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### The maintenance of variation in avian personality

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# Chapter 5

Handling stress is associated with survival of juvenile great tits (*Parus major*) in a fluctuating environment

Eva Fucikova, Piet J. Drent and Kees van Oers



**Abstract**

The maintenance of variation between individuals in the wild is one of the main themes in evolutionary biology. Environmental heterogeneity and particularly negative frequency-dependent selection are proposed to play a key role in the maintenance of the variation in personality. However, selection can vary over age classes, which may be also important for this maintenance. Although former studies have shown that selection acts on personality through adult survival, information about the impact of personality on juvenile survival of passerines is still lacking. Until recently it was only possible to estimate juvenile personality through an indirect measure by using the parental personality score. A recently developed handling stress test allows us to test the personality of passerines already in the nestling phase, which enables us to study survival and selection on personality directly over the whole period after fledging. Using this handling stress test we analysed the impact of a juvenile's handling stress and the exploratory behaviour of the neighbours of their parents. Juvenile local survival did depend on the juvenile's handling stress. Juveniles with high handling stress score (corresponding with fast exploring birds) had higher local survival compared to juveniles with low handling stress score. Selection on handling stress of juveniles was not related to juvenile population density or beech-mast crop. We found no evidence that negative frequency-dependent selection acted on handling stress via juvenile local survival. Their own handling stress and experience are therefore more important than the impact of exploratory behaviour of the neighbours of their parents. This contrasts with settled adults who experience more local conditions and frequency-dependent selection can act via direct social interactions with their neighbours. Hence, environmental heterogeneity in time and space combined with selection pressures which act differentially on different age categories may contribute to the maintenance of variation in personality.

## Introduction

How genetic variation in quantitative traits - like behavioural traits - is maintained in the wild is one of the main themes in evolutionary biology. Increasing knowledge of individual behavioural reactions to environmental stimuli enables us to analyze the importance of behaviour for evolutionary questions and to validate theoretical models. A concept that covers these consistent individual differences in physiological and behavioural reactions is referred as animal personality (Gosling 2001; Reale *et al.* 2007). Personality is a suite of behavioural reactions which are consistent in time within and between contexts. The personalities of individuals within a population show a continuum in physiological and behavioural reactions to challenges: e.g. in a shy-bold continuum there are phenotypes ranging from extremely bold to extremely shy individuals (Wilson *et al.* 1994). For example bold great tits are fast (Verbeek *et al.* 1994), but superficial and passive explorers (Marchetti & Drent 2000). They take more risk during feeding (van Oers *et al.* 2004b) and are more aggressive but recover slowly after they lose a fight (Verbeek *et al.* 1996). They do not respond to stress by increased corticosteroid levels as much as shyer phenotypes (Koolhaas *et al.* 1999; Carere *et al.* 2003), but their breath rate increases faster after handling (Carere & van Oers 2004; Fucikova *et al.* 2009). Shy animals in contrast are slow but thorough and active explorers, less aggressive but recover relatively fast after defeat and risk less. They react by increased corticosteroid levels in stressful situations, but their breath increases slower.

Personality affects individual reactions in ecologically relevant situations and challenges (Amy *et al.* 2010; Herborn *et al.* 2010). Thereby personality has fitness consequences (Reale & Festa-Bianchet 2003; Dingemanse *et al.* 2004; Smith & Blumstein 2008) and selection acts on variation in personality (Dall *et al.* 2004; Reale *et al.* 2007). Its impact varies over age categories and sexes (Chapter 3; Dingemanse *et al.* 2004). Personality of parents affects survival of juveniles and thereby parental fitness (Arnold *et al.* 2007; Boon *et al.* 2007; Reale *et al.* 2009). Personality is heritable (van Oers *et al.* 2004c; Penke *et al.* 2007b) and so the composition of the population can have evolutionary consequences (McDougall *et al.* 2006). Selection may differ between age categories and particularly selection on juveniles may be crucial because of the relatively high mortality rates in the weeks after fledging (Drent 1984; Naef-Daenzer *et al.* 2001; King *et al.* 2006). Selection on juveniles does not only affect the individual fitness of these juveniles but also the reproduction and fitness of parents. Thereby selection on juveniles affects the population composition for the next generations as a long-term effect. Therefore, it is very important to know what selective forces act on juvenile personality and how this differs from selection on adults. However, information on selection pressures on personality in early juvenile stages is lacking (Smith & Blumstein 2008). This is mostly due to the fact that it is hard to measure the personality of entire juvenile populations before selection takes place.

Researchers have used different strategies to cope with this lack of a measure of juvenile personality scores. One of them is to use exploratory score of parents (Chapter 3)

or mid-parent score (Dingemanse *et al.* 2004) since personality is partly genetically determined (Turelli & Barton 2004; van Oers *et al.* 2005a; van Oers & Mueller 2010). However, this does not directly show selection on juvenile personality itself, but only the impact of parental personality on number of recruits a pair produced (Chapter 2; Chapter 3; Both *et al.* 2005), because in these analyses individual juvenile personality itself is not used. Another option is to use the standard tests developed for adults after the fledglings have gained independence of their parents (Boon *et al.* 2007; Quinn *et al.* 2009). This is usually some time after the juveniles become independent of their parents, which implies that many individuals have already disappeared from the population and an important part of the period of strong selection has already taken place. Recently we have developed a handling stress test (HS) enabling us to test the personality of nestlings (Chapter 4). A higher score in the HS test corresponds with the higher exploratory score of faster explorers. This allows us to test the whole nestling population for personality. Hence, we can take within-nest individual differences into account when investigating juvenile survival after fledging until the next breeding season to answer questions related to the impact of personality on survival and selection in fledglings.

We use the great tit as our focal species, which is one of best studied species in personality research (Sih *et al.* 2004a; van Oers *et al.* 2005a; Reale *et al.* 2007) and a model species for ecology of wild animals. Selection acts on great tit personality differently in the sexes, age classes and between years (Chapter 3; Dingemanse *et al.* 2004; Quinn *et al.* 2009). Also, environmental heterogeneity has a high impact because the environment can form a chain of pressures which affects life history. For example beech-mast crop affects winter survival of both adult and juvenile great tits (van Balen 1980; Perdeck *et al.* 2000) and may effect selection on different personality types depending on sex and age as suggested by Dingemanse *et al.* (2004). After winters with a rich beech-mast crop a high population density arises, which normally leads to high adult and juvenile density. Increased density may increase competition that is important for nFDS (Sokolowski *et al.* 1997; Sinervo & Calsbeek 2006). Negative frequency-dependent selection (nFDS) is a type of social selection in which rarer phenotype has the highest fitness through e.g. lowest competition (Hori 1993; Roff 1998b; Bond & Kamil 2002). Hence, with increased density competition increases and this enables nFDS. We found in our former studies that the personality of adult great tits was under different selection pressures dependent on frequency in adult survival. However, the number of recruited juveniles was associated only with the social environment represented by the personalities of the direct neighbours and parental personality was not important (Chapter 3). These differences also show the importance of studies concentrating at selection acting at different age categories and on different life-history traits.

In this article we therefore want to test 1) the impact of juvenile personality on juvenile local survival, 2) how do juveniles of certain handling stress type interact with the personality of the direct neighbours of their parents and hence frequency-dependent selection may act on juvenile personality and 3) how this selection in combination with

environmental heterogeneity contributes to the maintenance of variation in personality in the wild.

## **Methods**

### **Study subject and area**

Great tits (*Parus major*) have broods containing between 5 and 12 nestlings. Nestlings are full grown after 13 days and fledge between 16 to 23 days after hatching. Fledglings become independent of their parents 2 to 3 weeks after fledging. The first three to four weeks after fledging, predation and starvation cause high mortality among fledglings (Drent 1984; Naef-Daenzer *et al.* 2001). Mortality of juveniles can reach up to 10% in the first days after fledging and even 30–50% in the week after reaching independence of parents. Soon after becoming independent of their parents, fledglings form hierarchical flocks. They disperse between flocks and areas in dependence on density, composition of the local population and food distribution. Thereby, juveniles are redistributed over a much larger area than used by their parents (Drent 1984). Also, in winter under worse food supply and foraging conditions a lot of juveniles (up to 80 %) starve or disperse (Perrins 1965; van Balen 1980). From September onwards juvenile males start to claim territories (Drent 1984).

### **Behavioural tests**

We tested personality of nestlings in our population by a handling stress test and personality of adult birds by a novel environment test. Thereby, we obtained the personality of both juveniles and breeding adults.

#### *Handling stress test*

We conducted a handling stress test (HS) on wild nestlings on day 14 after hatching between 0900 and 1600 hours following Fucikova *et al.* (2009). All nestlings were taken from the nest box and put in a cotton bag. In a shady location near the nest box, we took one nestling from the bag and held it in the hand loosely on its back. We fixed it by keeping its head between thumb and index finger and counted the number of breast movements (breath rate) during a one minute handling period in four 15-second bouts. After this we put each individual into a wooden box for 15 minutes. The second individual was taken from the bag right after the first handling minute of the first individual, until the whole brood was tested. After 15 minutes we measured the breath rate of the first individual for a second time in the same way as described above. When all birds of a brood were tested, we weighed them with a pesola to the nearest 0.1g, measured their tarsus with sliding callipers to the nearest 0.1 mm, and placed them back in the nest box. We measured air temperature in the shadow at the location of the test and recorded the time of the day.

*Exploratory behaviour*

To be able to determine the affect of the personality of the social environment (neighbour exploratory behaviour) on local juvenile survival, we measured exploratory behaviour using the novel environment test developed by Verbeek *et al.* (1994). Birds were released in a sealed room (4.0×2.4×2.3 m) with five artificial trees. We darkened the cage with a curtain, opened the sliding door and turned on the light in the test room; thereby birds flew into the room without handling. We used the total number of flights (movements between trees) and hops (movements within trees) within the first 2 minutes as a measure of exploratory behaviour. We corrected this score for date of capture based on the finding that behaviour changes with capture date within individuals (see Dingemanse *et al.*(2002)). After testing and weighing, all birds were released at the place of capture.

*Neighbour exploratory behaviour (NEB)*

We calculated Neighbour exploratory behaviour (NEB) as mean personality of all male neighbours sharing a boundary with the territory of a focal bird, to describe the social environment for each nest box as an indication of the local frequency of personalities. We used Dirichlet tessellations to estimate neighbouring territories. This technique 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. Territories created by the Dirichlet tessellation closely resemble the real territories (Chapter 2).

**Statistical analyses**

We used a generalized linear mixed-effects model approach (GLMM) using the software R 2.10.1 (R Development Core Team 2009) for all statistical analyses. Juvenile handling stress score was calculated following Fucikova *et al.* (2009). However, because we used 1249 juveniles in our analyses, our computer capacity was too small to calculate scores for all the juveniles in one go. Therefore, we calculated scores separately for each year. For analyses we used the estimates of the first handling period corrected for year differences (centralized around the year mean). All tests were two-tailed. The model of local juvenile survival contained juvenile local survival until first breeding (recruited or not) as the dependent variable with a binomial distribution and logit-link function. We tested the 3-way interaction between handling test score, parents' neighbour exploratory behaviour and year (HS×NEB×year) to test whether FDS acted as a consequence of differential local juvenile survival for birds with different personality scores due to variation in the social environment. We included year, since selection patterns are known to vary over years. Hatching day, number of fledglings in a brood, condition of the individual (residuals of the regression of weight on tarsus) and local density of breeding pairs (distance of the third closest nest box from the focal nest box, normalized for year) were used as covariates. We chose these covariates because hatching date correlates with the caterpillar peak which is important for the nestling condition (Naef-Daenzer & Keller

1999), weight correlates with the survival in tits (Tinbergen & Boerlijst 1990; Both *et al.* 1999) and tarsus length is a linear measure of body size (Garnett 1981) and number of fledglings in the brood shows juvenile density which affects juvenile recruitment as well as adult density (Both *et al.* 1999). To minimize the effect of pseudoreplication due to covariance between siblings, we included brood as a random factor. We did not include a measure for quality of the territory in the analyses, because we used a measure of juvenile quality at fledging itself, which is a more direct measure of individual quality.

#### *Standardized selection differential (SSD)*

To test the prediction that selection on juvenile personality is related to juvenile density and beech-mast crop we quantified selection on handling stress using standardized selection differentials (SSD). The SSD determines which phenotype has relative fitness advantage over the others. SSD for local juvenile survival was calculated as the difference between the mean HS score of the juveniles which locally recruited in our area in a given year and mean HS score of all juveniles which were born in a given year, divided by the standard deviation of mean HS score of all juveniles born in a given year (Falconer 1981).

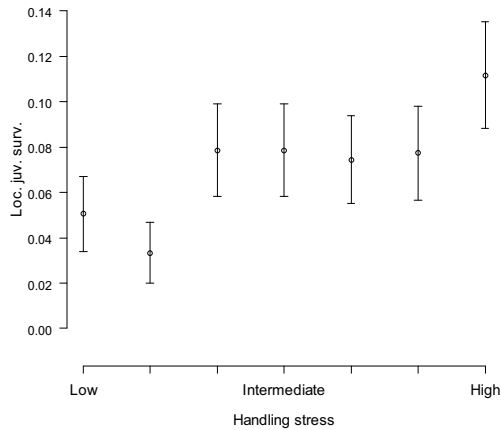
We then used a linear regression to relate the estimates of SSD with juvenile density (number of juveniles fledged in our area) and also beech-mast crop richness (beech-mast crop was calculated following Perdeck *et al.* (2000) as the number of full nuts per m<sup>2</sup>). Using these values, years were divided in three groups of rich, intermediate and poor crop). In the analysis we used the beech-mast crop for the winter following the spring in which the birds were born to test if selection for personality types is related to these environmental variables known to be important for juvenile survival.

## **Results**

We found evidence that selection acted on HS via local juvenile survival. Birds with higher HS score (corresponding with fast exploring birds) had higher local juvenile survival than birds with lower HS score and this was consistent over years (lmer, HS, estimate=0.26, df=11,  $\chi^2=8.03$ ,  $p<0.001$ ; Table 1, Figure 1). Overall, local juvenile survival differed between years (lmer, year, df=11,  $\chi^2=27.56$ ,  $p=0.004$ , Table 1). The highest survival was in winter 2004-05, intermediate survival in 2002-03, 06-07, 07-08 and very low survival in 08-09.

We did not detect FDS in our model when testing for an interaction of a nestling's HS score with neighbour personality (lmer, HS×NEB, df=15,  $\chi^2=4.07$ ,  $p=0.4$ ) and this pattern was not different for the different years (lmer, HS×NEB×year, df=26,  $\chi^2=1.98$ ,  $p=0.74$ ). Personality of neighbours around the nest box of their parents on its own did not affect local juvenile survival (lmer, NEB, df=12,  $\chi^2=0.6$ ,  $p=0.43$ ).



**Figure 1.**

Juveniles with higher HS score had higher local juvenile survival than birds with lower HS score in five years when tests were done. Raw handling stress scores were for the graph divided in seven groups. Error bars show local juvenile survival chance in these groups.

We found that Standardized selection differentials on handling stress (SSD) were positive for all years. This indicates that there was selection for individuals with high HS score in seasons 04-05, 06-07 and 07-08. However, SSD values in 02-03 and 08-09 were very low indicating very low selection on juvenile personality in these years (Table 2, Figure 2). There was no relationship between juvenile survival and juvenile density (lm,  $F_{1,3}=1.07$ ,  $R^2=0.263$ ,  $\beta=-0.001$ ,  $p=0.38$ ) or richness of beech-mast crop in a given year (lm,  $F_{1,3}=5.336$ ,  $R^2=0.6401$ ,  $\beta=0.3162$ ,  $p=0.104$ ).

### Discussion

The aim of this study was to investigate if the personality of juveniles affects their local survival. Moreover, we tested the impact of negative frequency-dependent selection (nFDS), which is together with habitat heterogeneity supposed to be the main factor explaining maintenance of variation in personality. In the case of nFDS due to the rearing environment, juveniles with opposite personality to neighbours of their parents have highest survival. We found that there was selection on handling stress, but we did not detect nFDS. We did not find an effect of social environment on local juvenile survival which is in contrast to what has been found before (Chapter 2; Chapter 3). This difference may be caused by the different research question in this chapter. In Chapter 2 and Chapter 3 we tested the impact of social environment on the reproductive success represented by the number of recruits a pair produced as an indication of parental fitness. The number of recruits a pair produced is probably dependent on the parental care which affects condition of all offspring in the nest. Juveniles in a good condition have a better chance to survive the winter (Both *et al.* 1999) and to recruit (Tinbergen & Boerlijst 1990). Hence, neighbours of the parents in the nestling phase could indirectly affect the recruitment probability of all siblings in a nest through interactions with parents. In contrast, a juvenile's own personality as studied in this chapter is probably more important for coping individually with the environment experienced by juveniles in their first year. Within nest variation in personality

could be therefore important for chance to survive within a brood. The effect of juvenile personality might actually overrule the effect of neighbour personalities during the nestling phase. The neighbours of parents may have impact on juvenile survival through the care of juveniles' parents. However, juveniles depend on themselves after gaining independence and their own behaviour affected by their personality is of higher importance. After gaining independence of their parents juveniles travel around a large area and hence they experience many territorial adults. Moreover, they have to compete for free territories with other juveniles with whom they share flocks and with adults (Drent 1984; Naef-Daenzer *et al.* 2001). Hence, although all juveniles from one nest may have similar fledging weight due to the rearing environment, their personality and life history varies and this variation gives space for selection on their own personality.

**Table 1.** Final model of the local juvenile survival in five years – model estimates. The  $\chi^2$  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                     | $\chi^2$ | df | p value | Level | Estimates |
|------------------------------|----------|----|---------|-------|-----------|
| Handling stress <sup>a</sup> | 8.03     | 1  | 0.005   | -     | 0.263     |
| Year <sup>b</sup>            | 27.56    | 4  | <0.001  | 2002  | 1.886     |
|                              |          |    |         | 2004  | 2.278*    |
|                              |          |    |         | 2006  | 2.120     |
|                              |          |    |         | 2007  | 0.585     |
|                              |          |    |         | 2008  | -0.661    |
| Hatching date                | 5.43     | 1  | 0.02    | -     | -0.106*   |
| Fledging date                | 0.03     | 1  | 0.86    | -     | -0.015    |
| Condition <sup>c</sup>       | 0.11     | 1  | 0.74    | -     | -0.001    |
| Local density <sup>d</sup>   | 0.09     | 1  | 0.77    | -     | -0.001    |
| NEB <sup>e</sup>             | 0.6      | 1  | 0.43    | NA    | NA        |
| HS×NEB×year                  | 1.98     | 4  | 0.4     | NA    | NA        |
| HS×NEB                       | 4.07     | 1  | 0.4     | NA    | NA        |
| HS ×year                     | NA       | 4  | NA      | NA    | NA        |
| NEB×year                     | NA       | 4  | NA      | NA    | NA        |

\*p<0.05

<sup>a</sup> Handling stress: score gained from HS test measure of personality in nestlings normalized for year

<sup>b</sup> Year: year in which were juveniles born and tested for personality

<sup>c</sup> Condition: condition of the juvenile (residuals of the regression of weight on tarsus)

<sup>d</sup> Local density: local density of breeding pairs (distance of the third closest nest box from the focal nest box, normalized for year)

<sup>e</sup> NEB: Neighbour exploratory behaviour calculated as mean personality of all male neighbours sharing a boundary with the territory of a focal bird

We also did not detect FDS in juvenile local survival as found previously in adult survival (Chapter 3). A possible explanation is in the life history of adults and juveniles. Adult great tits are territory holders and their main contacts are with direct neighbours (Perrins 1979; Drent 1984). Direct neighbours affect their survival more than far neighbours with which they have occasional contacts (Chapter 3). Therefore nFDS acts in adults on an individual scale: territory owners with opposite personality to their neighbours have highest fitness.

If nFDS acted at juvenile age on an individual scale, juveniles with the opposite personality to neighbours of their parents would have highest survival. We offer three hypotheses why we did not detect FDS for juveniles on an individual scale but detected sole selection on handling stress of juveniles: i) This hypothesis is same as our explanation of the missing effect of the neighbour personality: the impact of a juvenile's own personality could be more important for juveniles than the impact of the rearing environment and moreover the environment experienced later in life could overrule the impact of rearing environment. ii) We tested local juveniles for HS but could not test immigrant juveniles whom may have a very important impact on local juvenile survival and thus may be important for FDS. The reason is that there is high immigration in our area and immigrants are generally faster explorers (higher HS) compared to local recruits (Dingemanse *et al.* 2003; Quinn *et al.* 2009). The variable numbers of juvenile immigrants over the years play an important role for personality composition of the juvenile population (Drent 1984). iii) There are differences in life history of sexes (Perrins 1965; Drent 1984) and so juvenile males and females could be under different selection pressures as found in adults (Chapter 3; Dingemanse *et al.* 2004; Quinn *et al.* 2009) which could mask nFDS. We could not use sex of the juveniles in our analyses because sex of most juveniles was not available. In our opinion, the first hypothesis is most likely to explain the lack of FDS and effect of neighbour personality because juveniles are generally very sensitive to experience (Talloen *et al.*). Social environment in winter flocks and fights for territory might be a much stronger experience than immigration or sex differences.

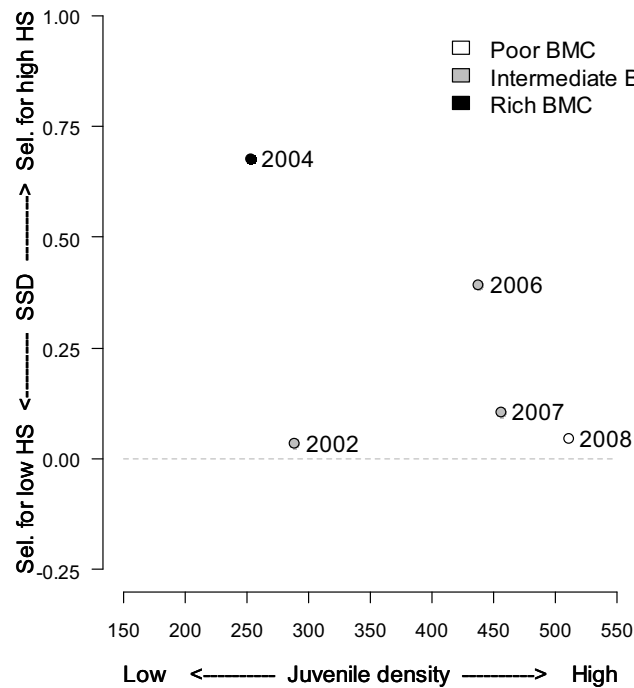
We found that an individual's handling stress used as an indication of own personality at an early age, had a significant impact on local juvenile survival: juveniles with high handling stress scores (HS) had a higher chance to survive than juveniles with low HS. To our knowledge this is the first study showing importance of passerine personality for survival already at early age. These results differ from the findings of Quinn *et al.* (2009) who did not find any selection on juvenile personality. A possible reason for this may be that Quinn *et al.* (2009) tested juvenile great tits for personality after the juveniles had already gained independence from their parents. However, strong selection acts already on the population exactly between fledging of juveniles and the time when they can be caught and tested for personality (Drent 1984; Naef-Daenzer *et al.* 2001). Therefore, studies like that of Quinn *et al.* (2009) could actually miss selection on juvenile personality.

**Table 2.** Standardized Selection Differential (SSD) - difference between mean raw HS score of the juveniles which locally recruited in our area in a given year and mean exploratory score of all juveniles which were born in a given year, divided by the standard deviation of mean HS score of all juveniles born in a given year. Positive SSD represent selection on the population scale for individuals with high handling test score. However, values in 2002 and 2008 were very low which represents very low selection on juvenile personality in these years.

| Year | Mean HS <sup>a</sup> of recruits | Mean HS of all juveniles | SD of HS of all juveniles | SSD   |
|------|----------------------------------|--------------------------|---------------------------|-------|
| 2002 | 0.177                            | 0.139                    | 1.089                     | 0.035 |
| 2004 | 1.487                            | 0.504                    | 1.452                     | 0.678 |
| 2006 | -0.072                           | -0.556                   | 1.231                     | 0.393 |
| 2007 | -1.555                           | -1.674                   | 1.119                     | 0.106 |
| 2008 | 0.363                            | 0.312                    | 1.140                     | 0.045 |

<sup>a</sup> Handling stress: score gained from HS test measure of personality in nestlings

**Figure 2.** Selection on handling stress was not related to juvenile population density. The x-axis shows juvenile density in the breeding season when the juvenile was born. The y-axis is Standardized Selection Differential - difference between mean raw HS score of the juveniles which locally recruited in our area in a given year and mean exploratory score of all juveniles which were born in a given year, divided by the standard deviation of mean HS score of all juveniles born in a given year. Colours of the points show richness of beech-mast crop in the given year.



To test the prediction that selection acting on handling stress through local juvenile survival is positively related to environmental variables related to great tit life-history we quantified this selection using standardized selection differential (SSD). SSD showed a higher survival of juveniles with high HS scores, which also confirmed results of the model in which we tested for role of personality and FDS. Looking at the biological context we related SSD to juvenile population density and beech-mast crop which are known to be important for juvenile survival (van Balen 1980; Both *et al.* 1999; Perdeck *et al.* 2000; Payevsky 2006). However, the selection on handling stress on a population scale (SSD) was related neither to juvenile population density nor to by beech-mast crop richness. The reason may be that we related always only one environmental variable to SSD. However, not only one environmental variable but an interaction of non-social and social environmental variables could differ between years and cause differences in selection (Svensson & Sheldon 1998; Sinervo & Calsbeek 2006). Environmental heterogeneity is known to have a very strong effect on survival and also on selection on handling stress in great tits (Chapter 3; Dingemanse *et al.* 2004). Moreover, there are many environmental variables important for great tits like e.g. food availability, emigration and immigration, population density or predation, which could affect juvenile survival and we could not test for them. Hence, we hypothesize that variation in multiple environmental effects might act on selection on juvenile personality. Generally variation in the non-social environment affects the social environment which then plays on life-history traits (Svensson & Sheldon 1998; Sinervo & Calsbeek 2006) and through them may act on personality. Therefore, every year may be unique in the combination of selection pressures and its impact on juvenile survival. The hypothesis of fluctuating selection pressures is supported by a vast literature (Chapter 3; Dingemanse *et al.* 2004; Sih *et al.* 2004b; Hedrick 2006, 2007; Clegg *et al.* 2008; Robinson *et al.* 2008; Quinn *et al.* 2009). For example, in the bighorn ewes (*Ovis canadensis*) selection on personality was detected only after arrival of a predator (Reale & Festa-Bianchet 2003). In populations of Soya sheep (*Ovis aries*) fluctuating ecological conditions create several optimal scales for allocation toward reproduction versus survival and so create selection on a secondary sexual trait (Robinson *et al.* 2008). A long-term study of 4000 years on an island bird *Zosterops lateralis chlorocephalus* found fluctuating form and strength of directional selection (Clegg *et al.* 2008).

In conclusion, we have shown that a juvenile's own personality, as measured by HS is important for local juvenile survival, independent of the personality of their neighbours during the nestling phase. Thereby FDS does not play a significant role for juvenile survival. The variation in personality is probably maintained by several processes, like differences in life history of juveniles and adults which cause variability in selection pressures over age classes and over time. Although environmental heterogeneity does not have a straightforward impact on juvenile survival in dependence on handling stress it may play an important role for overall survival of the whole population and hence also have an indirect impact on social composition of populations and age categories.

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