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Published in:
 Ecology Letters

DOI:
[10.1111/ele.12584](https://doi.org/10.1111/ele.12584)

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Document Version
 Publisher's PDF, also known as Version of record

Publication date:
 2016

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):

Nicolaus, M., Tinbergen, J. M., Ubels, R., Both, C., & Dingemanse, N. J. (2016). Density fluctuations represent a key process maintaining personality variation in a wild passerine bird. *Ecology Letters*, 19(4), 478-486. <https://doi.org/10.1111/ele.12584>

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LETTER

Density fluctuations represent a key process maintaining personality variation in a wild passerine bird

Marion Nicolaus,^{1,2*} Joost M. Tinbergen,² Richard Ubels,² Christiaan Both² and Niels J. Dingemanse^{1,3}

Abstract

Heritable personality variation is subject to fluctuating selection in many animal taxa; a major unresolved question is why this is the case. A parsimonious explanation must involve a general ecological process: a likely candidate is the omnipresent spatiotemporal variation in conspecific density. We tested whether spatiotemporal variation in density within and among nest box plots of great tits (*Parus major*) predicted variation in selection acting on exploratory behaviour ($n = 48$ episodes of selection). We found viability selection favouring faster explorers under lower densities but slower explorers under higher densities. Temporal variation in local density represented the primary factor explaining personality-related variation in viability selection. Importantly, birds did not anticipate changes in selection by means of adaptive density-dependent plasticity. This study thereby provides an unprecedented example of the key importance of the interplay between fluctuating selection and lack of adaptive behavioural plasticity in maintaining animal personality variation in the wild.

Keywords

competition, coping styles, density-dependent selection, fluctuating selection, great tit, *Parus major*, personality, selection gradient, temperament.

Ecology Letters (2016) 19: 478–486

INTRODUCTION

The existence of repeatable individual differences in behaviour (so-called ‘animal personality’) implies that individual animals express limited plasticity (Sih *et al.* 2004). This phenomenon is fascinating because it raises the question of why different behavioural types coexist within the same population (Réale *et al.* 2007). Personality variation is heritable (Dochtermann *et al.* 2015), affects fitness (Dingemanse & Réale 2005; Smith & Blumstein 2008), and is subject to fluctuating selection in a wide diversity of taxa (Dingemanse & Réale 2013). However, we lack understanding of why these fluctuating selection pressures characterize so many animal populations, and what general ecological processes explain the maintenance of personality variation in nature.

Negative density-dependence is a general ecological process, reducing fitness when competition rises (Begon *et al.* 1990). Individual phenotypes are differentially affected by competition. Therefore, density-dependent selection is commonly evoked as an adaptive explanation for the maintenance of individual variation in reproductive tactics (Kokko & Rankin 2006) or morphology (Sinervo *et al.* 2000). Despite the general appreciation of density-dependent processes, density-dependence has rarely been investigated in the context of personality (Cote *et al.* 2008; Quinn *et al.* 2009; Le Gaillard *et al.* 2015). This is surprising because behavioural types differ in

their ability to cope with both the causes (e.g., changes in food distributions) and consequences of density fluctuations (e.g., changes in amount of intraspecific competition). For example, in our study species (the great tit *Parus major*), availability of beech (*Fagus sylvatica*) crop increases overwinter survival (Perdeck *et al.* 2000) which in turn leads to intensified competition for breeding space in spring (Both & Visser 2000), while behavioural types in this species differ in both foraging and competitive abilities (Verbeek *et al.* 1999; Dingemanse & de Goede 2004; van Overveld & Matthysen 2013). Their relative performance should thus logically covary with conspecific density (Both *et al.* 2005; Dingemanse *et al.* 2004). Given the ubiquitous nature of density fluctuations within and among populations (Begon *et al.* 1990), we propose that variation in density can maintain variation in personality in natural animal populations.

This study aims to test whether heterogeneous selection on personality in great tits (Dingemanse *et al.* 2004; Quinn *et al.* 2009) is related to density fluctuations. We focused on exploratory behaviour, a trait that is repeatable and heritable in West-European great tit populations (Dingemanse *et al.* 2002, 2012; Korsten *et al.* 2013; Nicolaus *et al.* 2012b; Quinn *et al.* 2009). In this species, relatively explorative individuals are also relatively likely to take risks (van Oers *et al.* 2004), and obtain higher social dominance ranks among territorial adults in the wild (Dingemanse & de Goede 2004); explorative

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tendency covaries positively with the ability to secure resources under competition (Cole & Quinn 2012). This notion leads us to predict that the net benefits of investment in competitive ability should be higher in competitive environments, such as under high densities. When competition is relaxed, net benefits may instead decrease because risky behaviours, including exploratory tendency, may be inherently more costly to maintain (e.g. because they require more energy; Mathot *et al.* 2015). We thus predict that fast-exploring breeders should enjoy higher fitness under relatively high densities and slow-exploring breeders under relatively low densities ('*competitive advantage*' hypothesis, Fig. 1Aa–c).

Interestingly, stress physiology research gives rise to the opposite prediction that relatively faster exploring individuals are negatively affected by population density. Studies conducted in the laboratory have shown that personality types differ fundamentally in environmental sensitivity, with fast-exploring great tits being less able to track environmental changes (Verbeek *et al.* 1994) and being more negatively affected by social defeat than slow-exploring great tits (Carere *et al.* 2001; Verbeek *et al.* 1999). These findings may explain why, in the wild, non-territorial fast explorers have lower dominance ranks (Dingemans & de Goede 2004) and longer natal dispersal distances (e.g. Korsten *et al.* 2013). Fast-exploring, aggressive phenotypes should thus be generally less able to anticipate and buffer changes in their social environment compared to slow-exploring, non-aggressive phenotypes (Duckworth 2012). Recent field experiments, further-

more, show that fast-exploring great tits are indeed less sensitive to environmental change (Stuber *et al.* 2013), less capable of taking optimal clutch size decisions (Nicolaus *et al.* 2015), and more willing to shift investment from the future towards current reproduction when given the opportunity (Nicolaus *et al.* 2015). This link between personalities and specific life-history strategies is consistent with the idea that fast-exploring, aggressive phenotypes, adopt 'fast' life-history strategies characterised by investment in current reproduction at the expense of self-maintenance (*pace-of-life* theory; Réale *et al.* 2010). Based on this *pace-of-life* hypothesis (Fig. 1Ab), we would thus predict that a fast *pace-of-life*, and lesser ability to buffer environmental perturbations, should result in more pronounced negative density-dependence of survival in faster (vs. slower) explorers (illustrated by the steeper relationship in fast vs. slow explorers in Fig. 1Ab): net benefits of fast exploration should be higher under low densities because it confers an advantage but lower under high densities due to high costs of social defeat. The predicted shorter lifespan of fast explorers (Réale *et al.* 2010; Smith & Blumstein 2008) would thus result from fast explorers suffering a larger variance in survival when faced with density fluctuations. Overall, the *pace-of-life* hypothesis would thus predict survival selection to favour fast explorers under low density and slow explorers under high densities when analysing selection gradients as a function of density (Fig. 1Ad), whereas the *competitive advantage* hypothesis would predict the opposite pattern (Fig. 1Ac).

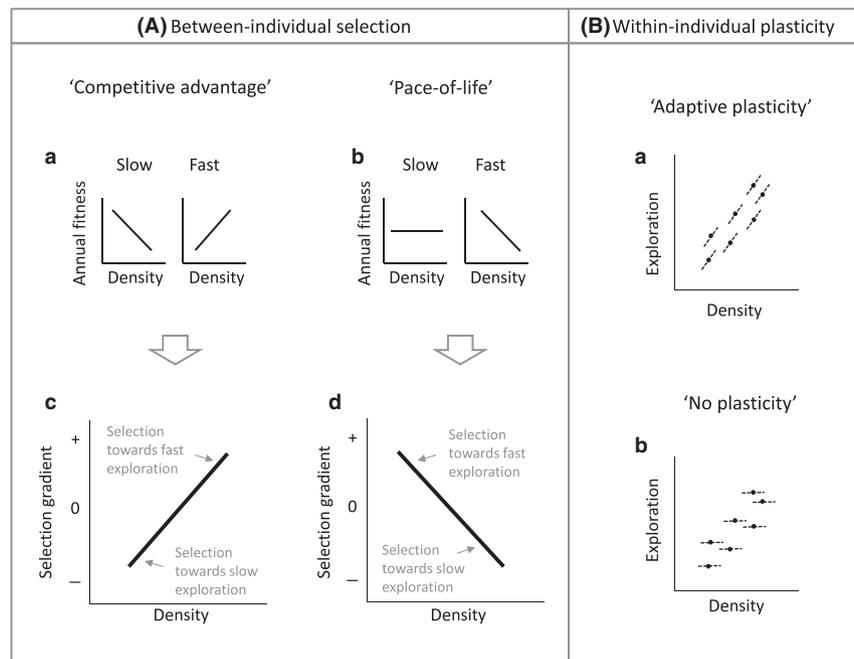


Figure 1 Predictions for between-individual selection (A) and within-individual plasticity (B). A) Under the '*competitive advantage*' hypothesis, fast-exploring individuals are expected to survive better in more competitive conditions than slow-exploring individuals (a). Increasing densities thus select for a higher speed of exploration (c). Under the '*pace-of-life*' hypothesis, slow-exploring (not fast-exploring) individuals are able to buffer environmental changes. Consequently, density fluctuations cause a larger variance in adult survival in fast explorers (b). In this case, increasing densities select for lower speed of exploration (d). B) If the between-individual patterns of selection are underpinned by adaptive plasticity (here illustrated for the hypothesised positive density-dependent selection gradients), individuals should adjust speed of exploration with density (a). If individuals lack behavioural plasticity, within-individual changes in exploratory behaviour are not expected (b). Individuals are represented by black dots and within-individual changes by dotted lines.

The existence of personality implies limits to – rather than lack of – within-individual plasticity (e.g., Sih *et al.* 2004), implying that there is scope for the presence of both personality and adaptive density-dependent plasticity in the same behaviour. We therefore further investigated whether individuals adjusted their exploratory behaviour to changes in annual densities. In great tits, various behavioural traits are known to show adaptive year-to-year density-dependent plasticity (e.g., Both 1998), suggesting that these birds are able to anticipate future breeding densities. Since exploratory behaviour in this study is measured in winter, this behaviour should only respond to density changes if cues indicative of density in winter predict breeding densities in the following breeding season (e.g. birds may respond to direct cues such as changes in encounter rates with conspecifics or indirect cues such as changes in food abundance). If such cues indicate that densities have changed, we expect individual birds to either increase or decrease their level of exploration as appropriate (i.e., adaptive within-individual plasticity, Fig. 1Ba). If, by contrast, individuals fail to express adaptive within-individual plasticity in response to changes in density (Fig. 1Bb), selection might instead favour the coexistence of a mix of personality types that all make the best of a bad job (Sih *et al.* 2004). In other words, the question of whether or not selection should favour the coexistence of personality types can be addressed by analysing both selection acting on individual phenotypes and patterns of within-individual plasticity within the same empirical study (Fig. 1).

MATERIAL AND METHODS

Study site

The study was carried out in a nest-box population of great tits in a fragmented forest in the Lauwersmeer (the Netherlands, 53°23' N, 6°14' E). The study site consisted of 12 woodlots ('plots') with a mean surface area of 10.39 Ha (± 1.39 SD) each fitted with 50 nest boxes placed in a regular grid. Plots were separated by open grassland; the minimal distance between plot edges ranged between 0.3 and 6.0 km (Nicolaus *et al.* 2009).

Data collection

We collected fitness and behavioural data for 4 years (2006–2009), using standard methods (Nicolaus *et al.* 2009). We quantified two main components of adult fitness: adult local survival probability (probability to breed in the study area in the following year) and annual number of recruits (number of offspring produced in a focal year that were found breeding in the study area in the following year). As each adult contributes only half of its genes to each offspring, annual adult fitness represents the sum of adult survival probability plus half the number of annual number of recruits (Charnov & Krebs 1974). We have previously shown that our plots do not differ in the number of recruits, that adult breeding dispersal is very limited (mean distance = 163 m), and that adult recapture probability is very high (0.90), implying that adult survival probability can be estimated without bias (Nicolaus *et al.* 2012a).

Outside the breeding season, individuals were caught using mist nets at feeding stations or when roosting in nest boxes (Nicolaus *et al.* 2012b). Exploratory behaviour was assayed in a 'novel environment room' in November–February following standard procedures established for this species (Dingemanse *et al.* 2012). The exploration score was calculated as the total number of flights and hops within the first 2 min after arrival in the room (Dingemanse *et al.* 2012). For details regarding housing and testing conditions, see Nicolaus *et al.* (2012b). Survival selection was measured from the breeding season following behavioural testing (year t) to the subsequent breeding season (year $t + 1$). Breeding adults were included in the analysis only if they were tested before the breeding season to prevent the results becoming biased by selective mortality occurring between testing and breeding (following Dingemanse *et al.* 2004). Most individuals were tested once, but surviving individuals were tested each year once ($n = 181$ out of 541 individuals had 2 scores or more in the selection analysis dataset). In the main analysis, we used the individual's first exploration score (i.e. its first test) as a measure for its 'personality'. We used the first score rather than a mean over all assays because long-lived individuals would inherently have more observations thus more precise behavioural scores, which could bias parameters in our survival analyses. Furthermore, analyses of means represent a form of 'statistics on statistics' known to lead to biased parameters. Finally, the usage of mean values would also come with the necessity to appropriately correct such scores for effects of test order which is not straightforward because individual great tits differ in patterns of habituation over repeated tests (Dingemanse *et al.* 2012). Reassuringly, our decision to use first scores did not bias our interpretation because first and mean scores were tightly correlated in individuals for which we had multiple behavioural scores [r (95% credible interval) = 0.79 (0.73, 0.84), $n = 181$ individuals]. As a consequence, analyses based on mean scores gave quantitatively similar results (Results not shown). Exploration score increases within individuals from autumn to spring (Dingemanse *et al.* 2012). Because not all individuals were caught in the same month (see above), first scores taken from individuals caught late in the season might be biased upwards, which could affect our survival analyses. This was not the case because analyses based on first scores corrected for test date effects (following approaches detailed in Dingemanse *et al.* 2002) yielded qualitatively similar results compared to 'uncorrected' scores (Results not shown). For simplicity, we thus used uncorrected scores in our analyses of viability selection. Our analysis focussing on within-individual plasticity in exploratory behaviour, in contrast, used all repeated measures (see below). See Table S2 for descriptive statistics of the exploration data.

Statistical analyses

Phenotypic selection analyses

Statistical analyses were performed in two steps using four years of exploration and fitness data ($n = 756$ observations of 541 individuals). First, to study whether survival selection on exploratory behaviour fluctuated between 'cohorts' (defined as the group of individuals breeding in the same plot in the same

year; $n = 4 \text{ years} \times 12 \text{ plots} = 48 \text{ cohorts}$), we analysed variation in adult survival probability, using generalised linear mixed-effects models (GLMMs) fitted with random intercepts and slopes (with respect to exploration score) at the cohort level. We used a GLMM with binomial errors and residual variance constrained to 1 (i.e. the default procedure for fitting GLMMs with binary errors; Nakagawa & Schielzeth 2010) as there was no evidence for overdispersion when it was modelled. Here, the variance in slopes represents the variance in viability selection acting on exploration score across cohorts. To test for personality-related density-dependence of survival, survival probability (measured between year t and year $t + 1$) was regressed as a function of exploration score, cohort density (local breeding density of year t) and their interaction. The exploration score followed a Gaussian distribution when square root transformed, and was further standardised within cohort (by subtracting the cohort mean from each individual's square-rooted observation and dividing it by the cohort's standard deviation). This particular within-cohort standardisation was applied because our primary aim was to compare variation in selection gradients among cohorts (Lande & Arnold 1983). Specifically, the applied within-cohort standardisation controls for any differences in scaling, and thereby allowed us to estimate how standardised selection gradients changed as a function of density. It further enabled us to formally compare patterns of density-dependent selection across spatial vs. temporal scales. Within-cohort standardisation was also warranted biologically because evolutionary processes are affected by variation in selection pressures acting on this spatiotemporal scale. Cohort density was centred on the grand mean of the whole dataset. Our results were notably not affected by decisions regarding transformation and standardisation (results based on untransformed data are given in Table S3). For example, statistical evidence for personality-related density-dependent selection reported in Table 1 was also found when exploration scores were standardised over the whole dataset (Table S3A). This implies that our findings did not hinge on how the data were standardised. Furthermore, mean exploration score over the whole cohort was not significantly correlated with cohort density (Fig. S2). Quadratic effects of exploration score were also considered in preliminary analyses but no evidence for nonlinear effects was found (Results not shown); we therefore solely present analyses of linear forms of selection (Table 1). Comparison of estimates of variance (σ^2) in random slopes (i.e. variance in selection) between models without (base model; Table 1a) vs. with the term 'cohort density \times individual exploration score' (expanded model; Table 1b) allowed us to quantify the percentage of variance in selection across cohorts due to density-dependent survival selection on personality. This percentage was quantified as $100 \times (\sigma^2_{\text{slopes in the base model}} - \sigma^2_{\text{slopes in the expanded model}}) / \sigma^2_{\text{slopes in the base model}}$.

As a second step, we formally calculated selection gradients to allow for a direct comparison of the strength of viability selection acting on exploratory behaviour across cohorts (Brodie *et al.* 1995; Lande & Arnold 1983). This was achieved by running the same models detailed above using 'relative survival' (i.e. survival probability (0/1) divided by the cohort's mean value) as the response variable (Lande & Arnold 1983)

Table 1 Personality-related density-dependent survival. Results of random regression models where variation in adult survival is regressed as a function of exploration score and cohort density either (a) without or (b) with accounting for personality-related density-dependence (i.e., by fitting individual exploration score \times cohort density as fixed effect). Estimates of fixed effects (β) and variance components (σ^2) are given with 95% credible intervals ($n = 756$ observations, 541 individuals and 48 cohorts)

Fixed effects	(a) β (95% CI)	(b) β (95% CI)
Intercept	-0.71 (-0.91, -0.50)	-0.69 (-0.90, -0.48)
Exploration score	0.05 (-0.13, 0.21)	0.06 (-0.11, 0.19)
Cohort density	0.00 (-0.31, 0.29)	0.02 (-0.31, 0.29)
Exploration \times cohort density	-	-0.35 (-0.60, -0.13)
Random effects	σ^2 (95% CI)	σ^2 (95% CI)
Cohort \times exploration score		
$\sigma^2_{\text{elevation}}$	0.18 (0.14, 0.31)	0.24 (0.15, 0.29)
σ^2_{slope}	0.019 (0.014, 0.027)	0.002 (0.001, 0.003)

instead (Fig. 4 and Table S1). Relationships between relative fitness and density can vary spatially (i.e. between-plots) and temporally (i.e. within-plots between-years). Therefore, we used centring techniques to separate within-plot from between-plot effects of density (Kreft *et al.* 1995; van de Pol & Wright 2009). For each plot, we calculated its mean density value over the four years ('mean density'; spatial component) and for each year the deviation from this plot mean ('density deviation'; temporal component) (Table S1). This centring procedure in the mixed-effects model enables the simultaneous estimation of within- and between-plot effects while avoiding problems associated with pseudo-replication (Kreft *et al.* 1995). Because studies in other populations found sex-specific patterns of selection acting on exploratory behaviour (Dingemanse *et al.* 2004; Quinn *et al.* 2009), the analyses were also rerun with data split between the sexes. These analyses yielded similar outcomes; there were no sex-specific patterns of selection (Table S4), which corroborates previous results showing that large-scale manipulations of social environments in this population did not illicit sex-specific effects on adult survival (Nicolaus *et al.* 2012a). We followed the same procedure to quantify strength of fecundity selection acting on exploratory behaviour across cohorts (see details in Table S1).

Plasticity analyses

To investigate whether individuals expressed adaptive density-dependent plasticity in exploratory behaviour, we modelled the sources of variation in square root transformed (see above) exploratory behaviour based on birds for which repeated measures of exploration behaviour were collected across years. We used a GLMM with Gaussian errors. We included three variables known to explain within-individual variation in exploratory behaviour (Dingemanse *et al.* 2012): time of year (days from July 1st, log transformed and grand mean centred), interval between tests (in days, log transformed and grand mean centred) and test sequence (1st vs. repeat test). We further fitted density as a covariate into the model. Relationships between exploration score and cohort density can exist at both the between- and within-individual

level. Therefore, we used within-individual centring to separate the within-individual effects due to phenotypic plasticity from between-individuals effects due to selective (dis)appearance (van de Pol & Wright 2009). For each individual, we calculated its mean value for cohort density ('individual mean cohort density') and for each observation of an individual the deviation from its mean (cohort density in year of observation t minus an individual's mean cohort density; 'individual cohort density deviation'). This procedure allows estimating both within- and between-level (here within- and between-individual) effects while avoiding pseudo-replication (see above). Because we were solely interested in within-individual effects, we only included the within-individual component (i.e., individual cohort density deviation) into the model. An effect of 'individual cohort density deviation' asks whether plastic adjustments in exploratory behaviour in response to changes in density from one observation (year) to the next are observed *within* the same individual. We fitted random intercepts for individual identity. In this analysis, we present results for all breeding adults including those not tested before the breeding season and those with one observation ($n = 572$ individuals and 737 observations) because doing so is known to improve the estimation of fixed-effect parameters and to increase accuracy and precision (i.e. statistical power) of random parameters (detailed in Martin *et al.* 2011). Note that because our environmental gradient was centred within individuals, excluding individuals with one observation should not affect our estimates of within-individual plasticity, which we confirmed by a rerunning the analysis after excluding individuals with a single observation; Table S5).

Model implementation

All GLMMs were constructed in R v.3.2.0, using the glmer function of the lme4 package. Estimates of fixed (β) and random effects (variance components) are given with their 95% credible intervals. We used the sim function of the arm package to simulate values of the posterior distribution of the model parameters (Gelman *et al.* 2012). 95% credible intervals (CI) around the mean (β) were extracted based on 1000 simulations (Hadfield 2010). The statistical significance of fixed effects and interactions were assessed based on these 95% CIs. We consider an effect to be significant in the frequentist's sense when the 95% CI does not overlap with 0. 95% CIs were defined as the 2.5 and 97.5% quantiles of the posterior distribution of parameter estimates.

RESULTS

Temporal and spatial variation in density

Local density varied spatially and temporally (Fig. 2): study plots were repeatable in density across years (spatial repeatability (r) adjusted for population-level year effects with 95% credible interval: $r = 0.68$ [95%CI = 0.57, 0.81]) and years were repeatable in density across plots (temporal repeatability adjusted for plot effects: $r = 0.71$ [95% CI = 0.58, 0.80]).

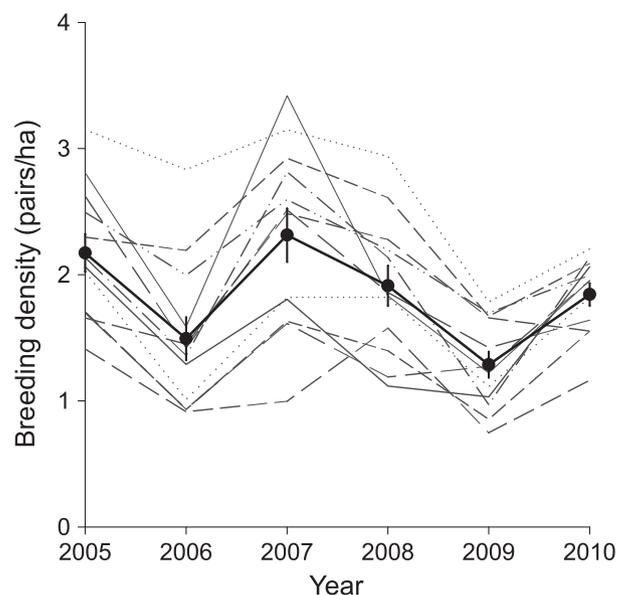


Figure 2 Cyclic variation in great tit densities. In the Lauwersmeer population, breeding densities vary significantly across study plots (each grey line is one plot) and exhibit cyclic variation across years (a high density year is usually followed by a low density year). The bold black line shows the average breeding density (\pm standard error).

Density-dependent selection on exploratory behaviour

We found substantial fluctuating selection in how exploration score affected annual adult survival in our study population (Fig. 3a), which we estimated statistically as the variance across cohorts in the effect of exploration score on survival (random slopes (σ^2_{slope}) = 0.019 in Table 1a). As predicted, spatiotemporal variation in density was an important factor explaining why survival selection on exploration score varied among cohorts. In agreement with predictions of the *pace-of-life* hypothesis (Fig. 1A), density negatively influenced the effect of exploration score on adult survival (interaction exploratory behaviour \times density (95%CI): -0.35 (-0.60 , -0.13); Table 1b): fast explorers survived better than slow explorers under low densities, but slow explorers survived better than fast explorers under high densities (Table 1b, Fig. S6), and exploration score was not under survival selection under average densities [main effect of exploration score (95%CI): 0.06 (-0.11 , 0.19); Table 1b]. (This interacting effect of exploratory behaviour and density was also found when exploration scores were standardised over the whole dataset [-0.27 (-0.54 , -0.07); Table S3], implying that our findings were not affected by data standardisation decisions]. The modifying effect of density was, notably, relatively strong (Kingsolver *et al.* 2001) as one unit increase in breeding density (pairs/ha; range 0.75–3.42) caused a shift of -0.25 (-0.41 , -0.05) units in the standardised selection gradient (Table S1, Fig. 4a). The patterns of density-dependent selection were primarily driven by within-plot year-to-year variation in density causing temporal variation in selection (interaction standardised exploratory behaviour \times within-plot deviation in density from plot-mean density (95%CI): -0.35 (-0.51 , -0.02); Fig. 4b, Table S1).

though also (somewhat) by repeatable among-plot variation in density, causing spatial variation in selection (interaction standardised exploratory behaviour \times long-term plot-mean density (95%CI): -0.23 ($-0.45, 0.08$); Fig. 4c, Table S1). Our results further revealed no personality-related density-dependent fecundity selection, i.e. the relative number of recruits did not vary as a function of cohort density, exploration score, or their interaction (Table S1).

Under the *pace-of-life* hypothesis, we had expected these patterns of negative personality-related density dependent viability selection to emerge due to stronger negative density-dependent survival in fast compared to slow explorers (Fig. 1Ab). As predicted, adult survival rates of fast explorers indeed decreased more steeply with increasing density (Fig. 3b; right panel) compared to those of intermediate phenotypes (Fig. 3b, middle panel). Against predictions, survival rates of slow explorers were as strongly affected by density as they were for fast explorers (Fig. 3b, left vs. right panel). In slow explorers, however, survival rates instead increased as a function of density. These patterns therefore confirm the over-

all predictions of the *pace-of-life* hypothesis though not the hypothesised underlying mechanism (Fig. 1Ab).

As predicted, spatiotemporal variation in breeding density appeared to represent a major causative factor as it explained a major proportion of the variation in adult survival selection: the inclusion of ‘cohort density \times individual exploration score’ reduced the random slope variance (σ^2_{slope}) from 0.019 (Table 1a) to 0.002 (Table 1b), suggesting that as much as 89.5% [i.e., $100 \times (0.019 - 0.002) / 0.019$; see Methods] of the estimated variance in survival selection on exploratory behaviour was caused by spatiotemporal variation in density. We note that our graphical illustration of the variance in selection gradients explained by density (Fig. 4a) suggests a much more modest effect partly because Fig. 4 is based on selection gradients and not on unstandardised adult survival and because variance components are notoriously difficult to estimate with precision (e.g., Dingemanse & Dochtermann 2013). Variation in standard errors of selection gradients in Fig. 4a, notably reflects variation in sample size across cohorts (i.e. more birds were caught and assayed in high-density cohorts).

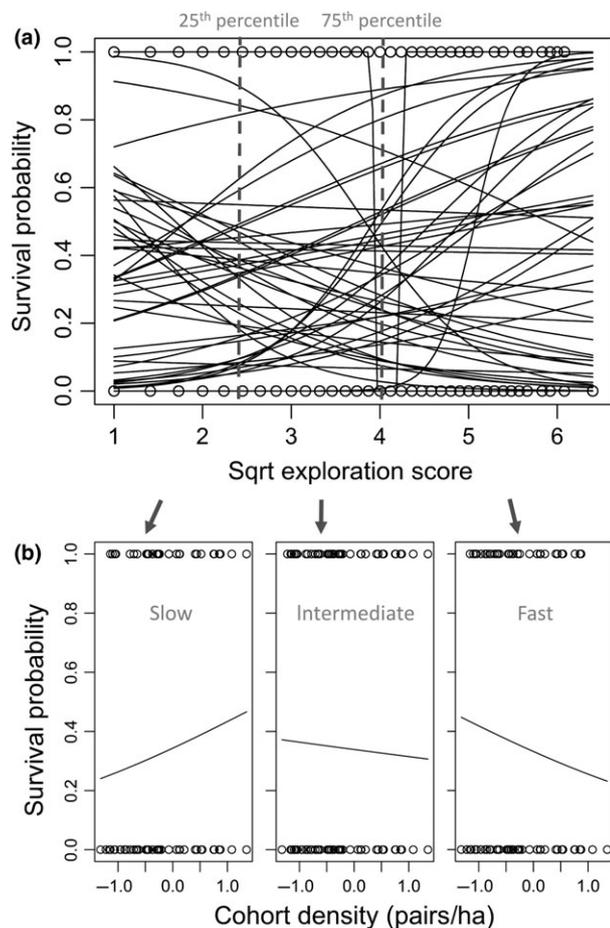


Figure 3 Personality-related density-dependent survival. In the Lauwersmeer population, variation in personality-related survival among the 48 cohorts (a) is largely explained by spatiotemporal variation in local density, with relatively slow explorers surviving better at high densities and the reverse for relatively fast explorers (b). For graphical purpose only, individuals have been grouped in three groups ‘slow’, ‘intermediate’ or ‘fast’ explorers based on the 25th and 75th percentile of the raw data.

Density-dependent plasticity of exploratory behaviour

Our repeated measures data revealed that great tits were capable of anticipating changes in density, as exploration score significantly changed with density within individuals assayed across multiple years (within-individual effect of ‘cohort density deviation’, Table 2). Interestingly, individuals failed to show adaptive phenotypic plasticity because they became more explorative with increasing cohort density (Table 2), whereas survival selection should instead have favoured them to become less explorative with increasing density (Table 1).

DISCUSSION

We investigated whether temporal and spatial variation in local densities underpinned patterns of fluctuating selection on exploratory behaviour. We detected strong density-dependent viability but no fecundity selection on personality: among the 48 episodes of selection fast explorers survived better in years with low local densities, whereas slow explorers survived relatively better in years with higher densities. Observed patterns of personality-related density-dependent survival combined with cyclic population dynamics further suggested that individuals should adaptively down-regulate their exploratory behaviour when facing density increases. However, we found no evidence for adaptive within-individual plasticity: individuals increased (instead of decreased) their speed of exploration when facing increases in density between years; this pattern is inconsistent with adaptive density-dependent plasticity (Fig. 1Ba).

Our study provides a clear example of density-dependent viability selection acting on personality variation in adults. In disagreement with the ‘*competitive advantage*’ hypothesis, high population densities (with presumably *higher* levels of intraspecific competition) selected for types thought to be *least* competitive (i.e., slow explorers) (Cole & Quinn 2012). In our population, low densities are typically followed by increased densities in the next year, implying that density in year t and

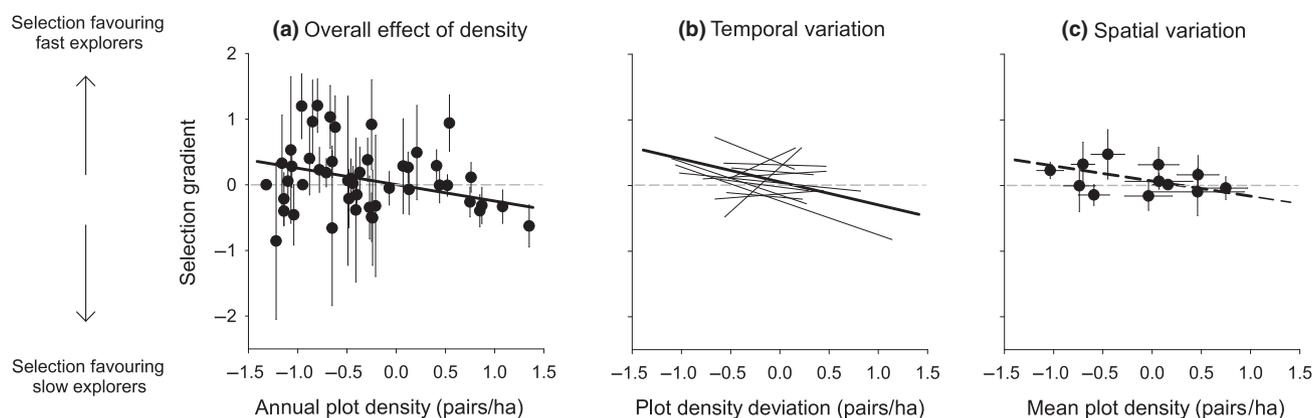


Figure 4 Density-dependent selection gradients. Selection gradients for exploration score as a function of (a) annual cohort density (each dot represents estimate for a unique combination of plot and year), (b) cohort density deviation (a year's density deviation from the mean over the 4 years for a focal plot; each line is a plot) and (c) plot mean density (mean density over the 4 years; each dot is a plot). Fast explorers survived best under low densities while slow explorers survived best under high densities. Raw data are plotted with regression lines taken from the model (bold lines). Parameters are shown with standard error (a and c). The grey dotted line represents no selection. Selection gradients were obtained by regressing an individual's relative survival probability against its within-cohort standardised exploration score (Table S1).

Table 2 Density-dependent plasticity of exploration behaviour. Results of a GLMM where exploratory behaviour (square-root transformed) is regressed as a function of time of year (days from July 1st), interval between tests (in days), test sequence and change in cohort density experienced by the individual ('individual cohort density deviation'). Estimates of fixed effects (β) and variance components (σ^2) are given with 95% credible intervals ($n = 572$ individuals and $n = 737$ observations).

Fixed effects	β (95% CI)
Intercept	3.19 (2.41, 3.78)
Time of year	0.16 (-0.06, 0.46)
Interval	-0.10 (-0.29, 0.14)
Test sequence	1.25 (0.07, 2.62)
Individual cohort density deviation	0.22 (0.00, 0.47)
Random effects	σ^2 (95% CI)
Individual	0.83 (0.77, 0.93)
Residual	0.73 (0.66, 0.78)

change in density from year t to year $t + 1$ were negatively correlated (Fig. 2). The viability selection pattern found with density in year t (Table 1) may thus have been an artefact caused by this correlation and fast explorers may instead have been selected when density (and presumably competition level) increases between years. To test this alternative explanation, we expanded our initial model (Table 1) by adding the interaction between exploratory behaviour \times the change in plot density from year t to year $t + 1$ (Table S7). This model confirmed our original analysis by providing conclusive evidence for a significant effect of density in year t (Table 1) whereas there was no effect of density change from year t to year $t + 1$; we therefore reject this explanation and the *competitive advantage* hypothesis.

Our findings support instead the overall prediction of the 'pace-of-life' hypothesis that fast exploration is detrimental at high densities (Fig. 1Ab). We originally hypothesised that density-dependence of personality originates from fast explorers being less able to anticipate and buffer changes in their

social environment (Fig. 1Ab). Our analyses show that the survival of both slow- and fast-exploring individuals was affected by density (Fig. 3). This finding implies that all phenotypes were affected by density fluctuations and that the prediction that fast explorers should live shorter (Réale *et al.* 2010) cannot be explained by a higher variance in survival. In agreement with this conclusion, lifespan was unrelated to personality in our population (Table S8). Predictions regarding the underlying mechanisms of the *pace-of-life* hypothesis are thus only partly supported: fast-exploring aggressive individuals may survive less well under high densities because of e.g. enhanced negative effects of social defeats (Carere *et al.* 2001; Verbeek *et al.* 1999) or other physiological aspects (e.g. negative effects of prolonged high testosterone levels; Dufty 1989). Given the descriptive nature of this study, manipulation of e.g. breeding density or competition level is required to shed light on the exact mechanisms underlying between-individual selection.

We detected strong density-dependent selection on personality acting via adult survival rather than offspring recruitment. This was unexpected, given that previous studies found fluctuating selection on personality acting via the number of recruits in other populations (Dingemans *et al.* 2004; Quinn *et al.* 2009). This discrepancy may be due to imprecision in our measure of recruitment caused by many locally born offspring dispersing away from this particular study area. Estimates of fecundity selection may also be inaccurate because of the known occurrence of personality-related differences in natal dispersal (e.g. Korsten *et al.* 2013). An interesting avenue for future research would therefore be to address the question of whether personality-related differences in natal dispersal also vary as a function of competitive regimes. One key question emerging from our findings is also whether personality-related density-dependent adult viability selection is sufficient to maintain genetic variation in personality in this population. The answer to this question will depend on the relative importance of adult survival vs. offspring recruitment in the genetic contribution to future generations: adult survival combined with half

the number of annual recruits should represent an adult's total annual fitness (Charnov & Krebs 1974). This simple calculation implies that patterns of personality-related density-dependent selection acting on adult survival should play a major role in maintaining variation in personality.

The existence of personality variation across many taxa suggests that species-general processes must be invoked to explain its maintenance. Because personality traits typically covary with aggression, sociality and exploration (Sih *et al.* 2004), we suggest that variation in social environments represents a prime candidate for this general process as demonstrated here. Whether the role of density-dependent selection in maintaining genetic variation in personality is more pronounced in species exposed to strong fluctuations in selection pressures acting via cyclic variation in winter food abundance (e.g. as for great tits and beech mast years (Perdeck *et al.* 2000) or North American red squirrels (*Tamiasciurus hudsonicus*) and spruce (*Picea glauca*) mast years (Taylor *et al.* 2014)) remains an interesting hypothesis to test.

Our findings also imply that density-dependent selection gradients result in the co-existence of different exploration types that perform best at different densities. The lack of (adaptive) plastic adjustment of individual behaviour to changes in social environments may explain why natural populations typically evolve multiple distinct personality types rather than one single plastic density-dependent type (Wolf & Weissing 2012). Interestingly, our findings support predictions made in psychology that in growing human populations, competitive environments should favour shy, non-explorative, non-aggressive individuals (e.g. Nettle 2005). In contrast, individuals with high levels of exploratory activity or aggression should perform relative better in declining populations (e.g. because of habitat loss). Whether this potential loss of personality variation affects the adaptive capacity of populations is currently unknown but represents an important question in both the social and natural sciences (Wolf & Weissing 2012).

ACKNOWLEDGMENTS

We thank K.M. Bouwman, T. Dijkstra, M. Keiser, K. Meijer, J. Oldenburger, R. Piault and S. van Schie for help in collecting exploration data, students of the University of Groningen for help in collecting fitness data, Staatsbosbeheer and the Royal Dutch Army 'Koninklijke Landmacht' for permission to work on their properties, and Jon Wright and Dave Westneat for discussion. Damien Farine and two anonymous reviewers provided useful feedback on earlier versions of the manuscript. M.N. and N.J.D. were supported by the Max Planck Society (MPG), and J.M.T., R.U. and C.B. by the University of Groningen. The study was supported by the Netherlands Organization for Scientific Research (NWO-ALW to C. Both) and carried out under license (DEC-4114 B) of the Animal Experimental Committee of the University of Groningen.

STATEMENT OF AUTHORSHIP

All authors have seen, and approved for submission, the current version of the manuscript and all persons entitled to

authorship have been named. M.N. and N.J.D. developed the rationale of this paper, all the authors collected the data and helped compile the database, M.N. analysed the data, and M.N., N.J.D. and C.B. prepared the manuscript with input from all authors.

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Editor, Greg Grether

Manuscript received 23 September 2015

First decision made 20 November 2015

Second decision made 5 January 2015

Manuscript accepted 14 January 2016