Turning Shy on a Winter's Day: Effects of Season on Personality and Stress Response in *Microtus arvalis*

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Abstract

Animal personalities are by definition stable over time, but to what extent they may change during development and in adulthood to adjust to environmental change is unclear. Animals of temperate environments have evolved physiological and behavioural adaptations to cope with the cyclic seasonal changes. This may also result in changes in personality: suites of behavioural and physiological traits that vary consistently among individuals. Winter, typically the adverse season challenging survival, may require individuals to have shy/cautious personality, whereas during summer, energetically favourable to reproduction, individuals may benefit from a bold/risk-taking personality. To test the effects of seasonal changes in early life and in adulthood on behaviours (activity, exploration and anxiety), body mass and stress response, we manipulated the photoperiod and quality of food in two experiments to simulate the conditions of winter and summer. We used the common voles (*Microtus arvalis*) as they have been shown to display personality based on behavioural consistency over time and contexts. Summer-born voles allocated to winter conditions at weaning had lower body mass, a higher corticosterone increase after stress and a less active, more cautious behavioural phenotype in adulthood compared to voles born in and allocated to summer conditions. In contrast, adult females only showed plasticity in stress-induced corticosterone levels, which were higher in the animals that were transferred to the winter conditions than to those staying in summer conditions. These results suggest a sensitive period for season-related behavioural plasticity in which juveniles shift over the bold–shy axis.

Introduction

Animal personality refers to individual differences in behaviour that are repeatable and correlated across contexts (Reale et al. 2007). In a broad sense, these consistent differences between individuals can involve any type of behaviour (Reale et al. 2010a). Personalities have been distinguished both along a shy–bold gradient and a proactive/risk-taking and reactive/cautious gradient (Sloan Wilson et al. 1994; Wolf et al. 2007; Bokony et al. 2012). Even though

the study of animal personality is currently a flourishing research field (Sih et al. 2004; Dingemanse & Reale 2005; Wolf et al. 2007, 2008; Biro & Stamps 2008; McNamara et al. 2009; Koolhaas et al. 2010; Gracceva et al. 2011), more specific questions about the development of animal personality have hardly been addressed in the literature (Stamps & Groothuis 2010a; Groothuis & Trillmich 2011). This is understandable considering that personality refers to individual consistency over time and across situations and the study of development (ontogeny) deals with

changes over time. However, as young animals often differ in their ecological or social niche from adult conspecifics, showing several ontogenetic adaptations, it is conceivable that not only behavioural traits but also their personality changes with age. Individuals do not only differ consistently in behaviour (personality), but they also differ in their behavioural plasticity, i.e. in the responsiveness that individuals may show to changes in the environment (Dingemanse et al. 2010). Interestingly, individual plasticity and personality can thus be considered complementary aspects of the phenotype. The question to what extent individuals can permanently adjust their behaviour (personality) to current circumstances during life is relevant both for the study of its causation as for its evolutionary implications. We studied this phenomenon by analysing the potential effect of a change in environmental factors that are related to seasonal changes in terms of photoperiod and food quality in a seasonal animal, the common vole.

Animals have evolved seasonally induced changes in physiology and behaviour to cope with these recurrent and predictable fluctuations in photoperiod, food abundance and temperature (Scherbarth & Steinlechner 2010; Eccard et al. 2011). Typically, in temperate environments, the winter is the adverse season as the temperature decreases together with the availability of food resources as the photoperiod shortens. Among mammals, many species have therefore timed reproduction and parturition to occur during the energetically favourable times of the year (spring, summer) (see Paul et al. 2008 for a review). For timing these life-history phases, the photoperiod seems to be the most important signal, although not the only one (see (Paul et al. 2008) for a review), that triggers the ability of animals to activate the correct set of gene expression and produce the suite of season-specific physiological and behavioural adaptations (see Walton et al. 2011a) for a review). In rodents, both the absolute and the incremental changes in day lengths contribute to the timing of seasonal behaviour and physiology (Gorman & Zucker 1995).

The effect of the photoperiod on reproduction in rodents has been extensively studied in long-day breeders (e.g. mice, hamsters, voles), with short-day lengths inducing a number of changes in physiology which result in suppression of breeding during the winter period (Walton et al. 2011a). In addition, exposure to short days increases anxiety-like and depressive-like behaviour (emotionality) in several diurnal and nocturnal rodents (Molina-Hernandez & Tellez-Alcantara 2000; Prendergast & Nelson 2005;

Pyter & Nelson 2006; Benabid et al. 2008; Ashkenazy-Frolinger et al. 2010; Workman et al. 2011). Both an increase (Badura & Nunez 1989; Jasnow et al. 2002) and a decrease (Andrews & Belknap 1993; Eccard et al. 2011) in aggression have been reported to occur in different rodents species during short days. In addition, short days can impair spatial learning and memory (Walton et al. 2011b).

It has been documented that the developmental stage at which a photoperiodic rodent encounters short days can strongly alter its life-history. Individuals born early in the breeding season (spring), experiencing long-day length, can achieve sexual maturity around 40–50 d of age. However, individuals born in late breeding season will delay sexual maturation until next spring (Forger & Zucker 1985; Gorman & Zucker 1995; Gorman 2001; Walton et al. 2011a). These data indicate that the season experienced early in life may affect a whole suite of traits (personality). Personality in terms of consistent behavioural differences has been already proposed to be related to life-history differences at the population level (see Reale et al. 2010b for a review). The common vole *Microtus arvalis* is a photoperiodic long-day breeder; in this species, most animals suppress reproduction during the winter season (Prendergast et al. 2001). As in many other small rodents, these voles undergo very different life-history trajectories during the summer and the winter period. During summer, populations face increasing densities (Krebs et al. 1973). As this is the main reproductive period, individuals might then benefit from a bold/aggressive and risk-taking personality type (summer personality type) to allow fast exploration, access to resources and reproduction opportunities (Eccard & Rodel 2011). During the winter season, however, when food is less abundant and mortality rates are higher, individuals might increase their chances of surviving to the breeding season by showing a shy, less explorative (in terms of distance travelled in the environment) and cautious personality type. This phenotype would have increased chance of survival over the winter and thus reproductive success in the following breeding season (winter personality type).

Our hypothesis is that personalities in this species are correlated to individual's seasonally constrained life history. Therefore, we expect personality to be determined by the season experienced during early life (developmental plasticity). Alternatively, it could also be that season affects adult personality independent of the timing of birth. In this case, we expect that adult animals adopt a less risk-taking behavioural type

during winter, while switching to a more risk-taking behavioural type in the spring/summer (adult plasticity). To test the effects of seasonal changes in early life (experiment A) and in adulthood (experiment B) on personality, we manipulated two key characteristics of a seasonal environment, photoperiod and food quality to simulate the conditions of winter and summer. At this stage, we aimed at testing whether the season has an influence on personality in voles rather than disentangling which specific seasonal factors may be responsible. We used the common voles *M. arvalis* as our study species as it is a seasonal breeder in which there is strong evidence for personality differences (Lantova et al. 2011; Herde & Eccard 2013). In the first experiment, we investigated the effects of the early life seasonal treatment on juvenile personality. Moreover, we also investigated the stress response as it has been shown in many species that differences in personality/coping style are related to differences in the HPA axis reactivity (Koolhaas et al. 1999; Baugh et al. 2012). To this end, in the first experiment (experiment A), we exposed half of the siblings present in each litter that received summer as a pre-natal and early post-natal treatment (until weaning time) to the winter environment, whereas the other half of the siblings was left in the summer environment matching their pre-natal experience. Both groups were tested two times, at the day of weaning before separation and 5 wk later in early adulthood, for activity, exploration, risk-taking behaviour and anxiety in three different tests. In addition, we measured the corticosterone response to novelty at adulthood.

In the second experiment (experiment B), we investigated the short-term effects of the same seasonal treatment on the same behaviours and hormonal response in adult female's personality to investigate whether also adult animals are capable of changing their personality regardless of their early life environment.

Methods

Animals and Housing

We used adult females and males and their offspring of the common voles (*M. arvalis*). The adults used for the present experiments (n = 55; 42 females; 13 males) were trapped with live traps [Ugglan special No2, Grahnab, Sweden, modified with a shrew exit (Eccard & Klemme 2013)] from different sites around Potsdam (Germany, 52°26′21.83″N, 13°00′44.14″O) and from the outdoor enclosures of the working

group Animal Ecology in Potsdam in Aug 2010 (only one individual) and between Jan to May 2011 (the rest of the voles). After capture, the voles were brought into the laboratory and individually housed in polycarbonate cages (Typ III: 42 cm × 27 cm × 16 cm; Ehret GmbH Germany) under natural light–dark condition, *ad libitum* food (ssniff V1594 R/M-H Ered II) and water until the beginning of the experiments. Cages contained wood shavings, hay and paper rolls as enrichment. Temperature in the room was kept around 18–23°C and humidity around 60%.

At the end of the experiments, all the animals were returned to the original trapping sites or were used for further experiments, as specified by our trapping license.

Ethical Note

The experiments were conducted under the permission of the 'Landesamt für Umwelt, Gesundheit und Verbraucherschutz Brandenburg' (reference number V3-2347-44-2011), and the voles were trapped under permission of the Landesumweltamt Brandenburg (reference number RW-7.1 24.01.01.10). During the capture sessions, traps were equipped with rolled oats and moist food (apples) and checked every approximately 6 h. Traps were moreover protected against predation and weather by wooden baskets. Captured voles were released from the traps into plastic boxes (45 cm × 22 cm × 25 cm) with ventilation and transported, within 30 min, into the laboratory where they were housed as described above.

Seasonal Treatment

To manipulate important seasonal cues, we choose to manipulate photoperiod together with food quality: in the 'winter condition', the voles were housed on 10:14 light–dark cycle (light on at 7:00 and off at 17:00) and fed with *ad libitum* hay, supplemented with a fixed amount of dried commercial barley grains (4 g/d). In the 'summer condition', the voles were housed on 16:8 light–dark cycle (light on at 5:00 and off at 21:00) and fed with *ad libitum* hay, daily supplemented with fresh barley sprouts grown from the same commercial grains, and fresh grass that in the vole habitat are plentiful in spring but absent in winter. Temperature and humidity were kept similar in both rooms (temperature around 20°C; humidity around 60%). Animals with their treatments were transferred every week between the two experimental rooms to avoid any confounding effect.

Experimental Design

Experiment A: Effects of early life treatment on juveniles' behaviours and physiology

In experiment A, we used for breeding 13 male–females pairs that were housed together in the summer conditions for a week. Next, males were removed from the female's cages. Before this social housing, both males and females were housed individually in standard laboratory conditions (see above for details). After 21.6 d (SD = 2.08), a number of seven litters were born in the laboratory summer condition from seven independent 'summer' mothers. The average litter size was 4.9 (SD = 0.8) and the sex ratio (males/females) 1.47 (SD = 1.44). At weaning (post-natal day 21), the offspring from each nest were randomly divided into (1) juveniles, continuing to live in summer conditions, (summer–summer life history: Su–Su, n = 16) and (2) their siblings, which were moved into winter conditions (summer–winter life history: Su–Wi, n = 13). From weaning onwards, all offspring were singly housed in a standard polycarbonate cage with sawdust as bedding and *ad libitum* water. At weaning (PT1), before the reallocations of half siblings to the winter condition, all animals were tested in a battery of behavioural tests and measured for body mass and sexual maturation. This 'baseline' measure of behaviours was used in the analysis to investigate the consistency of individual differences over time called 'differential consistency' (see further, Statistical Analysis section) of personality and the possible disruption of it due to the treatment. At this stage (PT1), there was no significant difference neither in behaviour nor in body mass between the two treatment groups randomly chosen. Later, at early adulthood (PT2), the Su–Su and Su–Wi group were tested a second time, in the same battery of behavioural tests, after approximately 5 wk of post-weaning treatment (for details see below). In this occasion also, the body mass was measured for the second time. Moreover, sexual maturation development was investigated, at PT1, PT2 and an intermediate time point between these, by external genital inspection. For females, the vagina opening served as a criterion of sexual maturation; for males, we checked whether the testes changed from abdominal to scrotal (sexually mature; Eccard & Ylonen 2001). After the last battery of tests, the two treatment groups were also tested in a stress test paradigm to assess the HPA response by analysing corticosterone concentration in faecal samples (for details see below).

Experiment B: Effects of the treatment on adult females' behaviours and physiology

In experiment B, adult females were housed in the two different seasonal conditions: winter (n = 16) and summer (n = 13). Groups were balanced for body weight. All females were singly housed in the same standard polycarbonate cages as in experiment A. After approximately 4 wk of treatment, summer and winter voles were tested in a battery of behavioural tests to assess personality (see below). Thereafter, both groups were also tested for stress response in the same procedure as used in experiment A (see below).

Behavioural Tests

To quantify common voles' behaviour, we used standard laboratory tests for mice and rats and adjusted these set-ups for the needs and skills of non-climbing, subterranean voles. The tests were already described for measuring animal personality in common voles (Herde & Eccard 2013) and in other species (see Gosling 2001 for a review). Variables that were recorded in barrier test (Prior & Sachser 1995; Lewejohann et al. 2006), open-field test (Archer 1973) and dark–light test (Young & Johnson 1991) reflect mainly boldness, exploration and activity of the tested animals (Herde & Eccard 2013).

Open-field test

A round open field of 100 cm diameter made of grey metal with a light linoleum floor was used as a test arena. The floor was virtually divided into three areas: a centre area of 35 cm diameter, named the unsafe area, the middle area of 32.5 cm and a peripheral area of 32.5 cm diameter named the safe area; only the movements of the animals in the 'unsafe area' have been included in the analysis. The test was carried out during the light phase between 10.00 and 18.00 h. On the test day, subjects were picked from the home cage in random order and placed in the centre area of the arena. The vole's movements in the arena were filmed and analysed using ANYmaze video tracking system (Stoelting Co., USA) for 10 min. After each test trial, the arena was cleaned with 70% alcohol. The following parameters were included in the analysis: total distance moved in the whole arena as a measure of exploration (Russell 1983) defined as 'exploratory activity'. The 'number of entries in the unsafe area' was used as a measure of boldness/risk-taking behaviour as we know that small prey animals show high levels of thigmotaxis and visit the unsafe

area only for short periods of time and do not stay there for longer periods (Archer 1973). We therefore assume that shy animals will have the smallest scores in this variable.

Barrier test

Spontaneous exploratory behaviour and activity were measured by slightly modifying the barrier test previously used in mice (Lewejohann et al. 2006) for our model species. A rectangular plastic box of 45 cm × 22 cm × 25 cm was filled with approximately 2 cm of sand as bedding. A plastic wall of approximately 4.5 cm height, parallel to the shorter side, divided the box into two parts of equal size. At the start of the test, each animal is placed at one side of the box and the 'latency to jump' over the barrier is recorded as a measure of boldness. Moreover, the total 'number of crossings' is scored over the test period of 5 min as well as whether the animal was mobile at the end of every 10-s interval ('activity'). Both measures reflect general activity of an animal.

Dark–light test

The dark–light test to measure anxiety is adapted from (Young & Johnson 1991) to our model species: a square white plastic box of 65 cm × 50 cm × 30 cm was used to perform the test. A second black plastic box (30 cm × 30 cm × 15 cm) half the size of the big box is placed upside down in the middle of the white box, providing a dark shelter. A small entrance (4 cm × 5 cm) was available on one side of the black box. Each animal was placed inside the dark box through the entrance at the beginning of the test. The 'latency to emerge' from the black box with its entire body was measured. Moreover, the total 'time spent in the light' compartment is measured over 10 min.

HPA Reactivity

Test design

One day before the stress test, all voles received food pellets (ssniff V1594 R/M-H Ered II), fresh grass and sprouts and barley grains were, respectively, removed from summer and winter animals cages to ensure a similar content of the digestive tract. One hour after the light went on (T0 = 8:00 for the winter treatment and T0 = 6:00 for the summer treatment), each vole was singly placed in the sampling cage (30 cm × 13 cm × 11.5 cm) after being chased by the experimenter's hand for 3 min in a unfamiliar plastic box (45 cm × 22 cm × 25 cm), mimicking a predation

attack. The sampling cage had a metal grid floor equipped with a plastic tray underneath and a paper towel to allow collection of faecal pellets. In experiment A, faecal samples were collected immediately after placing the vole in the new environment at T0 (to assess pre-stress levels) and after 2–4 h after the stressful event (to assess the stress levels) and stored in a −20°C-freezer. In experiment B, faecal samples were collected and stored in a −20°C-freezer every 2 h from the stressful event throughout the entire light phase (T1 = 8:00, T2 = 10:00, T3 = 12:00, T4 = 14:00, T5 = 16:00, T6 = 18:00; winter: T1 = 10:00, T2 = 12:00, T3 = 14:00, T4 = 16:00). The paper towel was changed after each sampling.

Corticosterone metabolite assay

Faecal corticosterone metabolites were extracted with 80% methanol and analysed using a 5α-pregnane-3ß,11ß,21-triol-20-one enzyme immunoassay according to the method described by Touma et al. (2003, 2004) and used in other studies with common voles (Liesenjohann et al. 2013).

Statistical Analysis

SPSS 18 PC package was used to perform statistical analyses. Two-tailed p-values ≤ 0.05 were considered statistically significant. According to the Shapiro–Wilk test, normality of data was accepted or rejected. If normality was not achieved after transformation (log or square root) nonparametric statistics were applied.

Experiment A

The effect of the early life treatment on behavioural variables at PT2 was tested by a mixed model using type of treatment (Su–Su vs. Su–Wi), sex and their interaction as fixed factors. Also, body mass and sexual maturation were tested by the same statistical model. Mother identity was used as a random effect to control for independence between offspring of the same mother participating in the experiment. Interactions were excluded when not significant. A similar approach was used to test the effect of the treatment on corticosterone metabolites after a stress challenge measured at PT2. In this case, hours after stress were used as repeated measure in the mixed model; the interaction between the repeat and season was also tested.

In addition to testing the effect of season on single behaviours, we also tested its effect on personality. To

this end, we tested two key aspects of personality, contextual generality and differential consistency (Stamps & Groothuis 2010b). Contextual generality refers to the extent to which scores for behaviour expressed in one context are correlated across individuals with scores in behaviour expressed in one or more other contexts when the behaviour in each context is measured at the same age (Stamps & Groothuis 2010b). This was tested for both treatment groups separately after the end of treatment at PT2 by Pearson (or Spearman when variables were not normally distributed) correlations between the expected behavioural linkages. These expectations were based on contextual generality results of an agglomerative cluster analysis previously conducted with the same kind of data in this species (Herde & Eccard 2013). To investigate a possible difference in contextual generality due to the treatment, we used the z test procedure to compare the correlation coefficients between the treatment groups (Cohen 2003). The following expected correlations have been analysed:

1. Barrier test, *number of crossings*/open field, *exploratory activity*.
2. Barrier test, *number of crossings*/dark light, *latency to emerge*.
3. Barrier test, *latency to jump*/open field, *number of entries in the unsafe area*.
4. Barrier test, *latency to jump*/dark light, *time spent in the light*.
5. Barrier test, *activity*/open field, *exploratory activity*.

The repeatability of behaviours will be named here 'differential consistency' meaning the extent to which scores for a given behaviour in a given context at PT1 on the first behavioural measurements are correlated across individuals with scores for the same behaviour in the same context at PT2 after the treatment (Stamps & Groothuis 2010b). Expected consistency was tested by Pearson correlations (or Spearman when variables were not normally distributed) between the same behaviours at the two different time points (PT1 and 2). The two treatments were also in this case tested separately, and a z test procedure was used to compare correlation coefficients between the treatment groups (Cohen 2003). As for contextual generality, when looking at differential consistency, we only tested those parameters for which repeatability was shown previously in this species (Herde & Eccard 2013) to avoid too much multiple testing without having a specific hypothesis. The following parameters were included in the analysis: *latency to jump* in the barrier test; *number of crossings* in the barrier test;

exploratory activity in the open field and *latency to emerge* in the dark–light test.

Experiment B

The effect of the treatment on single behaviours was tested by independent samples unpaired t test or Mann–Whitney when data were not normally distributed. The effects of the treatment (summer vs. winter cues) on the corticosterone metabolites after the stress challenge were tested by a mixed model with the seasonal treatment as a fixed factor and the hours after stress as a repeated measure. The interaction between the hours after stress and the seasonal treatment was also tested. Contextual generality as defined above was tested by Pearson (or Spearman) correlations on the expected linkages (see above). Also in this case, only the expected linkages according to previous analysis (Herde & Eccard 2013) were tested. With the same reasoning as experiment A, the z test procedure to compare independent correlation coefficients was applied.

Results

Experiment A

Body mass and sexual maturation
At PT2, Su–Wi ($\bar{x}$ + SE = 18.625 + 1.252 g) voles were lighter than Su–Su ($\bar{x}$ + SE = 22.611 + 1.295 g) ones (mixed model: $F_{1,21.154} = 12.165$, p = 0.002). No effect of sex on the body mass was found (mixed model: $F_{1,25.39} = 1.923$, p = 0.178). Both Su–Su and Su–Wi became sexually mature at the same age (mixed model: $F_{1,21.513} = 137$, p = 0.715) without any effect of sex (mixed model: $F_{1,25.662} = 0.367$, p = 0.850) nor of the interaction between sex and treatment (mixed model: $F_{1,20.885} = 0.125$, p = 0.727) .
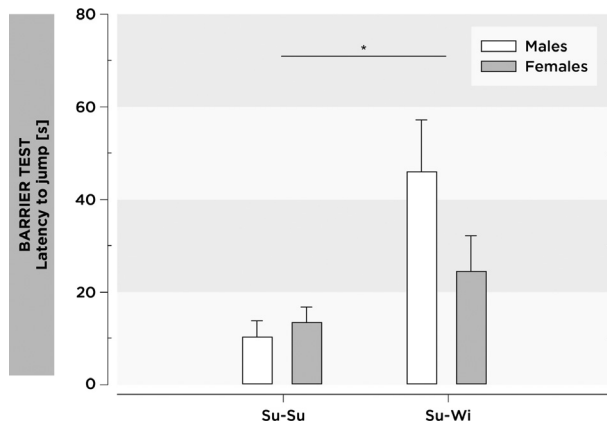
Single behaviours
The Su–Wi voles moved significantly less in the open-field arena than the Su–Su ones (mixed model: $F_{1,21.33} = 6.176$, p = 0.021, Fig. 1) after excluding the interaction (mixed model: $F_{1,20.438} = 2.337$, p = 0.142) also sex (mixed model: $F_{1,23.150} = 4.364$, p = 0.048) had an effect on exploration activity; males ($\bar{x}$ + SE = 53.52 + 9.7 cm) moved more than females ($\bar{x}$ + SE = 48.52 + 6.2 cm). No difference in the number of entries in the unsafe area was found (mixed model: $F_{1,22.77} = 0.338$, p = 0.566), after excluding the interaction (mixed model: $F_{1,20.803} = 0.040$,
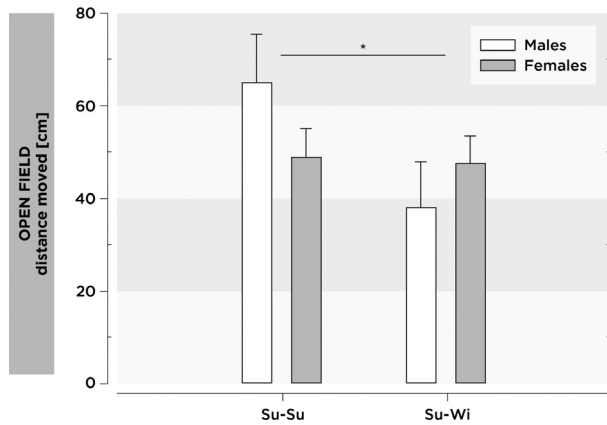
Fig. 1: Exploratory activity in the open-field test performed after the seasonal switch treatment period (experiment A). Bars represent the total distance moved (average and SEM), expressed in centimetres, of the Su–Su and Su–Wi groups for males (white bars) and females (grey bars), respectively. *p < 0.05.

number of crossings. The activity did not differ between sexes (Mann–Whitney: $U = 78.000$, p = 0.239), and no effect of treatment was found (Mann–Whitney: $U = 92.000$, p = 0.619).

The two groups did not differ in any of the variables measured in the dark–light test. After excluding the interaction (mixed model: $F_{1,25} = 1.765$, p = 0.196) and the effect of sex (mixed model: $F_{1,26} = 0.000$, p = 0.996), the treatment had no effect on the latency to emerge from the box (mixed model: $F_{1,20.724} = 0.001$, p = 0.972). Likewise, no effect of the treatment was found on duration in the light compartment (mixed model: $F_{1,21.434} = 0.002$, p = 0.966) after excluding the interaction (mixed model: $F_{1,20.913} = 1.435$, p = 0.244) and the sex (mixed model: $F_{1,21.359} = 0.021$, p = 0.887).

Corticosterone response

The Su–Su voles had lower concentrations of corticosterone metabolites both at time zero and at 4 h after the stress procedure was applied compared to the Su–Wi ones, and in both groups, the stressor increased the metabolites (Fig. 3). Indeed, a main effect of hours after stress (mixed model: $F_{1,23.583} = 8.660$, p = 0.007) and of season switch (mixed model: $F_{1,23.583} = 7.300$, p = 0.013) was found in the levels of corticosterone metabolites of the offspring. No significant effect of the interaction (mixed model: $F_{1,24.668} = 0.503$, p = 0.485) was found.

p = 0.843) and the effect of sex (mixed model: $F_{1,22.33} = 2.233$, p = 0.149).

In the barrier test, after removing the interaction (mixed model: $F_{1,20.67} = 0.271$, p = 0.609), the latency to jump the partition was longer for Su–Wi voles compared to the Su–Su ones (mixed model: $F_{1,21.4} = 10.58$, p = 0.004; Fig. 2), and sex did not have any effect on the latency to jump (mixed model: $F_{1,25.99} = 0.005$, p = 0.943). After removing the interaction (mixed model: $F_{1,21.323} = 0.214$, p = 0.649), neither sex (mixed model: $F_{1,25.968} = 0.058$, p = 0.812) nor the treatment (mixed model: $F_{1,21.581} = 0.488$, p = 0.492) had an effect on the
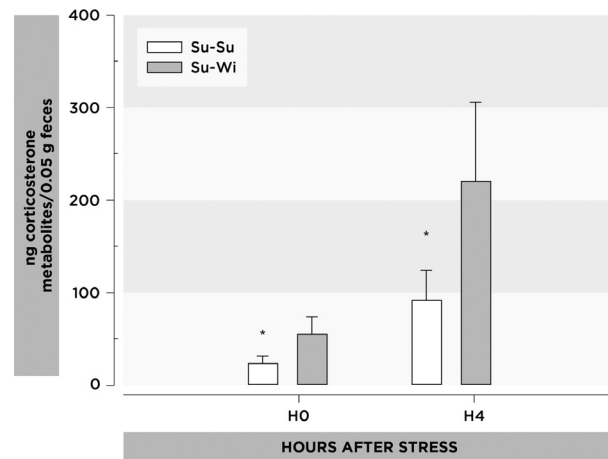

Fig. 2: Barrier test performed after the seasonal switch treatment period (experiment A). Bars represent the latency (average and SEM), expressed in seconds, to jump over the barrier of the Su–Su and Su–Wi groups for males (white bars) and females (grey bars), respectively. *p < 0.05.

Fig. 3: Stress response in young males and females voles after the seasonal switch treatment (experiment A). Bars represent mean and SE of corticosterone metabolites (nanograms per 0.05 g of faeces), in the two experimental groups Su–Su (white bars) and Su–Wi (grey bars) at baseline (H0) and 4 h (H4) after the stress was applied. *p < 0.05.

Contextual generality

A significant correlation between *number of crossings* in the barrier test and the *exploratory activity* in the open field was found when analysing both groups together (Pearson correlation: $r = 0.625$, $p \leq 0.01$). Similar correlation coefficients for both groups when analysed separately (Su–Su: Pearson correlation $r = 0.5670$, $p = 0.022$; Su–Wi: Pearson correlation $r = 0.748$, $p = 0.03$; Fig. 4 panel a and b); no significant difference is found between the coefficients ($Z = -0.773$, $p = 0.439$), suggesting that the personality linkage is not affected by our seasonal switch. A significant negative correlation between the *latency to jump* in the barrier test and the *number of entries in the unsafe area* of the open field was found for both treatment groups together (Pearson correlation: $r = -0.429$, $p = 0.02$). When testing the correlations separately for the two groups, a trend in the difference ($Z = -1.84$, $p = 0.064$) between the correlation coefficients of both groups was found. While a strong negative correlation was found in the Su–Su group (Pearson correlation: $r = -0.734$, $p = 0.001$; Fig. 4 panel e), no correlation was found in the mismatched Su–Wi group (Pearson correlation: $r = -0.159$, $p = 0.604$; Fig. 4 panel f).

There is no contextual generality (Spearman rank correlation: $r_s = -0.137$, $p = 0.480$) between the *latency to jump* in the barrier test and the *duration in the light* compartment in the dark–light test. When the two groups were analysed separately, no evidence for a correlation was found (Su–Su: Pearson correlation $r = -0.178$, $p = 0.511$; Su–Wi: Pearson correlation $r = -0.265$, $p = 0.381$; Fig. 4 panel g and h) and there was no difference between the correlation coefficients ($Z = 0.217$, $p = 0.827$). Similarly, no significant correlation (Pearson correlation: $r = -0.35$, $p = 0.856$) was found between the *number of crossings* in the barrier test and the *latency to emerge* in the dark–light test. This was also the case when the two groups were tested separately (Su-Su: $r = -0.024$, $p = 0.929$; Su-Wi: $r = -0.058$; $p = 0.85$; Fig. 4 panel c and d) and no significant difference was found between the two ($Z = -0.080$, $p = 0.935$). Only a trend was found when testing both groups together for a correlation between the *activity* in the barrier test and the *exploratory activity* in the open field (Spearman rank correlation: $r_s = 0.333$, $p = 0.077$). In this case, correlation coefficients were not different ($Z = -0.176$, $p = 0.860$) between the two groups when analysed separately (Su–Su: Pearson correlation $r = 0.317$, $p = 0.232$; Su–Wi: Pearson correlation $r = 0.382$, $p = 0.198$; Fig. 4 panel i and j).

Differential consistency

There was a clear differential consistency on *activity* in the open field as PT2 is strongly with the activity scores measured before the switch in treatment at PT1 (Table 1). Interestingly, when the two groups are tested separately for consistency, it revealed a significant correlation in the Su–Su animals whereas no consistency was present in the Su–Wi group although the correlation coefficients were not different ($Z = 0.905$, $p = 0.364$). A reverse situation was found for the *number of crossings* in the barrier test when the two treatments were tested separately: the consistency is not found in Su–Su animals, whereas consistency is shown in the Su–Wi group, although the two correlation coefficients were not significantly different ($Z = 1.448$, $p = 0.147$).

Likewise, also the *latency to emerge* from the box in the dark–light PT2 is predicted by the same behaviour before the season switch. Nevertheless, when the two groups are tested separately, only the Su–Su showed consistency over time whereas Su–Wi did not. However, also in this case, when testing the difference between coefficients, no significant difference was found ($Z = 0.913$; $p = 0.361$). Opposite to what was shown before in wild-caught animals (Herde & Eccard 2013), no consistency was found for the *latency to jump* over the partition in the barrier test. When the two treatments are tested separately, the consistency is found neither in Su–Su animals nor the Su–Wi group, and the correlation comparison ($Z = -1.300$, $p = 0.193$) did not show a significant difference between the two correlations either (correlations are shown in Table 1).
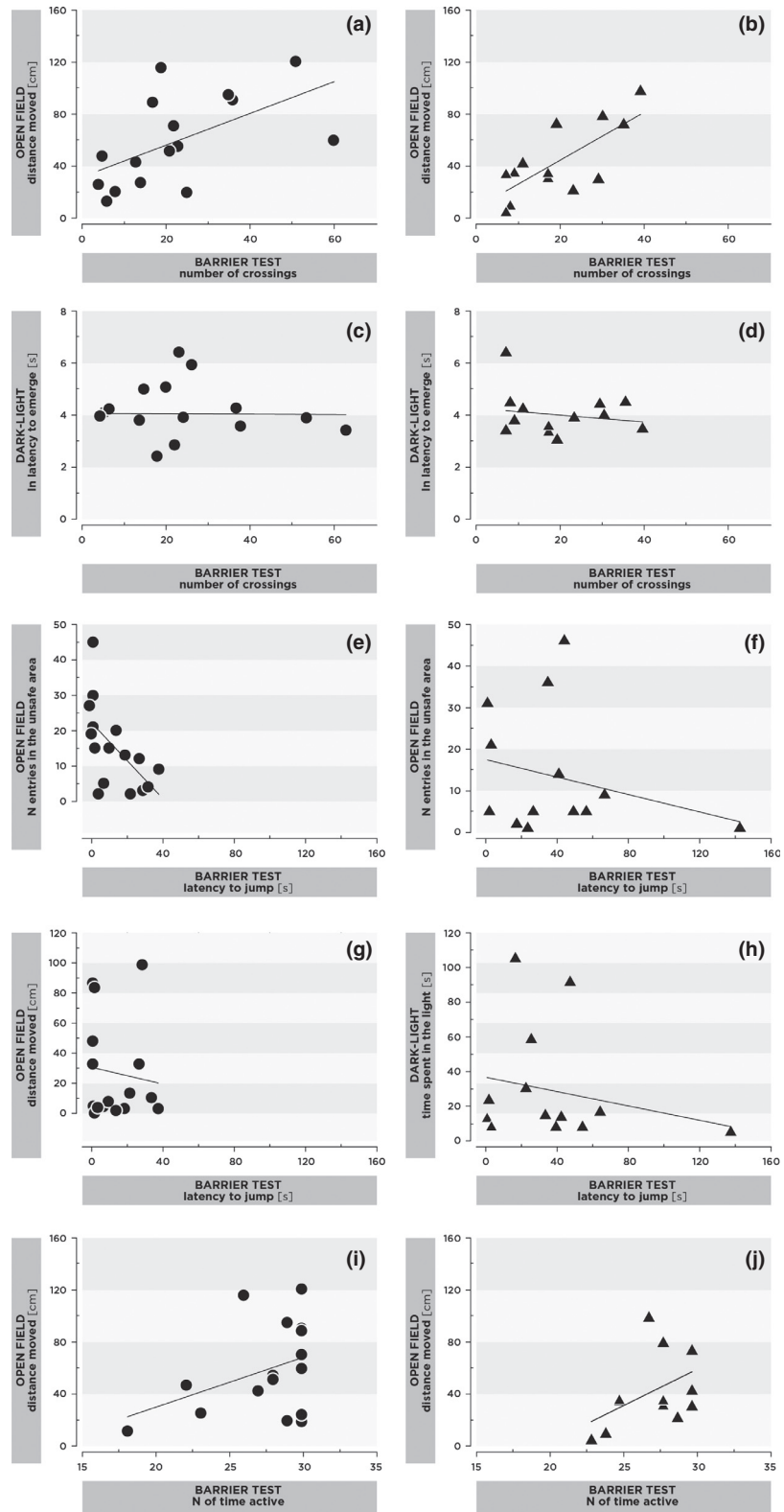
Experiment B

Single behaviours and corticosterone response

After 4 wk of the 'season treatment', there was no effect on body weight (*t*-test: $t = -1.285$, $p = 0.210$; winter females: $\bar{x} + SE = 20.67 + 1.05$ g; summer females: $\bar{x} + SE = 22.45 + 0.82$ g) of the female common voles. There was also no significant effect of the treatment on any of the behaviours measured in any of the three behavioural tests (Table 2).

A significant interaction between the treatment and the hours after stress (mixed model: $F_{3,20.717} = 3.3$, $p = 0.038$) was found on the levels of corticosterone metabolites in adult females. When the two groups are analysed separately, no effect of hours after stress was found for the summer animals (mixed model: $F_{3,10.015} = 1.277$, $p = 0.335$), while a significant increase in CORT metabolites over time is found in

Fig. 4: Contextual generality in young common voles (experiment A). Scatter plots represent the expected linkages between different behaviours in young voles after the seasonal treatment. On the left side (white dots), the Su–Su group; on the right side (dark triangles), Su–Wi group. See the text for the description of the panels (a–j).

Table 1: Consistency over time in behaviour (differential consistency) of juvenile common voles (experiment A)

		All groups		Su–Su		Su–Wi	
Test	Variable	r	p	r	p	r	p
Open field	Activity	0.587	0.001	0.665	0.004	0.377	0.205
Barrier test	Number of crossings	0.395	0.038	0.258 (r_s)	0.354	0.703	0.007
Dark–light test	Latency to emerge	0.389	0.045	0.488	0.055	0.100	0.770
Barrier test	Latency to jump	0.067 (r_s)	0.736	0.304 (r_s)	0.270	0.229	0.451

Pearson correlations, or Spearman correlations were differently indicated (r_s), are shown in the overall group and in the summer–winter (Su–Wi) and summer–summer (Su–Su) experimental groups (experiment A).

Table 2: Effect of treatment on single variables in the three different behavioural tests after 4 wk of season treatment in adult females

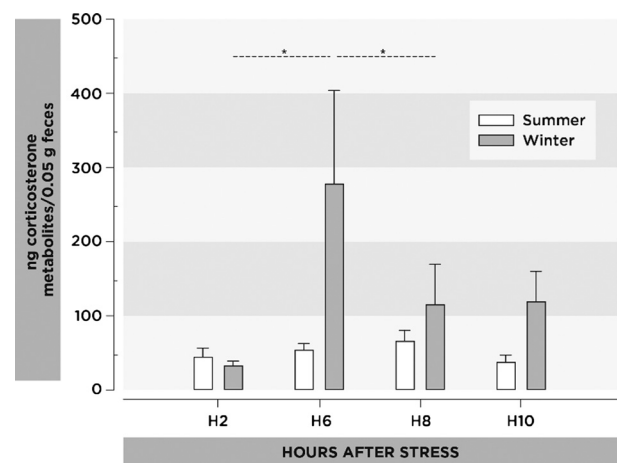| Behaviour	Summer ($\bar{x}$ + SE)	Winter ($\bar{x}$ + SE)	t	p
Open field – exploratory activity	43.5 + 4.77	55.87 + 5.88	1.6	0.122
Barrier test – number of crossings	9.92 + 1.98	14.43 + 2.22	1.541	0.136

	$\bar{x}$, 25th, 75th)	$\bar{x}$, 25th, 75th	U	p
Open field – entries in unsafe area	11, 6, 11	11, 8, 14	105.50	0.287
Barrier test – latency to jump	23, 1.5, 80	2.5, 1, 46.75	66.500	0.239
Dark light – latency to emerge	41, 23, 342.5	57.5, 342.5, 152	104.00	0.550
Dark light – time spent in the light	8, 3.5, 316.5	16.5, 9.25, 43	117.0	0.220

Summer and winter average ($\bar{x}$) and standard errors (SE) or median ($\bar{x}$) followed by 25th and 75th percentiles; Statistic: Mann–Whitney (U) or t-test (t) followed by p-value.

Fig. 5: Stress response in adult females (experiment B). Bars represent mean and SE of corticosterone metabolites (nanograms per 0.05 g of faeces); in the two experimental groups, summer (white bars) and winter (grey bars) at two (H2), six (H6), eight (H8) and ten (H10) hours after the stress was applied. *p < 0.05.

the winter group (mixed model: $F_{3,12.286} = 9.250$, p = 0.002), with levels reaching baseline at 10 h after stress (Fig. 5).

Contextual generality

When analysing linkages between different behaviours in different contexts, we found, as already found in wild-caught animals, a significant positive correlation between the *number of crossings* in the barrier test and the *activity* in the open-field test (Pearson correlation: r = 0.685, p < 0.001). When the two treatments are analysed separately, correlations hold for both summer (Pearson correlation: r = 0.816, p = 0.001) and winter (Pearson correlation: r = 0.569, p = 0.027) treatment; although the correlation coefficient is lower in the winter, the two correlations do not significantly differ (Z = −1.164, p = 0.244). A

significant negative correlation was found between *number of crossings* in the barrier test and *latency to emerge* in the dark–light test (Pearson correlation: r = −0.391, p = 0.044); in winter (Pearson correlation: r = −0.334, p = 0.206) and summer-like conditions (Pearson correlation: r = −0.370, p = 0.158), correlations between these two behaviours do not significantly differ (Z = 0.313, p = 0.753). Also, the *latency to jump* the barrier and the *number of entries in the unsafe area* are significantly negatively correlated (Spearman rank correlation: r_s = −0.391, p = 0.048) but the two correlations (Spearman rank correlation summer: r_s = −0.594, p = 0.043; winter: r_s = −0.347, p = 0.205) do not significantly differ (Z = −0.751, p = 0.452). Likewise, the *activity* in the barrier test and the *exploratory activity* in the open field showed the expected correlation (Pearson correlation: r = 0.554, p = 0.002). In this case, the summer-like treatment (Pearson correlation: r = 0.781, p = 0.002) revealed a significant correlation, whereas the

correlation in the winter-like treatment (Spearman rank correlation: $r_s = 0.451$, $p = 0.091$) was much weaker, although the two correlations do not significantly differ from each other ($Z = 1.33$, $p = 0.181$). Opposite to what we expected, the *latency to jump* in the barrier test and the *time spent in the light* in the dark–light test were not significantly correlated to each other (Spearman rank correlation: $r_s = 0.106$, $p = 0.583$). When analysing the treatment separately, in the summer (Spearman rank correlation: $r_s = 0.514$, $p = 0.072$), a trend is found, whereas in the winter (Spearman rank correlation: $r_s = -0.238$, $p = 0.374$) group, no significant linkage is found. The correlation comparison showed that the two linkages almost significantly differ ($Z = -0.192$, $p = 0.053$).

Discussion

Animal personalities are characterized by consistent individual differences in suites of traits. Nevertheless, it can be expected that animals, certainly during development, can adapt their behaviour to profound environmental changes. For animals living in the temperate zone, adjustment to the different seasons may require a seasonal change in a suite of behaviours and physiology. We therefore tested experimentally to what extent a change in cues related to a change in season (photoperiod and food) may affect single behaviours and suites of traits, including stress reactivity. We hypothesized that the winter period (short-day length and low-quality food) may require a cautious risk-aversive phenotype, whereas the summer period a more bold and risk-taking phenotype. Overall, we found evidences for the season modulating single behaviours, suites of traits and HPA reactivity. However, whereas young voles (experiment A) showed a clear response in behaviour, body mass and corticosterone to the experimental change in seasonal cues, adult females only showed a response in the latter.

Juvenile Plasticity

Young voles, reallocated to the winter 'environment' (Su–Wi treatment) directly after weaning, were less active in the open-field test and showed a longer latency to jump in the barrier test. Although no effect was found in an anxiety test, these data suggest that early life change from summer to winter environment induces a less active and more cautious behavioural phenotype. In line with this, we found that our winter condition induced also a higher level of both basal- and stress-induced corticosterone levels, indicating an increase in corticosterone response that may be causally linked with more cautious behaviour. Such a correlation between the degree of shyness and HPA reactivity has been found in several animal species, including mice (Veenema et al. 2003a,b) rats (Koolhaas et al. 2010; Diaz-Moran et al. 2012) and great tits (Carere et al. 2003; Carere & van Oers 2004). It has been shown before that shy individual have a higher stress-induced corticosterone levels than bold individuals (Carere et al. 2003; Cavigelli & McClintock 2003; Veenema et al. 2003b). Seasonal variation in glucocorticoids secretion (baseline) has been found in various vertebrate species including mammals (Ransone & Bradley 1992; Dunlap & Wingfield 1995), but in the latter, no clear consistent pattern seems to emerge (for a review see Romero 2002). Like in our case, in some photoperiodic rodents, for instance male Siberian hamsters, short-day lengths induce a higher cortisol concentration both at baseline and in response to a stressor (Bilbo et al. 2002). However, in the golden hamster, exposure to short-day lengths leads to a decreased secretion in circulating glucocorticoids or shutoff of stress responses when compared to long-day lengths (Ronchi et al. 1998). The finding that winter cues increased corticosterone and also lowered body mass may suggest that the latter is the cause of the former, as low body condition is often associated with increased corticosterone production (Dallman et al. 2004; H. Bobby Fokidis et al. 2011). However, this seems unlikely as in experiment B we found a similar effect of corticosterone but no effect on body mass. It is therefore unlikely, to our opinion, that a shift in energy balance related to the food component of our treatment has induced the observed changes in corticosterone response. The effect of our treatment on body mass is interesting as both treatments received *ad libitum* food, but the Su–Wi group is significantly lighter in body mass at PT2 when compared to Su–Su. The effect could be due to the difference in food quality. However, other studies have experimentally shown that photoperiod alone can function as a key cue to promote a reduction in body weight (Ho et al. 2012). In free-living photoperiodic rodents, a reduction in body mass in winter conditions has also been reported (Chen et al. 2012). The fact that we found both an effect of seasonal cues on personality traits and body mass is in line with the suggestion of Biro and Stamps (2008) that boldness and activity may correlate with, for instance, food intake rate.

We found no effect in sexual maturation of young voles in the post-weaning environment, which is not

in line with what has been reported for other seasonal breeders (see Walton et al. 2011a for a review). For example, although in the Siberian hamster perinatal effects of photoperiod are present, an overruling effect of post-weaning environment on the pre-weaning photoperiodic environment has been reported (Weil et al. 2006). However, in that study, sexual maturation was measured in terms of testis and uterine mass, perhaps a more sensitive measurement. Moreover, the post-natal treatment lasted 8 wk, twice as long as ours. Alternatively, it might be that the effect of the early environment (summer season) and potentially maternal effects (effect of the summer season during pregnancy) induced a long-lasting programming effect for a fast sexual maturation at the time of the seasonal switch (weaning).

In several aspects, differential consistencies (correlations in behaviour over time across individuals or repeatability) and contextual generalities were found, indicating that personality differences exist in this species. In all three cases where we found differential consistency among all individuals, the correlation was significant only in one treatment group and not in the other. The difference in these correlations between the treatments was never significant, but it is likely that our sample size was too limited for proper testing. Therefore, negative results should be taken with caution, but it is interesting that despite this low power, we still found several of the expected correlations to be significant in this study. Moreover, the conservative statistical approach we used to measure differential consistency and contextual generality in both experiments, mainly imposed by the distribution of the data and the experimental design, might have posed some limitations in the interpretation of the results. Future studies of this type should therefore be designed to allow a more advanced statistical approach (see Dingemanse & Dochtermann 2013) that includes assessments of repeatability in personality and improved comparisons of both between- and within-individual variation in behaviour.

In the case of contextual generality, where we tested four possible correlations, in three of them was a (nearly) significant correlation found. Only in one of these cases, the correlation coefficient showed a substantial difference but, probably due to low power, this difference only approached significance. So while effects of the treatment on single behaviours were significant, no statistically significant effect on correlations among traits was found. Although these results have to be taken with caution, they suggest that there might be no change in differential and contextual generality despite change in single behaviours. This

finding suggests that personality in the Su–Wi group has shifted from bold to shy without breaking the linkages between the behaviours involved but more extensive studies may well show that also these linkages show plasticity.

Adult Plasticity

Adult females (experiment B) did not show any change in single behaviours following the seasonal treatment suggesting that adult females in reproductive state are not as plastic, in behaviour, as juveniles with respect to seasonal changes. Also, no effect on body mass was shown. Two explanations may be applicable for the observed adult unresponsiveness: first, it has been shown that although adult Siberian hamsters can exhibit a suit of physiological changes when exposed to short days, the winter phenotype is strongly influenced by the previous photoperiodic history (Goldman et al. 2000). Second, it has also been shown for that species that responsiveness to short days is at least partially age related (Bernard et al. 1997; Benabid et al. 2008). It has been hypothesized that this age-related change in responsiveness can have an important role in the reproductive success of animals in the wild and can constitute an adaptive strategy used by organisms to maximize reproductive success (Goldman et al. 2000). Eccard and Herde (2013) showed that adult common voles show bolder and less variable behaviour in spring compared to summer, winter and autumn, when population variability in measured behaviour is high. A change from summer to winter conditions may not induce such a drastic change in behaviour. Nevertheless, similar to the young voles, an effect of the seasonal treatment on the stress response was found: summer females seem to be unresponsive to the stress test whether winter females show a significant increase in faecal CORT metabolites 6 h after stress. The effect of the winter treatment is therefore in the same direction in young and adult voles.

Contextual generality over all animals was found in four combinations of behaviours, three being the same as in the young voles. This suggests that the outcome of these tests was not just significant by chance alone. In one of these, the treatment seemed to affect the correlation coefficient, but due to low power, the test yielded only a non-significant trend; Interestingly, the treatment affected the strength of the correlation significantly in a fifth case, suggesting that an almost significant positive correlation in the Su animals changed into a non-significant negative one due to the winter treatment.

Conclusions

Our data suggest that the juvenile phase, after the weaning period, is still a sensitive phase to adjust both behaviours, body mass and HPA axis sensitivity to a change in seasonal cues. Due to power limitation, it is less clear whether personality's main characteristics (differential consistency and context generality) were affected by our treatment. Winter conditions, as presented in our treatment, seem to induce a more cautious personality in the juvenile phase although at this stage is not possible to know whether photoperiod or food quality induced these changes. Adults seem to be responsive in their HPA axis and not in their body mass and behaviour. Our data therefore show that personality may be a trait that can be adjusted during late development by a shift over the bold–shy axis. Whether a more fundamental reorganization of personality in terms of contextual generality or differential consistency can change due to changing seasonal cues is less clear and should be tested more extensively. Follow-up studies should also test (1) whether the 'winter' cues rather than any drastic environmental change during early life can cause the phenotype shift we did observe in the juvenile experiment, and (2) whether one or both seasonal cues we used (photoperiod and food quality) contribute, and to what extent, to trigger the changes observed in the current experiment.

Acknowledgements

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