The maintenance of variation in avian personality

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Chapter 2

Fitness consequences
of neighbour personality

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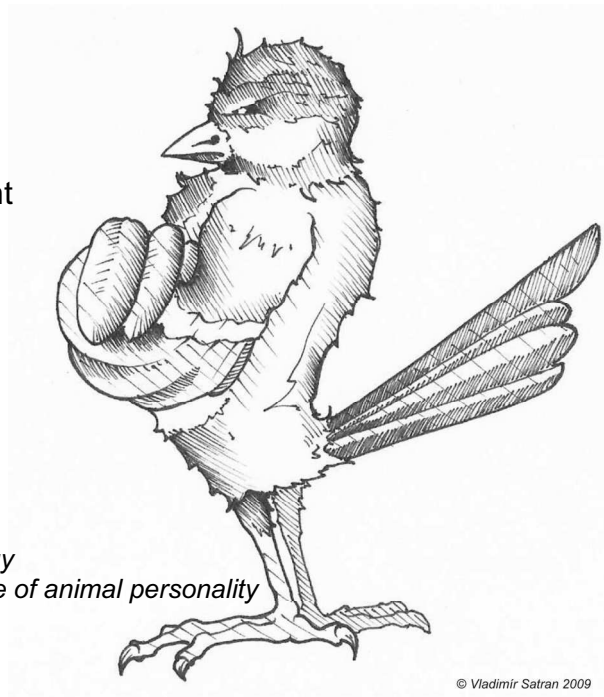
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Abstract

Apart from an individual's characteristics, also the social environment can affect its fitness, especially in socially living or territorial species. Although it has been proposed that personality included in the social environment might play an important role for fitness, it has not been tested in passerines. Here we show in a wild passerine bird that the personality of neighbours, measured through exploratory behaviour, is associated with the fitness of breeding individuals independently of their own personality. We found that neighbour personality was not associated with their survival but the reproductive success and thereby the total fitness of a breeding bird. The effect on reproductive success varied over years, but could not be assigned to yearly variables like beech-mast crop and population density. These results indicate that personality as an environmental source of phenotypic variation can be an important factor influencing individual fitness.

Introduction

Apart from an individual's own characteristics, also the social environment can be an important source of variation in fitness of many socially living organisms. Individuals must choose the best reproductive strategy on the basis of information they have about conspecifics (Lott 1984; Sutherland 1996; Fryxell & Lundberg 1998). For instance, male mites perform adult moult only in presence of receptive females (Nehring & Muller 2009), side-blotched lizards increase their clutch sizes in the presence of many neighbours (Svensson *et al.* 2001) or cotton rats accelerate or delay their sexual maturation in dependence on presence of male or female (Evans & McClure 1986). However, social environment may affect individual behaviour independent of its own traits. For example a hyper-aggressive male water strider may drive all females out of the group and decrease their mating activity independent of their behavioural type (Sih & Watters 2005). The blue-banded goby (*Lythrypnus dalli)* determine their sexual phenotype on basis of a hierarchical rule: the subordinate individuals express themselves as females and dominant individuals express themselves as males (Rodgers *et al.* 2007). Thus, intraspecific variation in the social environment is important for understanding variation in the allocation of reproductive effort and fitness differences. While many studies have shown that variation in e.g. density or position in hierarchy affect behaviour and fitness, the field of animal personality poses the hypothesis that the personality of neighbours should also affect fitness.

Animal personality is generally defined as a suite of correlated traits reflecting individual consistency in behaviour across situations and time (Reale *et al.* 2007). Variation in personality traits affects fitness (Smith & Blumstein 2008), which can be mediated by social competition (Cote *et al.* 2008). Social competition is affected by habitat heterogeneity, since this causes context dependent trait expression (van Oers *et al.* 2005a). This may result in variation in e.g. parental quality (Reale *et al.* 2007) and has possible consequences for recruitment (Dingemanse *et al.* 2003). Therefore the personality of neighbours may be very important in explaining differences in survival and reproductive success as consequence of success in competition for food and territory occupancy (e.g. (Sih & Watters 2005; Kurvers *et al.* 2009)). However, to our knowledge this has not been tested in a natural population.

In this study we investigate the impact of the behavioural phenotype of the direct neighbour (as a component of the social environment), on fitness in a wild bird population. Our study species, the great tit (*Parus major*) is territorial during the breeding season and outside this period birds develop place dependent dominance hierarchies (in relation to their former territory) in flocks consisting of adults and juveniles wandering through the territories (Drent 1984; Payevsky 2006). We therefore predict that variation in the exploratory behaviour of neighbours in the breeding season could be associated with survival and the number of recruits of breeding pairs.

Materials and methods

Breeding population assessment

We used data from seven year cycles (2000/1-2006/7; 258 breeding pairs for adult survival and 243 pairs for reproductive success) of a nest-box population in Westerheide near Arnhem, the Netherlands. From April onwards we checked nest boxes twice a week until females were incubating full clutches, and each day from the expected hatching date onwards. Nestlings were banded with an individual metal ring on day 10 after hatching. We caught parents on their nest when the juveniles were 10 days old. Nest boxes were checked again a week after the expected day of fledging to assess the exact number of fledglings. No correction has been made for capture probability of breeding birds, since it is extremely high in our population (97.5% for females and 86.3% for males, see also Both *et al.* (1999)). After the fledglings reached independence, birds were caught in mist nets and their exploratory behaviour was tested in a novel environment test.

Exploratory behaviour

Exploratory behaviour was measured the morning after catching using the novel environment test (Verbeek *et al.* 1994). Individuals were tested alone in a room (4.0×2.4×2.3 m) with five artificial trees the morning after the capture date. We used the total number of flights (movements between artificial trees) and hops (movements within trees) within the first 2 min as a measure of exploratory behaviour (Dingemanse *et al.* 2002). Faster explorers have higher scores compared to slower explorers. We corrected data for date of capture based on the finding that behaviour changes with capture date within individuals (Dingemanse *et al.* 2002). To control for year variation in exploratory behaviour, we centralized exploratory score per year by subtracting the year mean of the exploratory score from all measured exploratory scores. After all birds had been tested and weighed, they were directly released at the place of capture.

Social environment assessment

As a measure of the social environment, we used the mean exploratory behaviour of all males directly neighbouring the focal individual (neighbour exploratory behaviour). To identify which males were actual neighbours of a breeding pair, we used GIS software (ArcGIS Desktop 9.2). The GIS technique of Dirichlet tessellations assigns space to a given point that is closer to this point than to any other point (here the inhabited nest boxes) and thus fills the space with theoretical territories. We used the nest boxes in which the birds were breeding to determine territories. To verify the accuracy of the GIS territories we compared the calculated territories with actual territories obtained by noting singing activity and border conflicts of males in 2000. We compared neighbour exploratory behaviour obtained from maps estimated by GIS and from maps of actual territories, showing the comparability of these methods. There was a strong relationship between the neighbour exploratory behaviour around focal breeders in the GIS and actual territory maps (GLM, ß = 0.87, R^2 = 0.77, $F_{1,23}$ = 78.6, p<0.001), which shows the comparability of these

two methods. To explore whether this measure was associated with varying distances between the nest boxes in which these neighbours bred, we corrected the mean for the distance between the nest box of the neighbour and the focal. We subsequently ran the final model again to check whether the two-way interactions between NEB and year were affected. We found that our conclusions would not change from these analyses, but models with neighbour exploratory behaviour corrected for distance had higher AIC values, indicating a lower fit of the data points to this model (final model; year×NEB, χ^2=13.3, df =6, p=0.038; AIC=345.82; original AIC=343.82).

Statistical analyses

We used a generalized linear mixed-effects model approach (GLMM) using the software package R 2.7.2 (R Development Core Team 2007) for all statistical analyses. All tests were two-tailed.

The model of local *adult survival* contained adult survival until next year (survived or died) as the dependent variable with a binomial distribution and logit-link function. Since breeding dispersal is very low in great tits (8%) (Andreu & Barba 2006), we used adult birds in our analyses on survival and assume that adult survival in our analyses is approximately the same as the actual survival. We tested the 2-way interaction of neighbour exploratory behaviour with year, using age of breeding (1year old or older), exploratory behaviour of the territory owner, sex, local density (the deviance of the distance of the third closest nest box from the focal nest box in the given year, from the overall mean of distances of the third closest nest box in that year), nest box quality (mean fledgling weight of fledglings produced over 10 years in a nest box) as covariates. Because most of next boxes were used more years for breeding we used nest box as a random factor. We used age of breeding (1year old or older) because life history of juvenile and adult tits greatly differs (Perrins 1979). Exploratory behaviour of the territory owner and sex are important for adult survival (Dingemanse *et al.* 2004). Local density determines interactions between individuals and also survival (Tinbergen *et al.* 1985), nest box quality shows success of the territory owners in the long-time span. Female neighbour exploratory behaviour was no good predictor for survival or reproductive success (GLMM models with female neighbour exploratory behaviour, p>0.2). Thus, we concentrated on the impact of male neighbour personality. Since adult survival probability is stable over age and neighbour exploratory behaviour can change for an individual present as focal in different years, we have not included individual as a random factor in the model.

Reproductive success was defined as the number of juveniles fledged in our population and breeding there in any of the next breeding seasons during the period 2000-2007. We used the number of locally recruited juveniles a pair produced for the reproductive success, since we know that next to a high juvenile mortality (up to 70%) juveniles might also disperse over long distances where we are not able to track them. Only a dataset of pairs having fledglings (243 breeding pairs out of 258) was used for the

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analyses, because we were interested in impact of the neighbour exploratory behaviour between fledging and recruitment of the juveniles. The neighbour exploratory behaviour of the sample with fledglings did not differ from the sample without fledglings (ANOVA, $F_{1,256}$ =2.08, p=0.151). The model contained number of recruits per pair as the dependent variable with a Poisson error structure. We tested the 2-way interaction of neighbour exploratory behaviour with year, using local density, nest box quality and hatching date as covariates, and nest box as random effect. We chose these covariates because adult density affects juvenile recruitment (Both *et al.* 1999), hatching date correlates with the caterpillar peak which is important for the nestling condition (Naef-Daenzer & Keller 1999) and nest box quality shows success of the territory owners in the long-time span right on number of fledglings.

Table 1. Final model of the reproductive success - model estimates. The χ^2 and P values are calculated by comparing the final model without the factor and factor included in the model. The model contained number of recruits per pair as the dependent variable with a Poisson error structure. Estimates are given for all levels of discrete variables.

Variable	χ^2	df	p value	Level	Estimates
Year × NEB [a]	15.93	6	0.01	2000	-0.038
				2001	-0.193*
				2002	0.043*
				2003	-0.689*
				2004	-0.029*
				2005	0.070*
				2006	0.072
Density	0.73	1	0.39	-	0.003
Hatching day	4.34	1	0.04	-	-0.055
Nest box quality	3.19	1	0.07	-	0.085

* $p < 0.05$
[a] NEB – Neighbour exploratory behaviour

The *fitness* of an individual was defined as the sum of its survival until the next year (0 dead/1 alive) plus half of the number of recruits. We tested the 2-way interaction of neighbour exploratory behaviour with year, using age of breeding, sex, density, nest box quality and hatching date as covariates, and nest box as random effect with a normal error structure. Because fitness is a combination of survival and reproductive success together, we used covariates from both former models. The significance of the associations in Figure 1, 2 and 3 was calculated by regression of the fitted values against frequency.

To clarify the results of the analysis on reproductive success with our available data, we tried to explain the between year variation in the effect of neighbour exploratory

behaviour on reproductive success by environmental variables. Thus, we exchanged the variable "year" in our final models of survival and reproductive success for one of the environmental year variables: beech-mast crop (beech-mast crop was calculated following Perdeck *et al.* (2000) as the number of full nuts per m^2; using these values, years were divided in rich/poor) and breeding density (high/low).

We are aware of a potential source of bias due to spatial autocorrelation, since individuals are used as focal and as neighbours in the same analysis. However, since neighbouring individuals can interact with multiple focal individuals independently, this is a biologically valid way of analysing the data. Each neighbour can affect more focal nest boxes, contributing to the mean exploratory score around that nest box. Hence, we used the mean neighbour personality, which is a measure describing the social environment that is unique for each nest box, which are therefore independent data points. To formally test for the possible effect spatial autocorrelation we ran a Monte-Carlo simulation randomly assigning a neighbour exploratory behavioural score to a focal. By doing this for 10.000 runs, we created 10.000 datasets with randomly assigned neighbourhoods to focal animals. Our empirical correlation between focal and neighbour exploratory score (0.029) did not deviate significantly from the distribution derived from this Monte-Carlo simulation (p=0.51), indicating that our distribution of focal-neighbour pairs did not deviate from a random distribution.

Results

Reproductive success did depend on neighbour exploratory behaviour and this effect varied among years (year×NEB, χ^2=15.9, df =6, p=0.01; Table 1; Figure 1). The same pattern was reflected in fitness (year×NEB, χ^2=14.2, df=6, p=0.03; Figure 2).

Annual variation in the effect of neighbour exploratory behaviour on reproductive success and fitness could not be explained by beech-mast crop or population density (for complete results see Table 2). Only annual differences in overall survival (year, χ^2=34.1, df=6, p<0.001) and reproductive success (year, χ^2=78.1, df=6, p<0.001) independent of neighbour exploratory behaviour could be explained by the richness of the beech-mast crop (survival: χ^2=5.43, df=1, p=0.02; reproductive success: χ^2=7.7, df=1, p=0.006), which concurs with former research (van Balen 1980). The population density explained some of the variation in annual reproductive success (population density: χ^2=3.83, df=1, p=0.05).

Local adult survival, however, did not depend on neighbour exploratory behaviour (NEB, χ^2<0.001, df=1, p=0.98) and this was consistent for the seven years (year × NEB, χ^2=8.37, df=7, p=0.30; Table 3, Figure 3).

The neighbour exploratory behaviour was not correlated with the exploratory behaviour of the territory owners (r_p=-0.029, df=514, p=0.52), and this did not deviate significantly from the distribution derived from a Monte-Carlo simulation (p=0.51), which signifies a limited effect of spatial correlation due the multiple use of neighbours and focal birds.
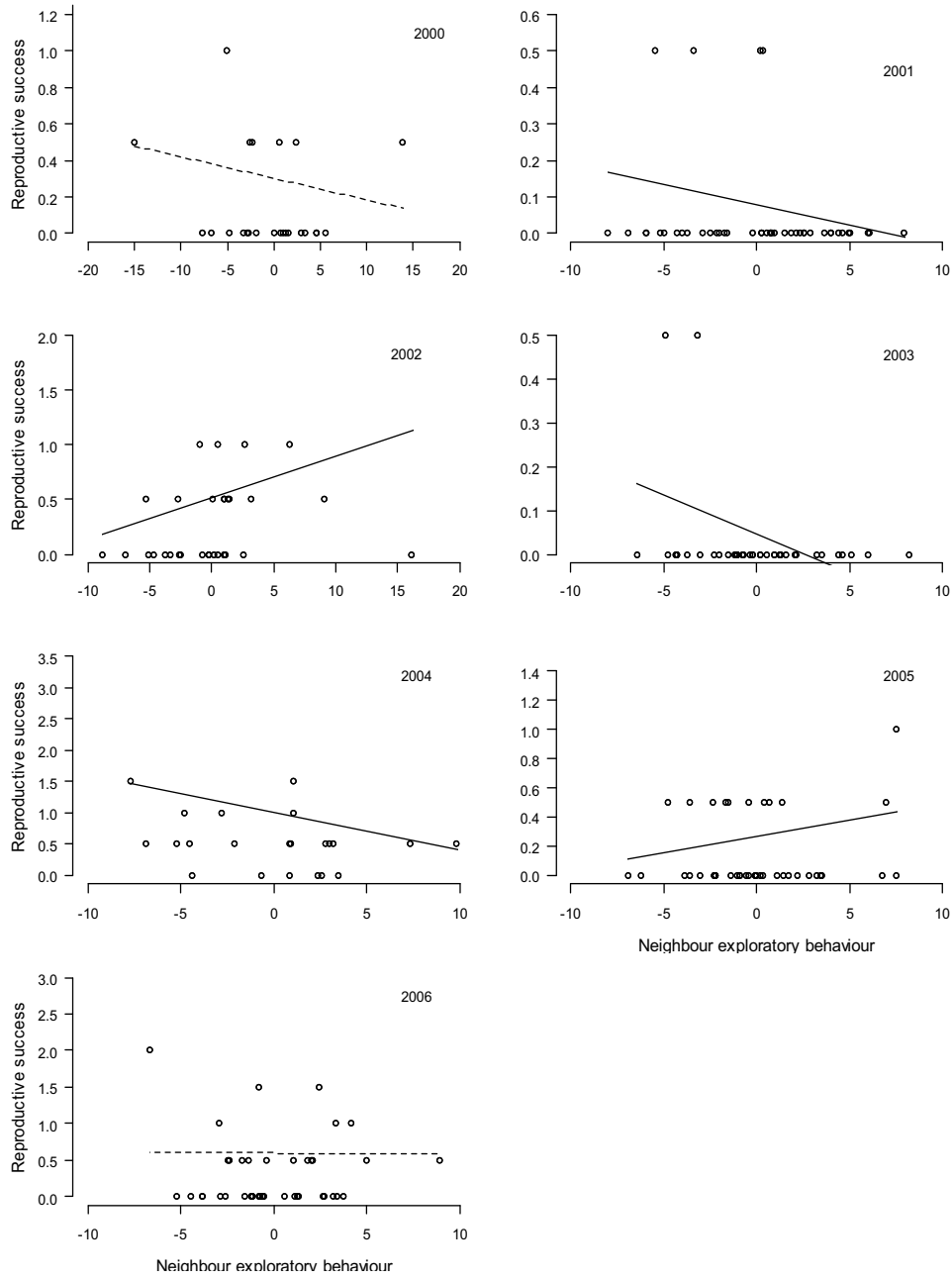
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Figure 1. The effect of neighbour exploratory behaviour on the reproductive success, plotted for the years 2000-2006 separately. Data points are raw values of reproductive success (number of recruits a pair produced). Low neighbour exploratory behaviour reflects slow environment around the focal birds, high reflects fast environment. For illustrative purposes axis lengths are adapted to the distribution of data for each year. Lines are regression lines of fitted values for reproductive success from the final model on neighbour exploratory behaviour. Solid lines indicate significant and dashed lines non-significant relationships.

Table 2. Model effects and likelihood-ratio tests resulting from models used to explain the year differences by yearly variation in beech-mast crop and population density. The χ^2 and p values are calculated by comparing the model without the factor and factor included.

Dependent variable →	Adult survival		Repr. success		Repr. success		Fitness		Fitness	
	Year		Year×NEB[a]		Year		Year×NEB		Year	
Predictor ↓	χ^2	p	χ^2	p	χ^2	p	χ^2	p	χ^2	p
BMC[b]	5.43	0.02	0.98	0.32	7.70	0.006	0.01	0.9	6.68	0.01
Population density	0.82	0.36	0.01	0.94	3.83	0.05	0.02	0.9	1.9	0.16

[a]NEB – Neighbour exploratory behaviour
[b]BMC – Beech-mast crop

Table 3. Final model of the local adult survival – model estimates. The χ^2 and p values are calculated by comparing the final model without the factor and factor included. Estimates are given for all levels of discrete variables.

Variable	χ^2	df	p	Level	Estimates
Year × NEB[a]	8.37	6	0.3	-	NA
NEB	<0.001	1	0.98	-	NA
Year	34.1	6	<0.001	2000	0.46
				2001	0.32
				2002	0.50
				2003	0.23
				2004	0.76
				2005	0.49
				2006	0.78
Age breeding	7.63	1	0.006	1 year	0.46
				Older	0.67
Sex	0.63	1	0.43	Female	0.46
				Male	0.41
Density	6.14	1	0.013	-	1.00
Nest box quality	3.9	1	0.048	-	1.00

* $p < 0.05$
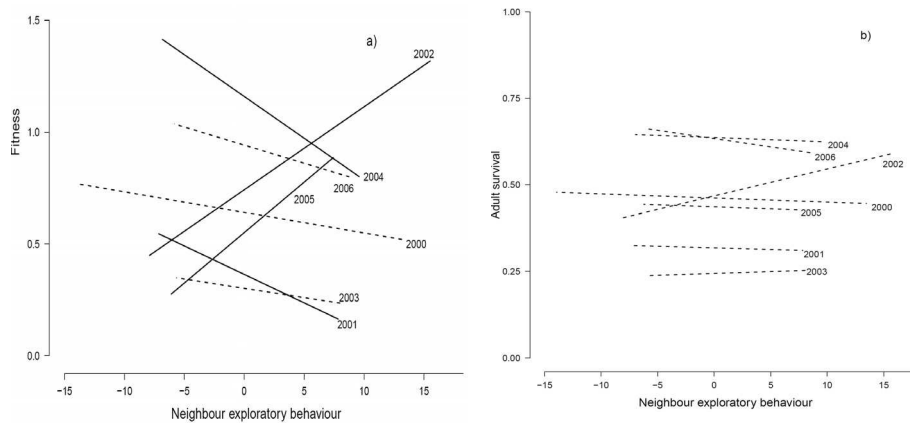[a]NEB – Neighbour exploratory behaviour

Figure 2. The effect of neighbour exploratory behaviour on (a) the fitness and on the (b) adult survival in years 2000-2006. Data points are the fitted values from the final model for fitness (adult survival + half of the number of recruits per pair). Low neighbour exploratory behaviour reflects slow environment around the focal birds, high reflects fast environment. Lines are regression lines of reproductive success on neighbour exploratory behaviour. Solid lines indicate significant and dashed lines non-significant relationships.

Discussion

Local adult survival did not depend on the mean neighbour exploratory behaviour and this was consistent for all seven years. Probably conditions in winter when birds form flocks and territory owners interact and compete with birds from a much larger area (Drent 1984; Matthysen 1990), may affect adult survival more than the competition with the direct neighbours during the breeding season. Hence, changes in the group composition due to selection in winter may strongly depend on environmental conditions during winter, independent on the neighbour exploratory behaviour during breeding (Perdeck *et al.* 2000).

In contrast, reproductive success and consequently fitness did depend on neighbour exploratory behaviour and this effect varied among years. This implies that the behaviour of the social environment is expected to change individual juvenile settlement decisions (Cote & Clobert 2007) and thereby their fitness prospects. The effect of neighbour exploratory behaviour is likely caused directly by interactions of the neighbours with the recruits' parents. This can be mediated by competition or cooperation between neighbours and parents before and during the nestling phase, which could affect nestling quality and by this means recruitment probability (Tinbergen & Boerlijst 1990). Alternatively, the effect could be just after fledging, since an important part of juvenile mortality occurs already in the first weeks after independence (Naef-Daenzer *et al.* 2001). Neighbour personality could also affect juvenile recruitment through the interactions with juveniles of these neighbours. After gaining independence fledglings join the juvenile

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flocks (Perrins 1979; Drent 1984), hence there is probability that these neighbouring juveniles might join same flocks.

The variation in the effect of neighbour exploratory behaviour on reproductive success and fitness over the years could not be explained solely by a single environmental or population characteristic (beech-mast crop or population density). Other factors or their combinations may cause variation in the direction of the effect among years and between age cohorts (Dall *et al.* 2004). Hence, e.g. the juvenile density may affect a juvenile's decision to either emigrate or to stay in the natal area (Payevsky 2006). The year differences may also arise due to temporal heterogeneity differing for particular territories; in other words, when some territories are more stable in e.g. quality than others.

These findings expand on previous studies by revealing the importance of the personality of conspecifics on individual fitness in a wild population. Although the interaction between various mechanisms during the year cycle may partly hide the effect under natural conditions, neighbour personality has an impact on fitness. The social environment could thus also play a role in e.g. frequency-dependent selection, which is often considered as one of the main processes contributing to the maintenance of variation in personality (Dall *et al.* 2004; Penke *et al.* 2007b; Wolf *et al.* 2008b). Because own personality is associated with adult survival (Dingemanse *et al.* 2004) interaction of personality with neighbour exploratory behaviour might be more important than effect of social environment alone. Field experiments that manipulate personality frequencies are therefore needed to directly test for the role of frequency-dependent selection for the maintenance of personality traits (Dall *et al.* 2004).