represent the 95% confidence interval around predicted values.

Table 2 Estimates of seasonal survival (Phi) and temporal recapture (P) rates along with 95% confidence intervals (CI) obtained from the best fitting model of chipmunk survival and recapture probability (Phi(season + (exp + $\exp^2$)) $P(t)$, see Table 1). Estimates also account for linear (nonsignificant) and quadratic effects (Beta estimate (logit): 0.52, 95% CI = 0.14 to 0.91) of exploratory behaviour on survival.

Parameter	Estimate	95% CI
Survival		
Summer	0.44	0.29–0.61
Winter	0.67	0.53–0.78
Recapture		
Late 2006	1.00	0.73–1.00
Early 2007	0.67	0.06–0.98
Late 2007	0.00	0.00–0.12
Early 2008	1.00	0.73–1.00
Late 2008	1.00	0.85–1.00
Early 2009	1.00	0.85–1.00
Late 2009	0.87	0.71–0.95
Early 2010	1.00	0.80–1.00

Discussion

We investigated the dynamic of viability selection over 5 years on a personality trait, exploration behaviour, in a population of eastern chipmunks living in a highly variable environment. We found no evidence of viability selection on juvenile personality but found strong disruptive viability selection on adult exploration behaviour, independent of seasonal variations.

No evidence for fluctuating selection related to environmental variability

We expected that fluctuating viability selection would be associated with variation in beech mast production, and more specifically that these conditions would favour different levels of chipmunk exploration behaviour. The environmental conditions on our study site are characterized by substantial temporal variation in resource abundance and climatic conditions (Bergeron *et al.*, 2011a). Variation in beech production is known to have massive effects on activity patterns in our population, including extensive late autumn activity and prolific food hoarding in years of high seed production contrasted with complete cessation of above-ground activity in midsummer preceding autumns of low seed production (Munro *et al.*, 2008; Bergeron *et al.*, 2011a). Also, Montiglio *et al.* (2012), found that OF exploration behaviour on resident adults from the same study population was correlated with above-ground activity in males and with the distance at which females were caught away from their burrow. Therefore, we expected that these major differences in resource and thus exploration conditions would lead to variation in the direction, or at least in the strength, of selection on OF exploration behaviour (see also Quinn *et al.*, 2009, 2012; Boyer *et al.*, 2010; Patterson & Schulte-Hostedde, 2011). Models allowing temporal interactions with exploration did not provide the best support to the data, and therefore, we found no support for the hypothesis that fluctuating selection is associated with highly variable environment. Although we acknowledge that our relatively small sample size (and therefore reduced statistical power) may have limited the detection of weak seasonal trends, we did find strong evidence that, across all seasons, animals with either low or high OF exploration behaviour enjoyed higher survival compared with individuals with intermediate exploration behaviour, resulting in constant patterns of disruptive viability selection on this trait. This result was supported by both the capture-mark-recapture analysis and by more traditional selection analyses.

Disruptive viability selection on adult exploration

We suggest that links between personality and coping style may partly explain the disruptive viability selection observed on adult exploration (Koolhaas *et al.*, 1999; Careau *et al.*, 2008; Wolf & McNamara, 2012). For instance, selection for individuals possessing particular combinations of extreme phenotype and anti-predator behaviour has been reported in other species. In garter snakes (*Thamnophis ordinoides*), Brodie (1992) found disruptive and correlational viability selection where juveniles possessing extreme colour pattern and escape behaviours were favoured by natural selection compared with individuals possessing intermediate colour patterns and behaviour. Here, although we found that individuals with average exploration levels suffered higher mortality compared with extreme phenotypes, the proximal causes of this relationship still remains to be further investigated. We can however speculate that if predation is a major mortality factor in chipmunks, slow explorers may survive by remaining in the safety of their nest. Conversely, fast explorers may spend more time outside their burrow but also be efficient at avoiding predators by being more proactive and have a better knowledge of the habitat and the location of refugees. Such extreme adaptive requirements to survive may be detrimental for individual with intermediate exploration scores. However, a multivariate approach taking into account the causes of mortality (e.g. extrinsic or intrinsic) and other relevant traits (behavioural, physiological, life-history) in combination with exploration behaviour is required to further understand the disruptive selection associated with individual exploration level observed here.

Persistent disruptive selection is recognized as an important force involved in the maintenance of intraspecific polymorphism (e.g. Smith, 1993; Hendry *et al.*, 2009). Exploration has previously been shown to be heritable in several species including rodents (reviewed in Taylor *et al.*, 2012). We measured episodes of selection on a rather short-time scale relative to the average lifespan of chipmunks (about 2 years) and acknowledge that the genetic basis of exploration behaviour in the population may carry the signature of a much more complex selective history over longer terms (Hoekstra *et al.*, 2001; Grant & Grant, 2002; Calsbeek *et al.*, 2009). However, the fluctuations observed here are likely representative of the fluctuations observed over the longer term and at a larger geographical scale given the similar patterns of fluctuations in food abundance observed in the study system and surrounding areas. Also, we cannot exclude the possibility that exploration behaviour may be genetically negatively correlated with other fitness components (Dingemanse & Réale, 2005; Wolf *et al.*, 2007; Biro & Stamps, 2008; Réale *et al.*, 2010) such that individuals with intermediate exploration level survive less but may, for instance, reproduce more than individuals possessing extreme level of exploration behaviour. A more comprehensive study involving fertility selection on exploration behaviour could help understanding the frequency distribution of exploration behaviour observed in juveniles.

Given the pattern of disruptive selection we documented and assuming that exploration is heritable in chipmunks as it has been reported in other sciurid (Taylor *et al.*, 2012), females could thus have produced higher fitness offspring by mating assortatively based on exploration behaviour. Preliminary results on mating patterns observed on our study population however revealed no evidence of assortative mating based on exploration behaviour: the exploration level of the females was not predictive of the exploration level of their mates (based on mating events that produced at least one juvenile; Fig. 2, Pearson's correlation: $r = 0.17$, t-value = 1.43, d.f. = 71, P-value = 0.16).

No viability selection on juvenile exploration

The lack of viability selection observed on juvenile exploration behaviour was also somewhat surprising. We have previously shown that mast strongly affects population-wide juvenile survival and that juveniles born in different seasons have vastly different schedules of hoarding and reproductive opportunities (Bergeron *et al.*, 2011a). We expected that such contrasted conditions associated with the season of birth and mast production would lead to variation in viability selection on exploration behaviour. A possible explanation for this result is that the strength of selection on exploration behaviour could be marginal compared with other non-discriminating (i.e. independent of exploration level) sources of mortality in juveniles, such as the overall food abundance, parasites and climatic conditions (see for instance Careau *et al.*, 2013). Also, our measures of viability selection are based on apparent survival which could be affected by juvenile sex-dependent dispersal towards males (Chambers & Garant, 2010; Dubuc-Messier *et al.*, 2012). Lower survival in juvenile males should thus be considered cautiously. In addition, if more exploratory juvenile individuals had a greater chance of dispersing outside the study grid, it could have partly masked the heterogeneous selection pattern expected on exploration (note that analyses on adults considered only resident individuals). Nevertheless, our results are similar to those obtained on juvenile great tits where no evidence of viability selection was found on exploratory behaviour (Quinn *et al.*, 2009). Further empirical studies on juvenile personality in the wild remains relatively scarce and are needed to provide further understanding of the dynamic of age-specific selection on personality.

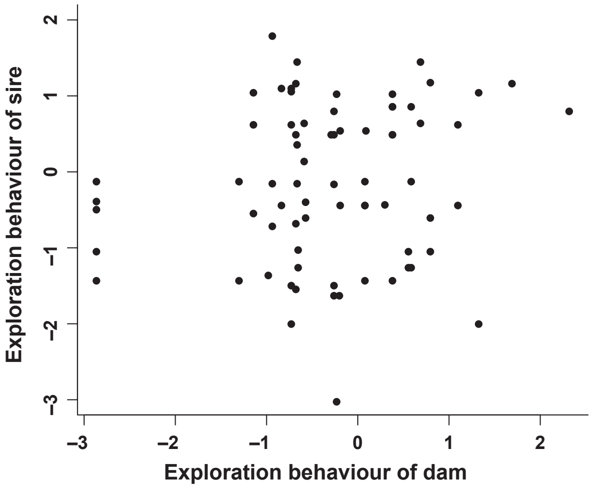

Fig. 2 Relationship between exploration behaviour of male (sire) and female (dam) mating partners that produced at least one juvenile in 2008 and 2009 (Pearson's correlation: $r = 0.17$, t-value = 1.43, d.f. = 71, P-value = 0.16).

Conclusions

Fluctuating directional selection associated with substantial temporal variation in environmental conditions is a typical observation in contemporary analyses of selection (e.g. Grant & Grant, 2002; Siepielski *et al.*, 2009; Bell, 2010; but see also Morrissey & Hadfield, 2012). It is also increasingly suggested that personality can be associated with a suite of correlated (positively or negatively) metabolic and life-history traits (Biro & Stamps, 2008; Réale *et al.*, 2010). Our results suggest that persistent disruptive selection can contribute to the maintenance of different personalities across temporally varying environmental conditions. We suggest that disruptive selection should not be overlooked in studies of selection and that understanding the proximal mechanisms underlying such selection may require a long-term multivariate approach based on multiple fitness components (i.e. viability and fertility selection measured on various phenotypic traits) on animals of various ages.

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References

Bell, G. 2010. Fluctuating selection: the perpetual renewal of adaptation in variable environments. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **365**: 87–97.

Bergeron, P., Réale, D., Humphries, M.M. & Garant, D. 2011a. Anticipation and response to fluctuating pulsed resources drive population dynamics in eastern chipmunks. *Ecology* **92**: 2027–2034.

Bergeron, P., Réale, D., Humphries, M.M. & Garant, D. 2011b. Evidence of multiple paternity and mate selection for inbreeding avoidance in wild eastern chipmunks. *J. Evol. Biol.* **24**: 1685–1694.

Biro, P.A. & Stamps, J.A. 2008. Are animal personality traits linked to life-history productivity? *Trends Ecol. Evol.* **23**: 361–368.

Boon, A.K., Réale, D. & Boutin, S. 2007. The interaction between personality, offspring fitness and food abundance in North American red squirrels. *Ecol. Lett.* **10**: 1094–1104.

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.

Brodie, E.D. III 1992. Correlational selection for color pattern and antipredator behavior in the garter snake *Thamnophis ordinoides*. *Evolution* **46**: 1284–1298.

Brodie, E.D. III, Moore, A.J. & Janzen, F. J. 1995. Visualizing and quantifying natural selection. *Trends Ecol. Evol.* **10**: 313–318.

Burnham, K.P. & Anderson, D.R. 2002. *Model Selection and Multimodel Inference: a Practical Information-Theoretical Approach*. Springer-Verlag, Berlin.

Calsbeek, R. & Smith, T.B. 2008. Experimentally replicated disruptive selection on performance traits in a Caribbean lizard. *Evolution* **62**: 478–484.

Calsbeek, R., Buermann, W. & Smith, T.B. 2009. Parallel shifts in ecology and natural selection in an island lizard. *BMC Evol. Biol.* **9**: 3.

Careau, V., Thomas, D., Humphries, M.M. & Réale, D. 2008. Energy metabolism and animal personality. *Oikos* **117**: 641–653.

Careau, V., Thomas, D.W. & Humphries, M.M. 2010. Energetic cost of bot fly parasitism in free-ranging eastern chipmunks. *Oecologia* **162**: 303–312.

Careau, V., Bergeron, P., Garant, D., Réale, D., Speakman, J.R. & Humphries, M.M. 2013. The energetic and survival costs of growth in free-ranging chipmunks. *Oecologia* **171**: 11–23.

Chambers, J.L. & Garant, D. 2010. Determinants of population genetic structure in eastern chipmunks (*Tamias striatus*): the role of landscape barriers and sex-biased dispersal. *J. Hered.* **101**: 413–422.

Choquet, R., Rouan, L. & Pradel, R. 2009. Program E-SURGE: a software application for fitting multievent models. In: Thomson, D.L., Cooch, E.G. & Conroy, M.J. (eds), pp. 845–865. *Environmental and Ecological Statistics*, Springer, New York.

Dingemanse, N.J. & Réale, D. 2005. Natural selection and animal personality. *Behaviour* **142**: 1159–1184.

Dingemanse, N.J., Both, C., Drent, P.J., Van Oers, K. & Van Noordwijk, A.J. 2002. Repeatability and heritability of exploratory behaviour in great tits from the wild. *Anim. Behav.* **64**: 929–938.

Dingemanse, N.J., Both, C., Drent, P.J. & Tinbergen, J.M. 2004. Fitness consequences of avian personalities in a fluctuating environment. *Proc. Biol. Sci.* **271**: 847–852.

Dubuc-Messier, G., Garant, D., Bergeron, P. & Réale, D. 2012. Environmental conditions affect spatial genetic structures and dispersal patterns in a solitary rodent. *Mol. Ecol.* **21**: 5363–5373.

Gimenez, O., Viallefont, A., Charmantier, A., Pradel, R., Cam, E., Brown, C. R. *et al.* 2008. The risk of flawed inference in evolutionary studies when detectability is less than one. *Am. Nat.* **172**: 441–448.

Grant, P.R. & Grant, B.R. 2002. Unpredictable evolution in a 30-year study of Darwin's finches. *Science* **296**: 707–711.

Hendry, A.P., Huber, S.K., De León, L.F., Herrel, A. & Podos, J. 2009. Disruptive selection in a bimodal population of Darwin's finches. *Proc. Biol. Sci.* **276**: 753–759.

Hoekstra, H.E., Hoekstra, J.M., Berrigan, D., Vignieri, S.N., Hoang, A., Hill, C.E. *et al.* 2001. Strength and tempo of directional selection in the wild. *Proc. Nat. Acad. Sci. USA* **98**: 9157–9160.

Kingsolver, J.G. & Diamond, S.E. 2011. Phenotypic selection in natural populations: what limits directional selection? *Am. Nat.* **177**: 346–357.

Kingsolver, J.G., Hoekstra, H.E., Hoekstra, J.M., Berrigan, D., Vignieri, S.N., Hill, C. *et al.* 2001. The strength of phenotypic selection in natural populations. *Am. Nat.* **157**: 245–261.

Koolhaas, J.M., Korte, S.M., De Boer, S.F., Van Der Vegt, B.J., Van Reenen, C.G., Hopster, H. *et al.* 1999. Coping styles in animals: current status in behavior and stress- physiology. *Neurosci. Biobehav. Rev.* **23**: 925–935.

Lande, R. & Arnold, S. J. 1983. The measurement of selection on correlated characters. *Evolution* **37**: 1210–1226.

Landry-Cuerrier, M., Munro, D., Thomas, D.W. & Humphries, M.M. 2008. Climate and resource determinants of fundamental and realized metabolic niches of hibernating chipmunks. *Ecology* **89**: 3306–3316.

Martin, J.G.A. & Réale, D. 2008. Temperament, risk assessment and habituation to novelty in eastern chipmunks, *Tamias striatus*. *Anim. Behav.* **75**: 309–318.

Montiglio, P.-O., Garant, D., Thomas, D.W. & Réale, D. 2010. Individual variation in temporal activity patterns in open-field tests. *Anim. Behav.* **80**: 905–912.

Montiglio, P.-O., Garant, D., Pelletier, F. & Réale, D. 2012. Personality differences are related to long-term reactivity in a population of wild eastern chipmunks, *Tamias striatus*. *Anim. Behav.* **84**: 1071–1079.

Morrissey, M.B. & Hadfield, J.D. 2012. Directional selection in temporally replicated studies is remarkably consistent. *Evolution* **66**: 435–442.

Munro, D., Thomas, D.W. & Humphries, M.M. 2008. Extreme suppression of aboveground activity by a food-storing hibernator, the eastern chipmunk (*Tamias striatus*). *Can. J. Zool.* **86**: 364–370.

Patterson, L.D. & Schulte-Hostedde, A.I. 2011. Behavioural correlates of parasitism and reproductive success in male eastern chipmunks, *Tamias striatus*. *Anim. Behav.* **81**: 1129–1137.

Quinn, J.L., Patrick, S., Bouwhuis, S., Wilkin, T. & Sheldon, B. 2009. Heterogeneous selection on a heritable temperament trait in a variable environment. *J. Anim. Ecol.* **78**: 1203–1215.

Quinn, J.L., Cole, E.F., Bates, J., Payne, R.W. & Cresswell, W. 2012. Personality predicts individual responsiveness to the risks of starvation and predation. *Proc. Biol. Sci.* **279**: 1919–1926.

Réale, D., Reader, S.M., Sol, D., McDougall, P.T. & Dingemanse, N.J. 2007. Integrating animal temperament within ecology and evolution. *Biol. Rev.* **82**: 291–318.

Réale, D., Garant, D., Humphries, M.M., Bergeron, P., Careau, V. & Montiglio, P.O. 2010. Personality and the emergence of the pace-of-life syndrome concept at the population level. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **365**: 4051–4063.

Rueffler, C., Van Dooren, T.J.M., Leimar, O. & Abrams, P.A. 2006. Disruptive selection and then what? *Trends Ecol. Evol.* **21**: 238–245.

Siepielski, A.M., Dibattista, J.D. & Carlson, S.M. 2009. It's about time: the temporal dynamics of phenotypic selection in the wild. *Ecol. Lett.* **12**: 1261–1276.

Sih, A., Bell, A. & Johnson, J.C. 2004. Behavioral syndromes: an ecological and evolutionary overview. *Trends Ecol. Evol.* **19**: 372–378.

Smith, T.B. 1993. Disruptive selection and the genetic basis of bill size polymorphism in the African finch *Pyrenestes*. *Nature* **363**: 618–620.

Smith, B.R. & Blumstein, D.T. 2008. Fitness consequences of personality: a meta-analysis. *Behav. Ecol.* **19**: 448–455.

Stamps, J.A. 2007. Growth-mortality tradeoffs and 'personality traits' in animals. *Ecol. Lett.* **10**: 355–363.

Stinchcombe, J.R., Agrawal, A.F., Hohenlohe, P.A., Arnold, S.J. & Blows, M.W. 2008. Estimating nonlinear selection gradients using quadratic regression coefficients: double or nothing? *Evolution* **62**: 2435–2440.

Taylor, R.W., Boon, A.K., Dantzer, B., Réale, D., Humphries, M.M., Boutin, S. *et al.* 2012. Low heritabilities, but genetic and maternal correlations between red squirrel behaviours. *J. Evol. Biol.* **25**: 614–624.

Wilson, D.S. 1998. Adaptive individual differences within single populations. *Philos. Trans. R. Soc. Lond. B Biol. Sci*. **353**: 199–205.

Wolf, M. & McNamara, J.M. 2012. On the evolution of personalities via frequency-dependent selection. *Am. Nat.* **179**: 679–692.

Wolf, M., Van Doorn, G.S., Leimar, O. & Weissing, F.J. 2007. Life-history trade-offs favour the evolution of animal personalities. *Nature* **447**: 581–584.

Yang, L.H., Bastow, J.L., Spence, K.O. & Wright, A.N. 2008. What can we learn from resource pulses? *Ecology* **89**: 621–634.

Appendix 1: Phenotypic measurements

We measured adult body mass to the nearest gram at each capture using a 300 g Pesola scale. We adjusted the mass of each individual, each year to 31 July, using a linear mixed-effect model with individual identity fitted as a random term. We estimated annual body growth as the individual slope of body mass over time extracted from the mixed model. Female body measurements taken during gestation were not included in the analysis. The number of parasites is the highest number of subcutaneous third instars bot fly (*Cuterebra emasculator*) larvae and scars observed during a season. These brown mature larvae can measure up to 25 mm and conspicuous scars remain for several days once they have left the animal.

Supporting information

Additional Supporting Information may be found in the online version of this article:

Table S1 Results of multivariate viability selection analysis conducted on eastern chipmunk traits. The statistical significance of each term was assessed using a generalized linear model with a binomial error structure.

Table S2 Correlation matrix between the phenotypic traits included in the multivariate viability selection analysis. Significance of each correlation (*P*-value) is shown in parentheses.

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