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DIPLOMARBEIT

Behavioural variation in the field cricket (*Gryllus integer*), what is the role of heritable components?

angestrebter akademischer Grad

Magistra der Naturwissenschaften (Mag. rer.nat.)

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Wien, im Dezember 2009

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Abstract

Individuals of the same size or sex, even within a single population, vary in the way they behave when facing challenges in their environment. Variation in behavioural responses is comparable to variation in human personalities. However, this variation is not necessarily random or haphazard. Like humans, animals show consistent behavioural styles both across time and situations. Consistent behavioural differences between individuals, occurring repeatedly within contexts, make up an overall personality that can be heritable. Further, behavioural styles may be consistent across contexts, i.e. they form a behavioural syndrome that may be observed at population level as a correlation between behaviours. One of the most familiar behavioural linkages is the aggressiveness-activity behavioural syndrome.

In this study I used sexually mature field crickets (*Gryllus integer*) from a laboratory stock as model animals to explore experimentally the relationship between individual variation in exploration activity and intrasexual aggression (indicating potential for dominance) and to estimate if behavioural traits are heritable. I tested my hypotheses using laboratory experiments that measured a) individual willingness to exit from a shelter into an unfamiliar, potentially dangerous environment and afterwards b) the individual's fighting success and the resultant dominance rank of males in male-male competition.

I used full-sib-half-sib analysis and parent-offspring-regression to study the heritability of the examined behaviours. In addition, I examined if life-history traits (i.e. mass, developmental time to maturity and mounting rate) were correlated with behavioural measures.

I found that latency to become active and latency to emerge were highly correlated in both generations, and could represent a single trait, exploration activity, but there was no correlation between exploration and aggressiveness, i.e. no detectable behavioural syndrome. Therefore, my study could not confirm the previous observations of presence of aggressiveness–activity behavioural syndrome in the *G. integer*.

However, there is still relatively little theory and data to explain the causes of behavioural correlations. There is evidence that behavioural syndromes may not be universal, even within a species. It is possible that because of the lack of predation pressure, competition for food or other natural stimuli, the syndrome will break apart. Individuals that I used in my studies were from F5 to F6 laboratory generation whereas in the previous work offspring of wild animals had been used. My results also suggest that shy individuals are both heavier and gain maturation faster than bold ones. Further, in contrast to previous studies, aggressive,

intrasexually dominant males did not obtain a higher mounting rate, i.e. female preference, than less dominant males.

In contrast to negative and therefore not reliable heritability estimates for behaviours derived from sib analysis, I found small heritable components using parent-offspring regression. Heritability estimates for latency to emerge derived from parent-offspring-regression ranged from 0.026 to 0.128. In the aggression dataset (males tested in the exploration as well as aggression trial) the heritability of the used PC for exploration derived from sire-son-regression was 0.042 ± 0.056 while heritability estimate of fighting success was 0.23 ± 0.40. Therefore, latency to emerge and fighting success seem to have small heritable components, which make them susceptible to evolutionary changes and facilitate behavioural adaptation to varying environments.

Introduction

Individuals of the same size or sex, even within a single population, use to differ in their behavioural tendencies (Clark & Ehlinger 1987; Magurran 1993; Wilson 1998; Bell 2007). However, between-individual variation in behaviour is not necessarily random or haphazard. In the last decade, behavioural ecologists have recognised that, like humans, animals show consistent behavioural traits both across time and situations (e.g. Gosling & John 1999; Drent et al. 2003; Reale et al. 2007). These consistent behavioural differences, when occurring repeatedly within single contexts, form personality traits (Gosling 2001) or when occurring across contexts, form behavioural syndromes (Sih et al. 2004 a,b; Bell 2007).

A behavioural syndrome is defined as a suite of correlated behaviours reflecting between-individual consistency in behaviour through time and/or across multiple situations which is exhibited by a population or species (Sih et al. 2004a,b; Reale et al. 2007). Within a syndrome individuals have a behavioural type (e.g shy or bold, more or less aggressive, etc.) that refers to the particular configuration of behaviours that an individual expresses (Sih et al. 2004a,b; Bell 2007). Behavioural syndromes are not only restricted to humans (Pervin & John 1999), and over the last few years several evolutionary and/or ecological studies have documented animal personalities in many species (Sih et al. 2004a,b), including mammals (e.g. Anestis 2005; Dochtermann & Jenkin 2007), birds (e.g. Carere et al. 2005; van Oers et al. 2005; Duckworth 2006), lizards (e.g. Stapley & Keogh 2005), amphibians (e.g. Sih et al. 2003), fish (e.g. Brown et al. 2005; Bell & Sih 2007) and insects (e.g. Hedrick 2000; Johnson & Sih 2005; Kortet & Hedrick 2007). However, behavioural syndromes may not always

occur, or be detectable, within a species or between populations of a same species (Coleman 1998; Bell 2005). It is still not clear why some individuals differ in their behaviour and are e.g. consistently bolder or more active than others (Biro & Stamps 2008). Main hypotheses for the maintenance of behavioural variation in a population of otherwise similar individuals were reviewed by Weissing & Wolf (2009). These hypotheses include mutation-selection balance, frequency dependent selection, spatiotemporal variation in environmental conditions, inaccurate environmental information, the idea that growth-mortality, and other life-history trade-offs may maintain differences in behavioural traits in nature (Stamps 2007, Wolf et al. 2007, Biro & Stamps 2008, Weissing & Wolf 2009).

Increasing interest in animal personality and behavioural syndromes has encouraged a new perspective on animal behaviour (Bell 2007). The traditional opinion in behavioural ecology has been that natural selection favours one optimal behaviour in each context. While this view is not mutually exclusive to the behavioural syndromes approach, the more recent studies within the field of behavioural ecology have begun to emphasize carryovers across contexts (Sih et al. 2004a,b; Bell 2007). Such carryovers are analogous to genetic trade-offs among life-history traits and may partially be caused by constrains, such as pleiotropy, in the genetic architecture of behaviours. An example of carryovers that cause correlations between behaviours exhibited in the same context but across different situations is foraging activity in presence versus absence of predators. Individuals that feed most actively without predators might also continue feeding relatively actively when they are present (Sih et al. 2003; Sih et al. 2004b). This example provides evidence for a trade-off between foraging and predator avoidance, and cost for behavioural inflexibility due to the activity carryover across situations (Sih et al. 2004b). Even sexual cannibalism could be explained as a non-adaptive carryover from a general feeding aggression syndrome (Arnqvist & Henriksson 1997). As a consequence, the idea of a behavioural carryover or spillover suggests that individuals show limited behavioural plasticity (Sih et al. 2004a,b). On the other hand, strong consistencies, when heritable, form a basis how evolution can shape behavioural traits.

To sum up, the central ideas above are that behavioural correlations may result from genetic trade-offs and potentially maintain individual behaviour variation in a variable environment, explain limited behavioural plasticity and also maladaptive behaviour that would be otherwise hard to understand (Sih et al. 2004a,b). Hence, personality has a major influence in many aspects of an individual's behavioural repertoire including habitat use, predation avoidance, dispersal or social behaviour (Dingemanse et al. 2003; Dall et al. 2004; Sih et al. 2004b; Dingemanse & Réale 2005). Behavioural syndromes often have underlying

physiological or neuroendocrine correlates (e.g. Koolhaas et al. 1999; van Riel et al. 2002; Carere et al. 2003; Bell 2007). Most importantly, recent studies show that an individual's behavioural type is related to its fitness (Dingemanse & Réale 2005; Bell 2007). Future research in personality could even inure to benefit humans (Cavigelli 2005) because of the link between specific personality traits, specific physiological mechanisms and health consequences that is recognised both in humans (e.g. Kagan & Snidman 1991; Dawe & Loxton 2004) and in animals (e.g. Gentsch et al. 1982; Koolhaas et al. 1999; Carere & van Oers 2004). Further work on individual differences across species may disclose universal elements of personality, also present in humans (e.g. shyness-boldness axis identified by Wilson et al. 1994; Cavigelli 2005).

Consistent intraspecific behavioural variations have been established along a number of axes (Sih et al. 2004b) such as activity (Sih et al. 2003), shyness/boldness (Wilson et al. 1994; Coleman & Wilson 1998; Wilson 1998; Fraser et al. 2001), aggressiveness (Riechert & Hedrick 1993; Maupin & Riechert 2001), fearfulness (Boissy 1995), exploratory behaviour (e.g. Verbeek et al. 1994) and proactivity/reactivity (Koolhaas et al. 1999; Reale & Festa-Bianchet 2003). One of the most familiar behavioural syndromes is an aggressiveness/activity syndrome, in which individuals behave more or less aggressive are respectively more or less active across many contexts (Sih et al. 2004a,b). Studies in funnel-web spiders demonstrated that some individuals are more aggressive with conspecifics than others, attack prey more vigorously, and expose themselves to higher predation risk because of their 'bold' or incautious behaviour in the presence of predators (Hedrick & Riechert 1989; Riechert & Hedrick 1993; Kortet & Hedrick 2007). In general, bold individuals tend to take risks, approach novel objects and explore novel environments. In contrast, shy individuals tend to be risk averse and are generally neophobic (Wilson et al. 1994; Brown et al. 2007b). Behaviour of shy individuals in novel situations is often accompanied by fear responses, such as freezing (Brown & Smith 1996; Budaev et al. 1999a,b; Templeton & Shriner 2004; Brown et al. 2007b). In many species, including stickleback fish (Huntingford 1976, 1982; Bell 2005) and fishing spiders (Johnson & Sih 2005) aggressiveness towards conspecifics is correlated with risky bold or noncautious behaviour under predation risk.

In field crickets (*Gryllus spp.*), certain species are known to form social dominance hierarchies, in which more aggressive males achieve higher dominance status by winning fights (Andersson 1994; Rantala & Kortet 2004, Kortet & Hedrick 2007). Success in these aggressive contests translates to high resource holding potential, i.e. helps males to ensure their access to resources and females. The recent results from a study by Kortet and Hedrick

(2007) suggest that a behavioural syndrome exists in offspring of wild collected crickets (*G. integer*): more aggressive males were generally more active, and possibly less cautious towards a predation risk. The previous data on the offspring of the wild collected mothers suggested that more aggressive males, who won more fights, had both shorter latencies to become active in a novel environment and to emerge from a safe refuge (Kortet & Hedrick 2007). Fighting success may also correlate with male's resistance against parasitism, and result in increased fertilization success for dominant males (e.g. Rantala & Kortet 2004; Kortet & Hedrick 2005). Fighting success is a heritable trait at least in one species of field crickets (*G. bimaculatus* De Geer; Wedell & Tregenza 1999).

Recent observations from various animals suggest that behaviours such as boldness or exploratory behaviour may have heritable components (Dingemanse et al. 2002; Drent et al. 2003; van Oers et al. 2004a,b). For example, in the dumpling squid consistent intraspecific behavioural variations have been established for shy–bold, activity and reactivity responses (Sinn et al. 2006). The same study also detected that behaviours from foraging contexts ($h^2 = 0.05 - 0.08$) and especially behaviours in antipredator contexts were statistically significantly heritable ($h^2 = 0.2 - 0.8$). Moreover, Brown et al. (2007b) suggested a heritable component in the boldness of a tropical poeciliid (*Brachyraphis episcopi*): the first-generation laboratory-reared fish resembled their wild parents in their behaviour. Differences between males and females were also sustained in the laboratory-reared generation indicating that there are heritable aspects in sex differences in boldness (Brown et al. 2007b).

In this study, as model animals, I used sexually mature field crickets (*Gryllus integer*) from a laboratory stock to explore experimentally the relationship between individual variation in exploration activity and aggression (indicating potential for dominance) and estimate whether there are heritable components in these behavioural traits / measures. Because these relatively small (< 1,2 g in weight), short-lived animals are easy to hold and rear, they are excellent subjects for this kind of research, especially to examine heritable components in behaviour. Based on current theory presented above I predicted that 1) individuals that spent a greater proportion of time until moving in the tube would also need more time hiding in the shelter, 2) aggressive and therefore dominant males would move and emerge from the vials into an unfamiliar environment sooner than less aggressive males, 3) aggressive, intrasexually dominant males would obtain a higher mounting rate than less dominant males, 4) behavioural traits would be heritable, and the behavioural syndrome would be present in both generations.

I tested my hypotheses using laboratory experiments that measured a) individual's willingness to exit from a shelter into an unfamiliar, potentially dangerous, environment and afterwards b) individual`s fighting success and the resultant dominance rank of males in male-male competition. My methodology was modified from the previous work by Kortet and Hedrick (2007). Ultimately, I aimed to examine if the studied behaviours are heritable.

For this purpose I used sib analysis and parent-offspring-regression. In addition, I examined if life-history traits (i.e. mass, developmental time to maturity and mounting rate) were correlated with behavioural measures.

Material and Methods

Crickets

The study was conducted during 2009. Field crickets used in the experiments were from approximately the 5th to 6th laboratory generation of the founder stock originating from wild populations in Davis, California, USA. The animals were maintained at the Experimental Unit of the Department of Biology, University of Oulu, Finland. They were kept under a constant 12 h : 12 h light-dark cycle and maintained at $27 \pm 1°C$ with *ad libitum* food (fish and reindeer pellets (Raisio, Finland) as well as fresh cabbage) and water. Crickets were derived from the bulk laboratory stock (population size more than 2000 individuals) as larvae/nymphs and reared individually (also with *ad libitum* food and water) in covered plastic containers (length 12.8 cm x width 9.8 x height 7.3 cm). There was a hole (3.2 cm in diameter) in the lids of these rearing containers which was covered with a plastic net for a better evaporation and ventilation. These boxes also contained a shelter out of cardboard, food and a drinking trough (smaller container 4 cm in diameter with a tiny hole in the lid where a stick out of cotton was put in). All the study animals were physically, but not acoustically, isolated from other individuals to control for their experience and ensure virginity. The second generation was housed individually in similar containers from 20 days post-hatching. All experiments were performed at approximately the same time.

Experimental trials

Experimental trials on activity in a novel environment and exploration

Methods of behavioural testing to assess the "cautiousness" of individual crickets were similar than previously used by Hedrick (2000) as well as Kortet and Hedrick (2007). Experimental trials were accomplished in a sound-proof, temperature controlled dark experiment room ($27 \pm 1°C$). Experimental set-up was composed of a computer, a desk and three arenas (length 18.8 cm x width 18.8 cm x height 11.2 cm) which were illuminated by red filter light (25 W red incandescent bulb). This light was used to mimic nocturnal conditions. Each arena was additionally placed in a 1.5 cm thick box (length 28.2 cm x width 27 cm x height 20.7 cm) out of polystyrene for acoustic shielding. Therefore, three trials could be performed next to each other at the same time.

The exploration trials were used to measure the latency of each cricket to become active and emerge from a shelter (a 7.7 cm long, 2.3cm in diameter translucent plastic vial with a small glass base: length 7.5 cm x width 2.1 cm x 2 mm) when placed in a novel, potentially dangerous environment.

Trials started after the crickets were acclimatized in the dark experimental room for 10 minutes. At the beginning of each trial, a cricket was placed in a transparent experimental tube which was set upright in the centre of the experimental arena. After two minutes, for acclimation of the crickets to the environment, vials were carefully laid down lengthwise in the arena and a plexiglass cover was set over the top of the arena to attenuate sounds from outside the arena and to bar crickets from escaping.

Each trial lasted for 10 minutes. If a cricket did not move within that time, the trials were ended because former experiments had shown that if a cricket did not emerge within 10 minutes, it often hid for another 10 minutes or more (Hedrick & Kortet 2006). During these trials two parameters "first movement" and "out of vial" were recorded using the software "AV Bio-Statistics 4.9 Professional" (copyright Anssi Vainikka). The time when a cricket first moved and the time at which a cricket's entire body was out of the vial were measured and used as measures for exploration behaviour.

After the trials, crickets were weighed with an electronic analytical balance and their mass was recorded to the nearest 0.001g. The mass data was then used to size match individuals in later intrasexual aggression trials. The inside of the box and the vial were carefully cleaned with 70% alcohol solution and dried after each trial to reduce the effects of residual pheromones.

For exploration trials, only mature, virgin crickets that had had their final moult a week ago were used to control for potential age-dependence in behavioural traits. We raised 300 crickets of the first generation to sexual maturity and 243 (124 males, 119 females) of them were tested. In total, 510 crickets of the second generation (271 males, 239 females) were used in the experiments. No cricket was used in more often than once in exploration trial.

Intrasexual aggression trial

Methods of testing the aggression and dominance rank of individual crickets were similar as described previously by Hedrick and Kortet (2007). Aggression trials were accomplished in the same sound-proof, temperature controlled dark experiment room (27 ± 1°C) than the exploration trials. Intrasexual aggression was quantified as frequency of battles won in six minutes. Fighting success was measured within 2-4 days, always one week after the exploration trial. During the intrasexual aggression trials, the experimental males, who were also tested in the exploration trials, were compared to reference males. These reference males were randomly removed from bulk boxes and thereafter housed individually. Most of the males got their maturity in isolation. For recognition in the trials, the experimental males were anaesthetized using carbon dioxide, and then marked on the left or right sides of the pronotum with enamel paint. Male body mass affects fighting success in some cricket species (*G. bimaculatus* and *Acheta domesticus* L.; Hofmann & Schildberger 2001; Savage et al. 2005). Therefore, all the males were matched by body mass. In this study, maximum 6% weight difference between experimental males and reference males was accepted. Because of the evidence that some males need to have a female present before becoming aggressive at all, a female was placed to the arena along the two males in each trial (Kortet & Hedrick 2007).

Trials started after the focal crickets had been acclimatized in the dark experimental room for 10 minutes. At the beginning of each trial one experimental male, one reference male and one female (to trigger males to fight) were placed under separate plastic vials (3.8 cm long and 6 cm in diameter) in an arena for two minutes to calm them down. The bottom of the arena approx. 25 cm in diameter was covered with sawdust and illuminated with red filter light (25 W red incandescent bulb). After each trial sawdust was replaced. After removal of the vials the male-male contest was observed for 6 minutes. Usually males started fighting immediately, sometimes even with the female. Time and frequency of two parameters "loss" and "mounting" were recorded using the software program "AV Bio-Statistics 4.9 Professional". An individual's level of aggression is related to its dominance rank (Huntingford & Turner 1987). Therefore, the within-pair dominance status of each male was

recorded by the number of times he lost aggressive encounters which included wrestling, biting but also chasing. Avoidance behaviour and retreat shown by one cricket after a fight, were regarded as signs of submission and thus as an indication about losing a fight. Every male's score was counted using a relative number of fights he won in every contest. The final aggression score was the average relative number of the fights a male won in three aggression trials.

Additionally the number of mountings was recorded to compare whether male attraction was depended on his dominance on fighting success. Females were not allowed to mate during these trials. They were immediately separated from males with a wood stick if they started mounting a male. Mounting score was defined by the same method as aggression score.

Each experimental male was used in three intrasexual aggression trials, always with different reference male and female.

22 male crickets of the first generation and 72 of the second generation were tested in aggression trials. All experiments were done at approximately the same time between 8.00 and 13.00 h to control for possible fluctuations of aggressiveness within a day.

Mating

After the behavioural trials of the first generation, 26 sires were each mated to three different virgin females (in total 78 females). Mate pairings between field crickets were performed blind with respect to behavioural phenotype and body size, but mates were chosen roughly on similarity in age. In order to ensure the fertility for reproductive analyses, female field crickets were mated up to three times with the male. A sire was placed, in random order, with one of his dams into an individual container for mating. The bottom of the arena 25 cm in diameter was covered with sawdust. They stayed there for an undefined time until they mated. Mated dams were established individually in containers out of plastic with a hatching box, a shelter out of cardboard, a drinking trough and food. The first individuals of the second generation eclosed from the hatching box approx. two weeks after the mating.

In total, the matings resulted in 62 full-sib families. For 19 sires, all three females had offspring. One male fertilized two of his dams and three males managed to fertilize only one dam. After the new generation emerged, 12 of the juvenile crickets from each female were randomly taken and raised individually from 20 days post-hatching.

Exploration tests were repeated using 510 individuals and aggression tests were repeated with 72 individuals of the second generation in the same way as in the former parent generation.

Heritability

Heritability (h^2) is a standardised index of the proportion of phenotypic variance that is explained by additive genetic variance of the trait and represents its evolutionary potential (Falconer & Mackay 1996). There are a number of techniques for the estimation of the components of variance in quantitative traits (Falconer & Mackay 1996; Lynch & Walsh 1998). In the present work I used parent-offspring-regression and sib analysis.

Parent-offspring-regression is one of the most common methods for estimating heritabilities. Advantages of the regression of offspring phenotypes on those of their parents are that neither dominance nor linkage influences the covariance between parents and offspring and it is unbiased by selection on parents. Further, resemblance (caused by shared alleles) between parents and offspring can be measured directly (Lynch & Walsh 1998). The slope of the regression is a direct estimate of the heritability (Falconer & Mackay 1996; Lynch & Walsh 1998). I estimated heritabilities of my aggression (males tested in the exploration as well as aggression trials) and exploration dataset (individuals tested only in the exploration trials) using one parent-offspring-regression and midparent-offspring-regression, where heritability is the proportion of total variance that is attributable to the additive effect of genes (Falconer & Mackay 1996). In the case of one parent-offspring-regression heritability estimates were calculated as twice the least-square slope of the regression for one parent and offspring

$$b_{op} = \tfrac{1}{2}\, h^2$$

whereas the slope of the midparent-offspring-regression is equal the heritability estimate (for detail explanations: Falconer & Mackay 1996). Both parent as well as offspring generation were measured in the same way. Since the family size was not equal and therefore not balanced, I used a weighted least-squares regression which can minimize the sampling error of the heritability estimate derived from parent-offspring-regression (Lynch & Walsh 1998).

An alternative to the parent-offspring regression is the analysis of sibs. There are three types of sib analyses: half-sib analysis, full-sib analysis, and a combination of both (Lynch & Walsh 1998). In the present work I used the combination of full-sib-half-sib analysis where each male is mated to several unique females, from each of which several offspring are tested. So all offspring of a female are full-sibs, while progeny of different females mated to the same sire are paternal half sibs (Lynch & Walsh 1998). These family structures permit one to partition the total phenotypic variance into within- and among-family components and both can be interpreted in terms of covariances between relatives (Lynch & Walsh 1998). The linear model for this nested design is

$$z_{ijk} = \mu + s_i + d_{ij} + e_{ijk}$$

where z_{ijk} is the phenotype of the kth offspring from the family of the ith sire and the jth dam, s_i is the effect of the ith sire, d_{ij} is the effect of the jth dam mated to the ith sire and e_{ijk} is the residual deviation (for detail explanations: Lynch & Walsh 1998). An advantage of the used method over only half-sib designs is its ability to provide insight into the potential significance of dominance and/or shared environmental effects (Lynch & Walsh 1998). As in half-sib design the best estimator of the heritability is

$$h^2 = 4t_{PHS}$$

where t_{PHS} is the intraclass correlation for paternal half sibs, since it is not inflated by dominance and/or maternal effects (Lynch & Walsh 1998). In the case, if variance among sires (var(s)) and variance among dams (var(d)) is approx. equal, then dominance and maternal effects can be ruled out as significant causal sources of covariance and then the average of var(s) and var(d) multiplied by 4/var(z) (total variance) provides an estimate of h^2 (for detailed explanations: Lynch & Walsh 1998).

Since the family size was almost equal, I did not correct the estimation of standard errors for unbalanced data. Data of all 510 individuals of the second generation were used for the parent-offspring regression as well as for the full-sib-half-sib design and 72 male offspring (aggression dataset) were used for the father-son-regression to estimate heritability of the behavioural variables.

Statistical Analysis

Normality of the studied parameters was checked using Kolmogorov-Smirnov test. For correlation of normally distributed variables I used Pearson's correlation tests (referred as r) and Spearman's rank correlation analysis (referred as r_s) for the others. To study the effect of X on Y I used a general linear model (ANCOVA), where mass and age were used as covariates. To examine between-sexes-differences in the mass and maturation time differences, I used ANOVA.

Linear regression was use to estimate heritability of parent-offspring-regression. Heritability estimations of exploration traits were done with a nested ANOVA in the statistical program "AV Bio-Statistics 4.9 Professional". This program estimates heritabilities according to equations presented in Lynch & Walsh (1998).

I used principal components analysis (PCA) to avoid type 1 error and to reduce the number of behavioural variables into two components, reflecting exploration behaviour (PC1). I combine the high positively correlated variables "latency to become active" and "latency to emerge" in to one PC to reduce the number of parameters for the heritability estimates. This PC explained

approx. 77 % of variance in these two variables. For all statistical analysis (except for full-sib-half-sib analysis) I used PASW Statistics 18.

Results

Explorative behaviour

I found a statistically significant positive correlation between latency to become active and latency to emerge from shelters into an unknown environment in the parent generation (Spearman, $r_s = 0.635$, $p < 0.001$, $n = 76$) as well as in the offspring generation (Spearman, $r_s = 0.502$, $p < 0.001$, $n = 510$) (Figure 1).
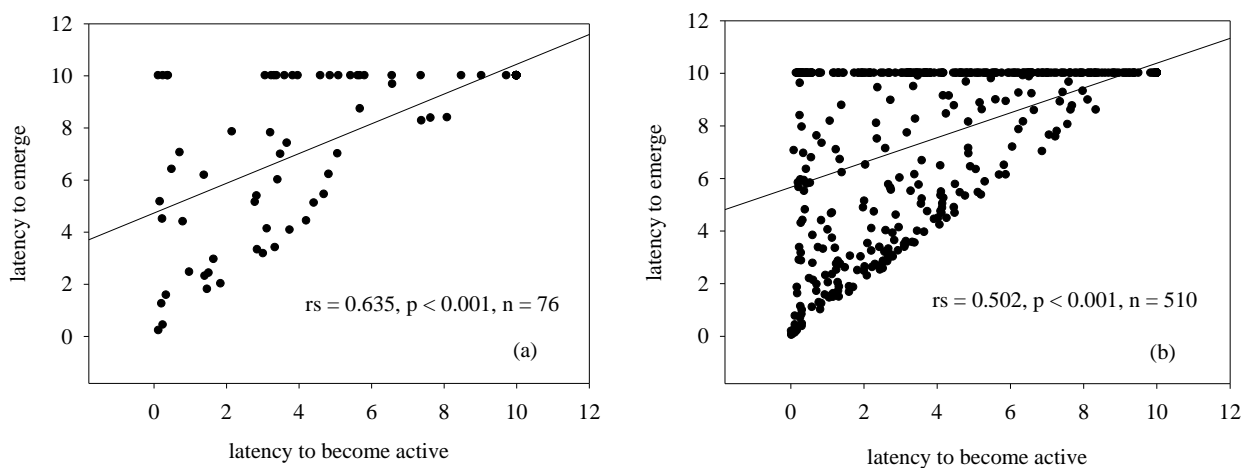
Figure 1. Results of correlations between latency to become active and latency to emerge in parent (a) and offspring (b) generation.

In the offspring generation body mass had almost statistically significant positive effect on latency to become active (ANCOVA, $F_{1,506} = 2.9$, $p = 0.089$) and a statistically significant positive effect on latency to emerge (ANOVA, $F_{1,506} = 7.489$, $p = 0.006$) suggesting that large individuals emerged last (Table 1 and 2). There was a significant negative effect of latency to emerge on development time to adult (ANOVA, $F_{1,506} = 13.61$, $p < 0.001$) suggesting that heavier and fast developing individuals had longer hiding times. I found no correlation between developmental time to adult and mass in the offspring generation (Spearman, $r_s = -0.025$, $p = 0.578$, $n = 510$) but in the parent generation there was a significant correlation between these variables (Pearson, $r = 0.237$, $p = 0.039$, $n = 76$). In neither generation gender had an effect on latency to become active (parent generation: ANOVA, $F_{1,72} = 0.021$, $p = $

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0.884; offspring generation: ANOVA, $F_{1,506} = 0.663$, p = 0.416) nor to emerge (parent generation: ANOVA, $F_{1,72} = 0.252$, p = 0.617; offspring generation: ANOVA, $F_{1,506} = 2.237$, p = 0.135). Males and females differed significant in their development time (U-test, Z = -3.231, p = 0.001, $n_1 = 271$, $n_2 = 239$), i.e. females gained maturity earlier than males (males: 103.46 days ± 17.7 days; females: 98.9 days ± 18.21 days). There was no difference in the body mass between males and females (T-test, F = 0.23, p = 0.880, $n_1 = 271$, $n_2 = 239$).

Table 1. Summary of GLM results of latency to become active.

Source of variation	Parent generation					Offspring generation				
	F	d.f.	Sig.	Estimate (B)	Partial η^2	F	d.f.	Sig.	Estimate (B)	Partial η^2
Intercept	9.654	1, 72	0.464	8.512	0.118	8.839	1, 506	0.003	4.114	0.017
Gender	0.021	1, 72	0.884	0.135	0	0.663	1, 506	0.416	0.270	0.001
Development time	1.824	1, 72	0.181	-0.028	0.025	2.489	1, 506	0.115	-0.014	0.005
Body mass	0.247	1, 72	0.621	-1.751	0.003	2.9	1, 506	**0.089**	2.845	0.006

Table 2. Summary of GLM results of latency to emerge.

Source of variation	Parent generation					Offspring generation				
	F	d.f.	Sig.	Estimate (B)	Partial η^2	F	d.f.	Sig.	Estimate (B)	Partial η^2
Intercept	9.544	1, 72	0.003	7.988	0.117	43.08	1, 506	< 0.001	8.001	0.078
Gender	0.252	1, 72	0.617	-0.423	0.003	2.237	1, 506	0.135	0.435	0.004
Development time	0.641	1, 72	0.426	-0.015	0.009	13.61	1, 506	**< 0.001**	-0.028	0.026
Body mass	0.178	1, 72	0.674	1.356	0.002	7,489	1, 506	**0.006**	4.006	0.015

Aggressive behaviour

I found no effect between the number of fights won and the latency to become active (parent generation: ANCOVA, $F_{1,6} = 1.119$, p = 0.331; offspring generation: ANCOVA, $F_{1,66} = 0.203$, p = 0.654) (Table 3). There was also no relationships between the number of fights won and the latency to emerge (parent generation: ANCOVA, $F_{1,6} = 1.470$, p = 0.271; offspring generation: ANCOVA, $F_{1,66} = 0.520$, p = 0.473). I found neither effect between number of fights won and number of mountings (parent generation: ANCOVA, $F_{1,6} = 0.703$, p = 0.434;

offspring generation: ANCOVA, $F_{1,66} = 0.222$, p = 0.639). Only in the offspring generation, development time to adult had a statistically significant positive effect on the number of fights won / aggression score (ANCOVA, $F_{1,66} = 10.58$, p = 0.002) suggesting that slower developing individuals were more aggressive and won more fights. Mass had no statistically significant effect on the number of fights won (ANCOVA, $F_{1,66} = 0.030$, p = 0.863) but on mounting rate in the offspring generation (ANCOVA, $F_{1,66} = 5.242$, p = 0.025) (Table 4) suggesting that heavier males have less mountings.

Table 3. Summary of GLM results of fighting success / aggression score

Source of variation	Parent generation					Offspring generation				
	F	d.f.	Sig.	Estimate (B)	Partial η^2	F	d.f.	Sig.	Estimate (B)	Partial η^2
Intercept	0.908	1, 6	0.377	-0.853	0.131	0.311	1, 66	0.579	-0.246	0.005
mounting	0.703	1, 6	0.434	0.238	0.105	0.222	1, 66	0.639	0.070	0.003
Body mass	0.852	1, 6	0.392	1.234	0.124	0.030	1, 66	0.863	0.095	<0.001
Latency to become active	1.119	1, 6	0.331	-0.054	0.157	0.203	1, 66	0.654	0.005	0.003
Latency to emerge	1.470	1, 6	0.271	0.077	0.197	0.520	1, 66	0.473	-0.009	0.008
Development time	0.222	1, 6	0.654	0.002	0.0036	10.58	1, 66	**0.002**	0.006	0.138

Table 4. Summary of GLM results of mounting scores

Source of variation	Parent generation					Offspring generation				
	F	d.f.	Sig.	Estimate (B)	Partial η^2	F	d.f.	Sig.	Estimate (B)	Partial η^2
Intercept	0.001	1, 6	0.973	-0.046	<0.001	14.51	1, 66	< 0.001	1.262	0.180
Body mass	0.252	1, 6	0.663	0.957	0.040	5.242	1, 66	**0.025**	-0.996	0.074
Latency to become active	0.015	1, 6	0.907	0.009	0.002	0.137	1, 66	0.713	-0.003	0.002
Latency to emerge	0.142	1, 6	0.719	-0.036	0.023	0.012	1, 66	0.912	0.001	< 0.001
Development time	0.021	1, 6	0.889	-0.001	0.004	2.264	1, 66	0.137	-0.002	0.033

Heritability

The nested analysis of variance included 19 sires, 3 dams per sire and approximately 9 offspring per dam in total of 510 offspring. The mean brood size in the full-sib-families (sibs within dams) was 8.94 ± 2.83 (range of 2-12). Since in my data variance among sires (var(s)) and variance among dams (var(d)) were never equal, the best estimator of the heritability was $h^2 = 4t_{PHS}$, which is the sire component (Falconer & Mackay 1996; Lynch & Walsh 1998). The heritability estimations of my data were negative because the variances among sires were small (Table 5-8). A negative estimate means that the results are unreliable (Lynch & Walsh 1998). Furthermore, almost none of the tests for the presence of additive genetic variance was significant. Only in the case of "latency to emerge", there seemed to be marginally significant additive genetic variance for the trait, however, h^2 was negative too.

Table 5. Summary of full-sib-half-sib analysis of latency to become active from the exploration dataset (n = 510). Heritability estimates were calculated according to equations presented in Lynch & Walsh (1998)

Factor	d.f.	Mean squares	Estimated variance components
Sires (s)	18	245.23	-0.623
Dams within sires (d)	38	157.19	0.484
Sibs within dams (e)	453	115.24	115.24
Total (z)	509	122.97	113.84
Estimates of heritability	**0 (-0.22 +/- 0.06)**		
Difference between var(s) and var(d) is 177.62 % (large values indicate strong dominance and maternal effects) Given that the difference is small, the h2, is (var(s)/var(z)*4 =-0.025 Otherwise, the estimate of heritability, h2, is **-0.22 +/- 0.06** (SE)			
Test for the sire effects in balanced set-up: F(18, 38) = 1.560, P = 0.123 Test for the dam effects: F(38, 453) = 1.364, P = 0.077 Test for the presence of additive genetic variance: F(19.6, 38) = 1.49, P = 0.145			

Table 6. Summary of full-sib-half-sib analysis of latency to emerge (n = 510). Heritability estimates were calculated according to equations presented in Lynch & Walsh (1998)

Factor	d.f.	Mean squares	Estimated variance components
Sires (s)	18	256.04	-0.903
Dams within sires (d)	38	130.29	0.474
Sibs within dams (e)	453	891.66	891.66
Total (z)	509	981.38	848.77
Estimates of heritability		**0 (-0.43 +/- 0.10)**	

Difference between var(s) and var(d) is 152.5 % (large values indicate strong dominance and maternal effects)

Given that the difference is small, the h2, is (var(s)/var(z)*4 =-0.10

Otherwise, the estimate of heritability, h2, is **-0.43 +/- 0.10** (SE)

Test for the sire effects in balanced set-up: F(18, 38) = 1.97, P = 0.04

Test for the dam effects: F(38, 453) = 1.46, P = 0.04

Test for the presence of additive genetic variance: F(19.2, 38) = 1.86, P = 0.05

Table 7. Summary of full-sib-half-sib analysis of PC exploration (n = 510). Heritability estimates were calculated according to equations presented in Lynch & Walsh (1998)

Factor	d.f.	Mean squares	Estimated variance components
Sires (s)	18	114.68	-0.030
Dams within sires (d)	38	0.723	0.028
Sibs within dams (e)	453	0.478	0.478
Total (z)	509	0.520	0.477
Estimates of heritability		**0 (-0.25 +/- 0.07)**	

Difference between var(s) and var(d) is 194.722 % (large values indicate strong dominance and maternal effects)

Given that the difference is small, the h2, is (var(s)/var(z)*4 =-0.0066

Otherwise, the estimate of heritability, h2, is **-0.249 +/- 0.067** (SE)

Test for the sire effects in balanced set-up: F(18, 38) = 1.587, P = 0.114

Test for the dam effects: F(38, 453) = 1.510, P = 0.029

Test for the presence of additive genetic variance: F(19.4183, 38) = 1.508, P = 0.138

Table 8. Summary of full-sib-half-sib analysis of mean of latency to become active and latency to emerge (n = 510). Heritability estimates were calculated according to equations presented in Lynch & Walsh (1998)

Factor	d.f.	Mean squares	Estimated variance components
Sires (s)	18	203.57	-0.637
Dams within sires (d)	38	113.67	0.421
Sibs within dams (e)	453	771.15	771.15
Total (z)	509	842.99	749.58
Estimates of heritability	**0 (-0.34 +/- 0.08)**		
Difference between var(s) and var(d) is 166.154 % (large values indicate strong dominance and maternal effects) Given that the difference is small, the h2, is (var(s)/var(z)*4 =-0.057 Otherwise, the estimate of heritability, h2, is **-0.34 +/- 0.08** (SE)			
Test for the sire effects in balanced set-up: $F_{(18, 38)} = 1.79$, P = 0.07 Test for the dam effects: $F_{(38, 453)} = 1.47$, P = 0.038 Test for the presence of additive genetic variance: $F_{(19.4183, 38)} = 1.693$, P = 0.08			

Father-son-regression included, as above, 19 sires, 3 dams per sire and approximately 9 offspring per dam in total of 510 offspring. The heritability estimations of the used PC (of latency to become active and latency to emerge) as well as latency to become active also were negative using parent-offspring regression (Table 9). In contrast, the heritability estimation of latency to emerge from father-son-regression was positive and ranged from 0.03 to 0.13. Heritability estimate derived from dam-offspring regression was much higher than heritability derived from sire-offspring-regression. In addition, I calculated the mean of latency to become active and latency to emerge to generate a new variable for boldness. In contrast to sib analysis, I got a positive estimation from parent-offspring-regression. Furthermore, all estimates had large standard errors which were partly even larger than the heritability estimates itself (which would mean that the h² doesn't differ significantly from 0).

Table 9. Summary of parent-offspring-regression on exploration dataset ($n_s = 19$, $n_d = 57$, $n_o = 510$). Heritability estimates were calculated as the slope of the regression (midparent-offspring) and as twice the slope (one parent-offspring regression).

	midparent-offspring-regression	sire-offspring-regression	dam-offspring-regression	Full-sib-half-sib analysis
PC exploration	-0.457 ± 0.140	-0.558 ± 0.31	-0.704 ± 0.272	-0.249 +/- 0.067
Latency to become active	-0.009 ± 0.057	0.020 ± 0.088	-0.048 ± 0.094	-0.219 +/- 0.061
Latency to emerge	0.070 ± 0.062	0.026 ± 0.088	0.128 ± 0.094	-0.426 +/- 0.097
Mean (latency to become active and emerge)	0.039 ± 0.056	0.052 ± 0.082	0.038 ± 0.092	-0.340 +/- 0.076

Father-son-regression included 12 sires and their 72 sons. The mean brood size per father was $6 \pm 2{,}9$. The heritability estimation of latency to emerge from father-son-regression and also the used PC (of latency to become active and latency to emerge) did not differ much from 0 and the estimation of latency to become active was even negative. (Table 10). Only the heritability estimate of fighting success ($h^2 = 0.23 \pm 0.40$) was higher, although their standard error almost overlaps with zero. In general, all estimates had large standard errors which were mostly even larger than the heritability estimates itself (which would mean that the h^2 doesn't differ significantly from 0).

Table 10. Summary of father-son-regression on aggression dataset ($n_1 = 12$, $n_2 = 72$). Heritability estimates were calculated as twice the slope of the regression for sons and fathers.

	father-son-regression ± standard errors (b ± SE)	Heritability ± standard errors ($h^2 \pm SE$)
PC exploration	0.021 ± 0.028	0.042 ± 0.056
Latency to become active	-6.37 ± 7.64	-12.74 ± 15.28
Latency to emerge	0.012 ± 0.095	0.024 ± 0.19
Fighting success	0.115 ± 0.20	0.23 ± 0.40

Discussion

Behavioural correlations

As expected, I found a strong correlation between latency to become active and latency to emerge in both generations (Table 1 and 2), indicating that these both measures reflected a single trait, exploration activity. Measurements of latency to emerge, the so called hiding time, quantifies, according to Kortet & Hedrick (2007), variation in antipredator behaviour rather than territoriality, since males never called within the shelter neither during their previous trials nor during my experiments. Results from the *G. integer* populations in Arizona and California also suggest that the latency to emerge from a refuge in a novel environment is related to the perception of predation risk (Hedrick & Kortet 2006). Significant differences of latencies to emerge were found in *G. integer* populations with different predator pressures. Longer latencies to emerge were found in male *G. integer* from Arizona, where predation pressure is very high, whereas in California, where predation pressure is much lower, latencies were significantly shorter (Hedrick & Kortet 2006). Hence, my results suggest that exploration activity is a consistent behavioural trait in field crickets, and may indicate individuals' incautiousness under a predation risk. In my trials, male and female behaviour did not differ statistically.

Bold individuals, which are characterized as risk takers, approach novel objects and explore novel environments quickly whereas shy individuals tend to be risk averse and are generally neophobic (Wilson et al. 1994). Behaviour of shy individuals in novel situations is often accompanied by fear responses, such as freezing (Brown & Smith 1996; Budaev et al. 1999a,b; Templeton & Shriner 2004) which I was subjectively able to observe during the trials, i.e. after an individual was placed in the plastic vial that functioned as a shelter. For this reason, explorative individuals could be classified as bold whereas individuals with long hiding times could be classified as shy.

Contrary to the previous findings in the same species (Kortet & Hedrick 2007), I could not find significant correlation between exploration behaviour and aggression (Table 3). In my data set aggressive, intrasexually dominant males did not start moving significantly sooner inside the vial or emerge sooner from a refuge in a novel, potentially dangerous environment than less aggressive males. Thereby, my results did not find evidence for a presence of aggressiveness–activity behavioural syndrome in the studied laboratory population of *G. integer*. A possible explanation of these contrasting results could be that the previous work suggesting a behavioural syndrome in this species was conducted using

offspring of wild animals (Kortet & Hedrick 2007), whereas in my study the used individuals were of 5th to 6th laboratory generation. This fact, due to laboratory evolution, but also the social isolation from 20 days post-hatching, due to lack of learning through social interactions, might have changed behavioural patterns and reduced aggression in this laboratory population. Compared to Kortet & Hedrick (2007), I also used a different methodological framework. In the present work, I used repetitive tests against several reference males in order to estimate the male aggressiveness, whereas the previous work was done using a pair-wise set up based on a single trial between two males. Males were also matched in a different way, in the previous study they were both size-matched (1.3 ± 0.16%) as well as age-matched (2.9 ± 0.35 days). For activity times Kortet & Hedrick (2007) also excluded values up to 2 s on the grounds that these probably did not reflect hiding behaviour but rather escape behaviour. Experiments by Kortet & Hedrick (2007) were also done later during the day (between 15 h–22 h), which could contribute to the fluctuation in aggressiveness.

However, the absence of a behavioural syndrome should not be taken as "bad news" because there is yet little theory to explain the causes of behavioural correlations. In addition, there is evidence that behavioural syndromes are not universal, even within a species. It is possible that because of the lack of predation pressure, competition for food or other natural stimuli, the syndrome will break apart. One example is a different food level and resulting competition for food. There is evidence that different food levels have an impact on behaviour (Riechert 1993; Pintor et al. 2007) and it is possible that because of the high food level, the general aggression level might decrease (Parker 1974).

For example, Riechert & Hedrick (1993) found that in funnel web spiders populations with low food availability were more aggressive across multiple contexts. Since in my experiment all individuals were fed *ad libitum* and equal states by food were expected, there might an effect on the general aggression level. Another example is predator pressure, the lack of which might also be a possible explanation for my results. Population comparisons have shown that there is a relationship between the strength of behavioural syndromes and predator pressure, so that boldness and aggressiveness tend to covary in high predation populations (Bell 2005; Bell & Sih 2007). For example, Bell (2005) found that due to differences in predation pressure between two stickleback populations a boldness-aggression syndrome was present in one but not in another. It is inferred by Bell (2007) that predation generated a behavioural syndrome. Brown et al. (2007b) also found that fish from high-

predation areas were bolder than those from low-predation areas and males were bolder than females.

Because of these findings above, researchers suppose that certain combinations of behaviours might be adaptive in some environments (Dall et al. 2004; Bell 2005; Bell 2007). Therefore it is possible that in the used laboratory crickets the unnatural environmental stimuli may not cause syndromes.

Life-history traits

Another interesting finding of this study was that contrary to my expectations aggressive, intrasexually dominant males did not obtain a higher mounting rate than less dominant males (Table 4). In many species females are generally assumed to prefer dominant males as mates (e.g. Rantala & Kortet 2004) and in some species, competition between males is even incited by females in order to mate with the most dominant one (Berglund et al. 1996). Indirect-benefit ('good genes') models (Andersson 1994) propose that females use male traits they prefer as indicators of male condition. Possible benefits of mating with these males are that they are more likely to protect females during and after mating, and may also provide access to superior resources (e.g. better quality territories in birds). Finally, there is a potential genetic benefit if traits that increase success during male-male competition are heritable (Cordero & Eberhard 2003). This is true, especially, if success in intrasexual competitions depends on males overall health and condition (Borgia 1979). Females could therefore gain indirect genetic benefits in terms of more viable offspring by mating with dominant males (Berglund et al. 1996). Rantala & Kortet (2004) found in a related cricket species, *G. bimaculatus* that dominant males were also more successful in obtaining matings and had stronger encapsulation response. Thus, their results suggest that a male's dominance status and fighting success may indicate his immunocompetence, i.e. health to females (Rantala & Kortet 2004).

A growing number of studies report that male fighting ability is not always correlated to attractiveness and mating success (Moore & Moore 1999; Moore et al. 2001; Shackleton et al. 2005; Duckworth 2006). This could occur because dominant males e.g. may provide less parental care (Forsgren 1997; Wong 2004), increase the risk of female injury while mating (Lebouef & Mesnick 1991). For example, Duckworth (2006) found that more aggressive males of western bluebirds, that also defend their nests more intensely, had the lowest reproductive success. The cost of nest defence was due to the correlated expression of aggression both in contexts of nest defence and male-male competition coupled with a trade-off between intrasexual aggression and parental care (Duckworth 2006). More aggressive

males could even be more likely to transmit diseases (Freeland 1981) or be sperm depleted (Pitnick & Markow 1994; Preston et al. 2001). Another possible reason for the lack of the female preference for dominant males could be that dominance has no effect on female or offspring fitness, or because there are other traits, uncorrelated with fighting ability, that predict better male's effect on female fitness (Shackleton et al. 2005). For example, in field crickets females prefer male traits such as courtship song. Hedrick (1986) found that in *G. integer*, males call to attract sexually receptive females and that they differ in their durations of uninterrupted calling and calls with longer calling bouts are favoured by females.

In addition, I found some interesting correlations between life-history traits (i.e. mass, developmental time to maturity and mounting rate) and behavioural measures. In most taxa, larger males are more likely to win fights (e.g. birds: Hagelin 2002; spiders: Kotiaho et al. 1997). However, I could not find a statistically significant effect of body mass on the proportion of fights won. Despite the approximate size-matching between male contestants, I found a statistically significant effect of mass on mounting rate, so that, my results suggest that smaller males receive more mountings. According to life-history theory (Stearns 1992), it is predictable that individuals that have longer development times until they become adults tend to be heavier as adults, i.e. there is a trade-off between maturation age and -size. Furthermore, individuals might also face different costs due to their different life-history strategies (Nylin & Gotthard 1998). I found different results within the two generations. There was a statistically significant correlation between maturation time and body mass at sexual maturity only in the parent generation within the exploration data that suggests as expected that heavier individuals gained maturity later than lighter ones. Within the aggression dataset of the offspring generation a different result can be found whereas lighter males gained maturity later but it has to be mentioned that these individuals were relatives and therefore not independent.

Maturation time still had a statistically significant positive effect on aggression. Maturation time had also a statistically significant negative effect on the latency to emerge but no effect on the latency to become active. These results suggest that aggressive and bold/explorative individuals reach maturity later compared to less aggressive and cautious individuals.

A prior study (Hedrick 2000) showed that lower body mass was correlated with longer hiding times in wild collected male individuals, but not in the F1 males in Davis, California, population . I found a contrary relationship for body mass and first movement as well as hiding times in the offspring generation, where heavier individuals seem to have longer hiding

times and are therefore classified as shy. This result contrasts many other studies (Reale et al. 2000; Sih et al. 2003; Bell & Sih 2007; Stamps 2007; Biro & Stamps 2008) that support the idea that more bold/explorative and aggressive individuals are heavier and gain maturation faster. It has been suggested that bold and explorative individuals might feed more than the fearful ones because they find food earlier and also take the risk to forage longer even under presence of predator. For example, Brown et al. (2007a) also found a significant correlation between body mass and boldness. Bold fish had a greater body mass at a given standard length than shy fish. Their results suggest that personality traits are strongly influenced by population-specific ecological variables and may have fitness consequences in wild populations (Brown et al. 2007a). However, my result suggests that shy individuals of the offspring generation are both heavier and gain maturation faster than bold/explorative ones. Indeed, my results support a new idea by Wolf et al. (2007). Their theoretical paper suggests that a trade-off between current and future reproduction leads to polymorphisms in populations, and that because of unequal fitness expectations individuals differ in their behaviour. My data clearly supports the idea that individuals with high future expectations should be more cautious because they have much to lose (Wolf et al. 2007). In this scenario, heavy, fast growing and rapidly developing individuals in this work have high future expectations and should indeed be more risk averse and shy than individuals with lower expectations which have little to lose.

Heritability

Heritability estimates derived from sib analysis were negative (Table 5–8) which means that the results derived from this method are unreliable (Lynch & Walsh 1998). Furthermore, almost non test for the presence of additive genetic variance was significant. If F-tests signals nonsignificance it most likely is a simple consequence of inadequate sample size (Lynch & Walsh 1998). Only in the case of "latency to emerge", there seems to be marginally significant additive genetic variance for the trait suggesting potential inheritance. The main reason for these results might be the inadequate experimental set-up. The main problem might be the individuals that did not move or emerged during the experimental trials. 127 individuals did not move at all and 343 individuals did not emerge from the shelter. However, these individuals were evaluated with 10 (duration of trials), which would actually mean that they moved and emerged at the end of the trial. Therefore these traits were not statistically normal distributed, which is an assumption of full-sib-half-sib-analysis (Falconer & Mackay 1996; Lynch & Walsh 1998). I tried several transformations but the distribution did not change. For that reason the used sib analysis might not work properly. For further

experiments it would be necessary to enlarge the duration of the trials and wait until individuals move and emerge to avoid this problem.

In contrast to heritability estimates derived from sib analysis, I found some small heritable components using parent-offspring regression. Advantages of parent-offspring-regression are that neither dominance nor linkage influences the covariance between parents and offspring, that the estimation is unbiased by selection on the parents and the resemblance between parents and offspring phenotypes can be measured directly (Lynch & Walsh 1998). I found negative heritability estimates in both latency to become active and the used PC using parent-offspring-regression as well as full-sib-half-sib analysis (Table 9). But heritability estimates of latency to emerge ranged from 0.026 to 0.128, so they did not differ much from 0 and had very large standard errors. Care must be taken when mother-offspring-regression are used to ensure that the maternal-progeny covariance is not inflated by maternal effects (Lynch & Walsh 1998). In the present work estimates of latency to emerge derived from dam-offspring-regression are actually higher because of maternal effects than sire- or midparent-offspring-regression. Compared to the exploration dataset, the aggression dataset was much smaller (72 sons). But also in this aggression dataset the heritability of latency to emerge was 0.024 ± 0.19 and in contrast to the exploration dataset the heritability estimate of the used PC was 0.042 ± 0.056 (Table 10). So all these estimates did not differ much from 0 and had very large standard errors too. But that should not be surprising because the sample size was relatively small. In comparison with the heritability estimates of exploration behaviour of great tits (Dingemanse et al. 2002) my results were much lower. Their heritability estimates of exploration score ranged from 0.22 to 0.61. My estimates are at least 10 times smaller than the results of Dingemanse et al (2002) but however, my data also suggests heritable variation in a behavioural reaction towards a novel situation. In addition, estimate of fighting success derived from sire-son-regression were quite high (0.23 ± 0.40). Therefore, offspring individuals in the present study tended to show similar behaviour and resemblance (caused by shared alleles) to their fathers suggesting that exploration activity and fighting success have small heritable components, which make them susceptible to evolutionary changes and facilitate behavioural adaptation to varying environments.

Anyway, compared to the results of other studies (e.g. Dingemanse et al. 2002) the heritability estimate of boldness in my study is quite low. In the work done by Dingemanse et al. (2002) more than thousand great tits were used for their measurements. In the present work I used only 510 individuals for heritability estimation of exploration and even less individuals (72) for heritability estimation of aggression. For that reason, my results about heritability

estimates, especially those from the aggression dataset, had very large standard errors. As in my thesis, studies with small sample size often report problems with large standard errors (e.g. Klindt et al. 2006). Since sample size has a large influence in the accuracy of estimations, increasing number of tested individuals would have reduced the standard errors (Köhler et al. 1996). Therefore, studies that estimate heritabilities should have a very large sample size.

A reason for the small heritability estimates could be that all the genetic components are influenced by gene frequencies and may therefore differ from one population to another, according to the past history of the population (Falconer & Mackay 1996). It is likely that in crickets, as in other animals, fitness-related consequences for personality traits will fluctuate through time and be mediated by current environmental conditions (Dingemanse et al. 2004; Dingemanse & Reale 2005; Sinn et al 2006). Since the used field crickets were of 5th to 6th laboratory generation, laboratory selection might already have lowered the heritability. Therefore these estimates may be affected by domestication or long-term maintenance under laboratory conditions (Sinn et al 2006). Heritability estimates are always highest during the first generations under selection and rapidly diminish in time. However, since heritability estimates in the present work were measured for laboratory populations, heritability could be insignificant in the wild because of large effects of environmental factors (Falconer & Mackay 1996) and therefore laboratory estimates may not predict heritability in natural populations well (Dingemanse et al. 2002; Drent et al. 2003). Thus, my results give alone a value for evolutionary potential over one single generation, and already in the second generation of laboratory individuals the evolution might slow down.

Since these estimations have not been studied many times, I feel that my data are highly valuable. The used sample size is, of course, not large enough for an extensively accurate estimation but can still be used to provide very first ideas of heritability of the studied behavioural traits in the field crickets and also form a good basis for future work.

Conclusion

In conclusion, I found a statistically significant correlation between latency to become active and latency to emerge in both generations of the used field crickets indicating that these both measures reflected a single trait, exploration activity. However, there was no correlation between exploration and aggressiveness. Therefore, my study could not confirm the previous observations of presence of aggressiveness–activity behavioural syndrome in the *G. integer.*

Further findings were that aggressive, intrasexually dominant males did not obtain a higher mounting rate than less dominant males, indeed smaller males receive more mountings

than large males in the present study. Furthermore, my results suggest that aggressive and bold/explorative individuals reach maturity later compared to less aggressive and cautious individuals.

I also found a positive relationship for body mass and first movement as well as hiding times in the offspring generation, where heavier individuals seem to have longer hiding times and are therefore classified as shy. My result suggests that shy individuals are both heavier and gain maturation faster than bold ones and supports the idea that individuals with high future expectations should be more cautious because they have much to lose (Wolf et al. 2007).

In the case of heritability my data indicated that all heritability estimates derived from the used sib analysis were negative and therefore unreliable. However, estimates derived from parent-offspring-regression suggest detectable heritable variation in a behavioural reaction towards a novel situation and fighting success.

Further studies should address whether there is influence of laboratory rearing on behavioural syndromes, and whether a larger sample size as well as adapted experimental set-up and balanced families provide more precise results about the studied heritability estimates. Moreover, further work would confirm, whether the correlations between life-history traits (i.e. mass, developmental time to maturity and mounting rate) and behavioural measures which I detected in this laboratory population are maintained under predator pressure.

Acknowledgement

This thesis could only be accomplished since many people kindly provided their time and knowledge. I wish to thank in particular the following persons for their substantial support and encouragement:

First of all, I thank Professor Dr. Hannes Paulus for supervising my diploma thesis and for giving me the chance to do my experiments in Finland; this project could not have been carried out in Austria.

Thanks to Professor Dr. Raine Kortet for supervising my experiments in Oulu and for many helpful comments on earlier drafts of my thesis. I thank Dr. Anssi Vainikka for his help with the estimation of heritability, as well as for answers to all my questions concerning statistics and, of course, for many comments on my thesis. I am grateful to Petri Niemelä, M. Sc. for assistance in the laboratory and commenting my thesis.

My thanks go further to my family for encouraging and supporting me in my decisions. Thanks to my parents, who accompanied me my whole life, for their ongoing support through the time at the university and especially during my work for the diploma.

Last but not least, I want to thank my friends in Vienna, Oulu as well as in my home town for their emotional support and patience.

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Appendices

Dataset of parent generation – exploration data

dam	gender	move	out	age	mass	sire	gender	move	out	age	mass
300	2	4.591	10.000	70	0.7434	**164**	1	10.000	10.000	71	0.6388
12	2	10.000	10.000	71	0.7337						
31	2	3.975	10.000	72	0.8515						
124	2	10.000	10.000	66	0.7143	**3**	1	0.249	0.428	67	0.6878
279	2	0.126	0.223	66	0.7338						
43	2	3.215	7.810	68	0.669						
33	2	10.000	10.000	84	0.6312	**1**	1	1.840	2.017	80	0.7376
175	2	3.241	10.000	83	0.6025						
243	2	3.119	4.123	82	0.7684						
135	2	7.368	10.000	74	0.7304	**87**	1	10.000	10.000	7	0.5998
161	2	0.979	2.466	74	0.6613						
191	2	8.478	10.000	76	0.6071						
291	2	10.000	10.000	74	0.7492	**274**	1	10.000	10.000	76	0.7991
55	2	10.000	10.000	75	0.8039						
R30	2	5.627	10.000	77	0.6186						
180	2	10.000	10.000	78	0.604	**210**	1	10.000	10.000	77	0.6613
312	2	0.232	4.499	78	0.7158						
229	2	3.339	3.406	75	0.6409						
206	2	5.684	10.000	82	0.7297	**32**	1	0.802	4.401	78	0.6759
89	2	9.032	10.000	77	0.07191						
101	2	0.389	10.000	76	0.705						
296	2	0.121	10.000	88	0.6527	**309**	1	2.789	5.141	89	0.6399
315	2	10.000	10.000	88	0.7844						
305	2	3.324	10.000	89	0.7724						
171	2	6.565	10.000	83	0.8084	245	1	3.827	10.000	84	0.8724
80	2	2.835	5.387	83	0.7667						
233	2	0.336	1.581	82	0.607						
116	2	10.000	10.000	88	0.5838	74	1	0.380	10.000	78	0.8121
150	2	5.095	10.000	88	0.5987						
163	2	1.473	1.802	88	0.6045						
295	2	3.387	10.000	90	0.8148	**200**	1	8.087	8.390	91	0.5754
119	2	0.716	7.051	90	0.7803						
R23	2	4.819	6.219	90	0.7586						
128	2	1.648	2.951	95	0.7677	**197**	1	0.166	5.167	95	0.6406
188	2	0.254	10.000	97	0.659						
136	2	3.490	6.985	96	0.7726						

ind.	gender	move	out	age	PC		ind.	gender	move	out	age	PC
105	2	1.405	2.303	99	0.7988		**306**	**1**	5.069	7.007	96	0.7207
252	2	3.065	10.000	99	0.7627							
77	2	5.810	10.000	101	0.6044							
202	2	7.634	8.377	103	0.6504		**167**	**1**	9.722	10.000	101	0.6396
216	2	10.000	10.000	103	0.7948							
184	2	7.378	8.275	101	0.67							
190	2	10.000	10.000	109	0.61		179	1	2.850	3.323	106	0.7076
222	2	1.513	2.426	108	0.5861							
48	2	10.000	10.000	108	0.9122							
231	2	3.016	3.174	106	0.7049		205	1	3.750	4.075	105	0.652
61	2	2.155	7.845	104	0.6433							
R34	2	1.385	6.179	105	0.661							
26	2	5.429	10.000	115	0.7329		299	1	6.578	9.678	111	0.9694
82	2	4.862	10.000	108	0.7706							
24	2	5.688	8.729	113	0.5616							
173	2	4.204	4.427	33	0.5775		126	1	3.669	7.412	122	0.8522
149	2	4.690	5.447	121	0.7927							
94	2	4.411	5.111	121	0.9153							
177	2	0.216	1.246	121	0.7381		121	1	3.607	10.000	119	0.8557
156	2	0.494	6.404	121	0.5865							
257	2	3.414	6.006	121	0.7723							

Dataset of offspring generation – exploration data

ind.	gender	move	out	mass	age	PC exploration
300-2	2	3,74	4,74	0,70	79	-0,71041
300-3	2	1,92	3,02	0,70	84	-1,32131
300-4	2	2,68	3,31	0,60	81	-1,14439
300-5	2	3,82	10,00	0,65	72	0,26302
300-7	2	2,73	8,97	0,58	75	-0,10283
300-8	1	1,30	10,00	0,63	91	-0,14802
300-9	2	4,10	5,35	0,61	85	-0,54031
300-10	2	4,82	10,00	0,65	81	0,42613
300-11	2	1,33	1,87	0,72	94	-1,62751
300-12	1	1,17	10,00	0,74	75	-0,16922
12-1	1	0,96	2,31	0,52	98	-1,60752
12-2	2	1,25	2,75	0,52	133	-1,47989
12-4	1	4,12	4,68	0,54	80	-0,65938
12-5	2	1,96	10,00	0,50	74	-0,04037
12-6	1	9,27	10,00	0,52	94	1,15196
12-7	1	1,06	1,46	0,45	82	-1,74641
12-8	2	0,48	10,00	0,45	91	-0,28177
12-9	2	3,45	10,00	0,51	104	0,20267
12-10	2	2,94	3,25	0,64	73	-1,11294
12-11	1	2,17	10,00	0,59	116	-0,00611

12-12	2	10,00	10,00	0,71	69	1,27103
31-1	1	0,44	10,00	0,63	89	-0,28829
31-2	1	7,77	10,00	0,64	79	0,9073
31-3	2	10,00	10,00	0,60	96	1,27103
31-4	1	1,63	3,04	0,55	112	-1,36496
31-6	2	4,67	10,00	0,61	96	0,40166
31-7	2	3,70	10,00	0,67	97	0,24344
31-8	1	9,12	10,00	0,56	89	1,1275
31-9	1	9,26	10,00	0,65	98	1,15033
31-10	2	0,27	10,00	0,51	94	-0,31602
31-11	1	3,29	10,00	0,63	101	0,17657
31-12	1	2,59	7,14	0,55	92	-0,45979
124-1	2	1,11	4,66	0,67	125	-1,15399
124-2	1	0,31	7,95	0,63	96	-0,68379
124-5	1	2,98	6,02	0,63	109	-0,60067
124-6	2	10,00	10,00	0,67	92	1,27103
124-7	2	0,71	1,96	0,71	71	-1,7122
124-8	1	0,33	4,40	0,73	125	-1,32869
124-9	2	5,52	10,00	0,57	68	0,5403
124-10	1	1,24	7,09	0,80	126	-0,68912
124-11	1	3,52	10,00	0,78	116	0,21408
124-12	1	0,85	7,34	0,70	89	-0,70708
279-1	1	4,06	10,00	0,52	68	0,30216
279-3	1	0,26	10,00	0,64	85	-0,31765
279-4	2	0,04	0,08	0,46	70	-2,16474
279-5	2	5,70	6,13	0,59	78	-0,13693
279-6	1	5,61	10,00	0,64	90	0,55498
279-7	1	0,29	10,00	0,67	92	-0,31276
279-8	1	0,53	5,83	0,72	112	-1,03498
279-9	2	0,23	10,00	0,50	99	-0,32254
279-10	1	0,24	10,00	0,54	101	-0,32091
279-11	2	0,83	10,00	0,46	102	-0,22468
279-12	2	0,03	0,06	0,47	70	-2,17002
43-1	2	5,58	10,00	0,58	60	0,55009
43-2	2	0,30	0,83	0,52	78	-1,9854
43-3	2	7,66	10,00	0,56	74	0,88936
43-4	2	0,37	5,92	0,55	122	-1,04464
43-5	1	4,32	9,14	0,61	87	0,18755
43-6	2	9,98	10,00	0,58	93	1,26777
43-8	2	6,51	10,00	0,62	90	0,70178
43-9	2	6,19	10,00	0,52	94	0,64959
43-11	2	3,82	10,00	0,69	87	0,26302
43-12	2	8,52	10,00	0,62	94	1,02963
33-1	2	0,44	5,79	0,32	106	-1,05696
33-4	2	0,05	0,07	0,47	74	-2,16493
33-5	2	1,20	10,00	0,50	129	-0,16433
33-9	2	9,16	10,00	0,73	149	1,13402
33-11	2	1,09	1,52	0,47	147	-1,73056
33-13	1	10,00	10,00	0,62	136	1,27103
33-14	1	2,66	2,94	0,64	107	-1,21521
175-1	1	2,65	2,83	0,74	78	-1,23693
175-2	1	5,11	10,00	0,76	124	0,47343
175-3	1	10,00	10,00	0,80	109	1,27103
175-4	1	5,88	8,93	0,74	95	0,40366

175-5	2	2,96	4,13	0,51	92	-0,94901
175-6	2	0,03	0,04	0,58	89	-2,17367
175-7	2	4,25	8,45	0,54	80	0,05015
175-8	2	0,24	10,00	0,50	113	-0,32091
175-9	1	3,11	3,49	0,66	108	-1,04139
175-10	2	7,57	8,05	0,55	90	0,51864
175-11	1	7,07	7,65	0,64	138	0,36406
175-12	2	0,57	10,00	0,57	89	-0,26709
243-3	1	2,53	2,85	0,50	130	-1,25285
243-5	1	1,16	1,48	0,58	131	-1,72644
243-6	2	4,18	5,25	0,68	144	-0,54552
243-7	1	6,87	7,02	0,67	134	0,21641
243-8	2	0,02	0,19	0,49	144	-2,14792
243-9	1	0,38	10,00	0,41	106	-0,29808
243-10	2	8,12	8,98	0,46	113	0,77815
243-11	2	0,18	1,86	0,45	87	-1,81691
135-1	1	0,19	1,61	0,61	96	-1,86092
135-2	1	0,62	2,12	0,87	100	-1,69767
135-3	1	1,71	1,85	0,74	103	-1,56918
135-5	1	3,65	3,95	0,65	90	-0,86933
135-6	2	9,94	10,00	0,68	74	1,26125
135-7	1	10,00	10,00	0,72	89	1,27103
135-8	2	5,48	9,80	0,72	87	0,49726
135-9	2	1,49	2,60	0,52	81	-1,46813
135-11	1	6,52	10,00	0,86	106	0,70341
135-12	2	5,88	6,14	0,63	93	-0,10574
161-2	2	8,15	10,00	0,69	114	0,96928
161-3	2	10,00	10,00	0,66	98	1,27103
161-4	1	2,71	10,00	0,68	88	0,08197
161-6	2	5,12	10,00	0,60	101	0,47506
161-7	1	10,00	10,00	0,67	94	1,27103
161-8	2	0,31	0,99	0,67	98	-1,95455
161-9	2	8,84	10,00	0,58	116	1,08183
161-10	2	3,50	10,00	0,51	97	0,21082
161-11	2	0,31	0,37	0,67	88	-2,06775
161-12	1	2,10	3,52	0,43	146	-1,20066
191-1	2	0,11	0,25	0,51	107	-2,12228
191-2	1	0,75	3,37	0,56	107	-1,44824
191-3	1	2,53	2,84	0,54	129	-1,25467
191-5	1	2,47	10,00	0,75	119	0,04282
191-7	2	3,39	3,54	0,49	115	-0,98659
191-8	1	0,60	3,83	0,61	125	-1,38872
191-9	2	0,56	6,78	0,50	97	-0,85663
191-12	2	3,83	10,00	0,62	134	0,26465
291-1	2	1,21	3,34	0,24	108	-1,37869
291-3	1	6,50	10,00	0,75	100	0,70015
291-5	2	4,50	5,77	0,56	111	-0,39839
291-7	1	2,03	2,64	0,22	147	-1,37275
55-1	1	5,12	5,46	0,87	111	-0,35386
55-2	2	3,65	10,00	0,60	87	0,23529
55-3	1	0,33	10,00	0,70	100	-0,30623
55-4	2	10,00	10,00	0,75	94	1,27103
55-5	2	2,31	2,72	0,78	122	-1,31247
55-6	2	3,93	10,00	0,65	104	0,28096
55-7	1	8,34	8,60	0,74	102	0,74466

55-8	1	4,77	5,33	0,73	82	-0,43468
55-9	1	0,25	8,39	0,75	94	-0,61324
55-10	2	5,83	6,50	0,72	104	-0,04817
55-11	1	8,33	10,00	0,76	102	0,99864
R30-2	2	0,27	10,00	0,54	92	-0,31602
R30-3	1	0,37	5,51	0,51	135	-1,1195
R30-4	2	0,44	10,00	0,60	108	-0,28829
R30-5	1	0,20	10,00	0,63	110	-0,32744
R30-6	1	0,24	10,00	0,67	117	-0,32091
R30-7	2	0,17	0,20	0,69	156	-2,12163
R30-8	1	4,63	5,46	0,47	117	-0,43378
R30-9	2	6,61	10,00	0,65	100	0,71809
R30-11	2	1,29	2,04	0,49	106	-1,60299
180-1	1	6,24	10,00	0,58	99	0,65774
180-3	1	4,86	6,93	0,67	90	-0,12787
180-4	2	10,00	10,00	0,57	112	1,27103
180-5	1	1,99	4,88	0,65	93	-0,97029
180-6	1	0,18	10,00	0,74	103	-0,3307
180-7	1	3,27	10,00	0,63	134	0,17331
180-8	1	10,00	10,00	0,70	74	1,27103
180-10	2	8,60	10,00	0,60	90	1,04268
180-11	1	10,00	10,00	0,65	93	1,27103
180-12	1	10,00	10,00	0,72	72	1,27103
312-2	1	10,00	10,00	0,57	106	1,27103
312-3	2	3,12	3,38	0,55	95	-1,05985
312-4	1	3,23	10,00	0,70	94	0,16678
312-5	1	3,20	10,00	0,66	94	0,16189
312-6	2	3,20	10,00	0,60	93	0,16189
312-7	1	1,36	2,74	0,58	93	-1,46377
312-8	2	2,43	3,38	0,62	81	-1,17239
312-9	2	0,24	3,37	0,64	76	-1,53143
312-11	1	2,79	3,92	0,68	100	-1,01508
312-12	1	4,47	4,89	0,67	117	-0,56395
229-1	1	10,00	10,00	0,76	101	1,27103
229-2	1	1,14	2,34	0,80	91	-1,57269
229-3	1	6,77	10,00	0,64	97	0,74419
229-4	2	0,51	2,19	0,59	88	-1,70283
229-5	1	10,00	10,00	0,64	117	1,27103
229-6	1	2,73	5,64	0,75	88	-0,71083
229-7	2	10,00	10,00	0,60	81	1,27103
229-9	2	0,17	0,24	0,57	90	-2,11432
229-10	1	10,00	10,00	0,72	101	1,27103
229-11	1	7,82	10,00	0,71	108	0,91545
229-12	2	2,45	2,52	0,48	89	-1,32615
206-1	1	0,40	4,81	0,57	141	-1,24241
206-3	1	2,04	6,51	0,68	103	-0,66453
206-6	1	0,11	0,27	0,48	159	-2,11863
206-8	2	2,68	5,76	0,54	120	-0,69707
206-12	1	1,02	4,05	0,66	128	-1,28005
89-1	1	1,74	10,00	0,67	99	-0,07625
89-3	1	9,20	10,00	0,79	67	1,14055
89-4	2	1,45	10,00	0,61	93	-0,12355
89-5	2	10,00	10,00	0,67	78	1,27103
89-6	2	10,00	10,00	0,45	91	1,27103
89-7	2	3,12	10,00	0,67	78	0,14884

89-8	2	2,28	4,73	0,55	116	-0,95037
101-3	2	5,04	10,00	0,58	102	0,46201
101-4	2	1,17	1,61	0,58	104	-1,70108
101-7	2	10,00	10,00	0,49	101	1,27103
101-8	2	5,98	10,00	0,57	87	0,61533
101-9	1	6,51	9,86	0,77	112	0,67622
101-11	2	8,91	10,00	0,64	108	1,09324
101-12	1	0,35	6,95	0,77	111	-0,85984
296-1	2	5,35	10,00	0,54	92	0,51257
296-2	2	0,20	10,00	0,56	78	-0,32744
296-4	1	0,60	2,77	0,60	78	-1,58226
296-5	2	0,28	10,00	0,53	97	-0,31439
296-6	1	0,58	10,00	0,58	97	-0,26546
296-7	2	6,60	10,00	0,53	74	0,71646
296-8	2	4,91	6,44	0,52	91	-0,20918
296-9	1	8,33	10,00	0,61	80	0,99864
296-10	2	0,12	0,76	0,51	86	-2,02754
296-11	2	1,39	8,78	0,51	80	-0,35609
296-12	2	7,40	10,00	0,48	78	0,84695
315-1	1	3,25	10,00	0,87	115	0,17005
315-2	2	1,14	3,73	0,55	89	-1,3189
315-4	1	7,44	9,27	0,77	92	0,72019
315-5	2	10,00	10,00	0,50	65	1,27103
315-9	1	4,17	10,00	0,51	100	0,32011
315-11	2	3,17	3,52	0,40	104	-1,02613
305-1	1	3,73	10,00	0,75	89	0,24834
305-3	1	10,00	10,00	0,73	100	1,27103
305-5	1	10,00	10,00	0,55	101	1,27103
305-6	1	0,27	1,12	0,63	99	-1,93734
305-7	2	6,35	9,90	0,67	79	0,65743
305-8	1	10,00	10,00	0,73	79	1,27103
305-10	2	0,22	5,66	0,52	96	-1,11658
305-11	1	3,16	3,60	0,57	101	-1,01315
305-12	2	4,27	4,48	0,57	78	-0,67143
171-1	1	3,41	8,25	0,79	127	-0,12337
171-2	1	8,42	10,00	0,77	104	1,01332
171-3	1	5,94	10,00	0,55	97	0,60881
171-4	1	5,30	10,00	0,72	111	0,50442
171-5	1	2,75	3,09	0,71	102	-1,17314
171-9	1	6,35	8,15	0,77	95	0,33791
171-10	1	5,60	8,98	0,70	106	0,36712
171-11	1	4,73	10,00	0,73	99	0,41145
80-1	2	0,78	10,00	0,63	80	-0,23283
80-2	1	0,26	10,00	0,63	84	-0,31765
80-3	2	0,31	10,00	0,62	106	-0,3095
80-4	2	10,00	10,00	0,59	94	1,27103
80-5	2	1,43	10,00	0,58	124	-0,12681
80-6	2	0,89	3,30	0,56	95	-1,43819
80-8	2	2,02	10,00	0,70	106	-0,03058
80-9	1	3,27	10,00	0,71	113	0,17331
80-10	1	3,03	10,00	0,59	78	0,13416
80-11	1	7,60	9,66	0,72	67	0,81749
80-12	1	0,52	10,00	0,72	84	-0,27524
233-1	2	2,67	2,97	0,49	120	-1,2081

233-3	1	10,00	10,00	0,71	84	1,27103
233-5	1	6,99	10,00	0,45	142	0,78007
233-6	2	10,00	10,00	0,51	107	1,27103
233-12	1	2,09	2,29	0,45	121	-1,42686
116-6	2	0,78	1,27	0,50	150	-1,82677
116-11	2	7,28	7,79	0,53	124	0,42387
116-16	2	0,94	1,56	0,54	106	-1,74772
116-17	2	10,00	10,00	0,63	134	1,27103
150-2	1	10,00	10,00	0,69	123	1,27103
150-6	2	9,40	10,00	0,59	132	1,17317
150-7	2	4,92	10,00	0,43	113	0,44244
150-8	2	10,00	10,00	0,50	132	1,27103
150-9	1	0,44	10,00	0,59	117	-0,28829
150-10	1	10,00	10,00	0,57	139	1,27103
163-2	1	10,00	10,00	0,54	92	1,27103
163-3	2	0,44	10,00	0,55	78	-0,28829
163-4	2	8,98	10,00	0,47	111	1,10466
163-9	1	10,00	10,00	0,55	108	1,27103
163-10	1	0,81	1,01	0,50	152	-1,86935
295-1	1	8,00	10,00	0,61	79	0,94481
295-2	1	7,63	10,00	0,69	99	0,88446
295-3	1	2,23	2,61	0,64	107	-1,3456
295-4	1	10,00	10,00	0,64	84	1,27103
295-5	2	10,00	10,00	0,62	91	1,27103
295-6	1	9,98	10,00	0,75	83	1,26777
295-7	2	10,00	10,00	0,57	80	1,27103
295-8	1	6,12	10,00	0,73	99	0,63817
295-10	1	2,75	5,56	0,67	115	-0,72217
295-11	2	10,00	10,00	0,63	89	1,27103
119-1	2	7,96	10,00	0,55	107	0,93829
119-2	1	4,95	10,00	0,60	115	0,44733
119-3	1	2,60	4,01	0,52	130	-1,02964
119-4	2	0,29	3,16	0,53	106	-1,56161
119-5	2	2,57	3,20	0,46	147	-1,18242
119-7	1	6,36	10,00	0,63	145	0,67731
119-8	1	4,14	10,00	0,61	120	0,31521
119-9	2	3,46	3,99	0,49	113	-0,89301
119-10	2	6,76	10,00	0,50	106	0,74256
119-11	1	4,80	9,67	0,61	99	0,36261
R23-1	2	0,24	10,00	0,51	89	-0,32091
R23-2	2	5,23	8,61	0,43	89	0,23921
R23-3	2	9,08	10,00	0,45	91	1,12097
R23-4	2	2,53	10,00	0,55	102	0,05261
R23-5	2	10,00	10,00	0,49	101	1,27103
R23-7	1	10,00	10,00	0,58	91	1,27103
R23-8	1	3,18	7,73	0,59	101	-0,25583
R23-9	2	7,69	8,76	0,39	82	0,66785
R23-10	1	4,18	10,00	0,59	91	0,32174
R23-11	2	2,52	2,57	0,46	91	-1,3056
R23-12	1	3,59	6,68	0,58	107	-0,38067
128-1	2	6,92	10,00	0,51	94	0,76866
128-3	2	7,65	8,60	0,35	114	0,63211
128-6	2	10,00	10,00	0,58	100	1,27103
128-7	2	9,96	10,00	0,54	96	1,26451
128-9	2	1,96	10,00	0,60	96	-0,04037

188-1	1	0,27	5,94	0,71	93	-1,0573
188-2	1	3,50	5,75	0,80	112	-0,56515
188-3	2	1,31	1,71	0,78	92	-1,65998
188-4	1	10,00	10,00	0,65	86	1,27103
188-5	2	10,00	10,00	0,71	121	1,27103
188-7	2	6,23	9,25	0,62	79	0,51917
188-8	1	7,05	10,00	0,59	89	0,78986
188-9	2	6,86	10,00	0,46	99	0,75887
188-10	2	2,84	3,63	0,74	101	-1,05987
188-11	2	0,34	10,00	0,63	98	-0,3046
188-12	1	8,84	10,00	0,65	98	1,08183
136-2	1	9,90	10,00	0,73	112	1,25472
136-4	2	4,10	4,74	0,71	101	-0,65169
136-9	1	4,86	8,14	0,76	121	0,09305
136-11	2	0,21	5,83	0,58	129	-1,08717
105-1	2	0,27	10,00	0,71	100	-0,31602
105-2	2	10,00	10,00	0,70	123	1,27103
105-3	1	5,55	10,00	0,74	109	0,5452
105-4	1	6,46	10,00	0,76	108	0,69363
105-5	1	4,15	4,86	0,69	96	-0,62162
105-6	1	8,21	10,00	0,67	128	0,97907
105-7	1	3,39	10,00	0,73	128	0,19288
105-8	1	1,30	2,86	0,55	110	-1,45165
105-9	1	5,17	8,87	0,74	123	0,2769
105-10	1	6,43	10,00	0,66	111	0,68873
105-11	2	3,59	5,22	0,76	125	-0,64724
105-12	1	10,00	10,00	0,65	73	1,27103
252-1	1	5,19	10,00	0,71	88	0,48648
252-2	1	1,94	10,00	0,70	76	-0,04363
252-3	1	4,51	10,00	0,81	84	0,37556
252-4	2	8,79	10,00	0,71	91	1,07367
252-5	2	6,58	10,00	0,70	93	0,7132
252-6	1	10,00	10,00	0,75	92	1,27103
252-7	1	4,54	10,00	0,73	85	0,38046
252-8	2	0,15	10,00	0,71	101	-0,33559
252-9	1	3,21	10,00	0,69	73	0,16352
252-10	1	10,00	10,00	0,74	78	1,27103
252-11	2	10,00	10,00	0,70	98	1,27103
252-12	2	0,21	10,00	0,69	101	-0,32581
77-1	1	10,00	10,00	0,37	146	1,27103
77-2	2	10,00	10,00	0,41	94	1,27103
77-3	1	10,00	10,00	0,48	128	1,27103
77-4	2	0,20	10,00	0,43	103	-0,32744
77-5	2	10,00	10,00	0,76	90	1,27103
77-6	1	3,56	10,00	0,65	97	0,22061
77-7	2	6,59	9,22	0,54	89	0,57242
77-8	2	10,00	10,00	0,58	83	1,27103
77-9	1	0,59	10,00	0,75	82	-0,26383
77-10	1	10,00	10,00	0,50	89	1,27103
77-11	1	7,49	10,00	0,78	107	0,86163
77-12	1	10,00	10,00	0,68	93	1,27103
202-1	1	3,67	10,00	0,68	119	0,23855
202-2	1	10,00	10,00	0,64	86	1,27103
202-4	1	3,39	6,14	0,63	101	-0,51188
202-5	2	0,12	0,13	0,63	81	-2,14256
202-6	1	1,35	6,72	0,67	113	-0,73873

202-7	2	0,26	10,00	0,58	100	-0,31765
202-8	1	2,00	2,47	0,65	109	-1,40868
202-9	1	8,32	10,00	0,61	91	0,99701
202-11	1	2,80	3,02	0,63	137	-1,17777
202-12	1	4,15	5,04	0,58	115	-0,58876
216-1	2	6,89	10,00	0,59	123	0,76376
216-2	2	4,92	10,00	0,44	140	0,44244
216-3	2	4,85	7,14	0,57	69	-0,09116
216-4	1	10,00	10,00	0,69	98	1,27103
216-5	1	6,59	10,00	0,69	119	0,71483
216-6	1	3,45	10,00	0,70	105	0,20267
216-7	1	1,31	10,00	0,55	71	-0,14639
216-8	1	2,66	10,00	0,71	105	0,07381
216-9	1	0,26	10,00	0,74	100	-0,31765
216-10	2	3,33	3,57	0,60	103	-0,9909
216-11	2	0,09	7,06	0,58	111	-0,88217
216-12	2	10,00	10,00	0,66	119	1,27103
184-2	1	10,00	10,00	0,67	98	1,27103
184-3	1	10,00	10,00	0,67	79	1,27103
184-4	1	1,60	1,88	0,67	94	-1,58164
184-5	1	10,00	10,00	0,61	108	1,27103
184-6	2	10,00	10,00	0,55	109	1,27103
184-7	2	4,65	10,00	0,59	101	0,3984
184-8	1	2,13	10,00	0,66	124	-0,01264
184-9	2	6,12	10,00	0,69	124	0,63817
184-10	1	0,58	10,00	0,61	94	-0,26546
184-11	2	0,22	10,00	0,58	89	-0,32418
184-12	1	8,38	10,00	0,66	98	1,0068
190-1	1	0,24	10,00	0,64	106	-0,32091
190-2	2	4,66	10,00	0,80	83	0,40003
190-3	2	9,38	10,00	0,58	80	1,1699
190-4	1	3,48	9,90	0,68	97	0,1893
190-5	2	4,13	10,00	0,64	84	0,31358
190-6	2	10,00	10,00	0,54	77	1,27103
190-7	2	3,06	10,00	0,75	94	0,13905
190-8	1	1,83	2,50	0,69	71	-1,43093
190-9	2	0,59	1,10	0,64	115	-1,8888
190-10	1	0,35	10,00	0,71	79	-0,30297
190-12	2	0,28	10,00	0,62	98	-0,31439
222-1	2	1,85	10,00	0,54	95	-0,05831
222-2	2	7,21	10,00	0,42	120	0,81596
222-5	1	0,23	2,90	0,77	98	-1,61887
222-6	1	0,12	0,43	0,50	101	-2,08779
48-1	2	4,61	10,00	0,62	82	0,39187
48-2	1	3,36	9,49	0,55	101	0,09487
48-4	2	5,63	10,00	0,55	96	0,55825
48-5	1	0,21	10,00	0,55	102	-0,32581
48-6	1	10,00	10,00	0,56	125	1,27103
48-8	1	1,32	1,49	0,51	122	-1,69852
48-10	2	8,69	10,00	0,50	105	1,05736
48-11	2	3,28	5,51	0,55	115	-0,64485
48-12	2	0,22	10,00	0,60	88	-0,32418
231-1	1	1,40	6,22	0,71	94	-0,82186
231-2	2	7,92	10,00	0,62	100	0,93177
231-3	1	2,18	10,00	0,65	88	-0,00448
231-4	2	0,21	10,00	0,41	95	-0,32581

231-5	1	0,28	10,00	0,65	90	-0,31439
231-6	1	7,00	10,00	0,64	97	0,7817
231-7	1	10,00	10,00	0,59	99	1,27103
231-8	2	10,00	10,00	0,62	107	1,27103
231-9	1	6,53	10,00	0,53	112	0,70504
231-11	1	2,17	10,00	0,59	85	-0,00611
231-12	2	0,21	10,00	0,44	91	-0,32581
61-1	2	2,36	7,50	0,46	114	-0,43157
61-2	2	0,29	2,87	0,64	100	-1,61456
61-3	1	0,71	1,70	0,51	102	-1,75968
61-4	2	0,26	9,62	0,43	97	-0,38703
61-5	2	1,33	10,00	0,62	103	-0,14312
61-6	1	10,00	10,00	0,50	100	1,27103
61-7	1	10,00	10,00	0,64	120	1,27103
61-8	1	8,23	10,00	0,63	91	0,98233
61-9	1	10,00	10,00	0,57	94	1,27103
61-10	1	10,00	10,00	0,66	98	1,27103
61-11	1	2,70	10,00	0,66	114	0,08034
61-12	2	10,00	10,00	0,64	136	1,27103
R34-1	2	4,07	4,23	0,56	72	-0,7497
R34-2	1	2,87	10,00	0,64	104	0,10806
R23-3	1	3,65	10,00	0,70	105	0,23529
R34-6	1	5,31	5,87	0,55	115	-0,24801
R34-7	1	3,24	10,00	0,46	112	0,16841
R34-8	2	10,00	10,00	0,56	101	1,27103
R34-9	1	5,07	6,33	0,49	93	-0,20317
R34-10	1	2,06	10,00	0,61	104	-0,02405
R34-11	2	4,80	10,00	0,49	110	0,42286
R34-12	1	6,06	10,00	0,62	106	0,62838
26-1	2	3,69	10,00	0,58	116	0,24181
26-2	1	2,34	8,10	0,81	115	-0,32529
26-3	2	7,63	10,00	0,64	84	0,88446
26-4	1	1,14	4,69	0,80	98	-1,14362
26-5	2	9,35	10,00	0,79	75	1,16501
26-6	2	10,00	10,00	0,59	94	1,27103
26-7	1	0,28	4,29	0,57	122	-1,35693
26-8	2	2,02	5,13	0,68	104	-0,91975
26-10	2	7,36	8,92	0,72	117	0,64324
26-11	2	0,58	10,00	0,69	127	-0,26546
26-12	2	10,00	10,00	0,57	70	1,27103
82-1	1	10,00	10,00	0,65	117	1,27103
82-2	1	5,77	10,00	0,63	119	0,58108
82-4	1	7,44	10,00	0,68	115	0,85347
82-6	1	9,84	10,00	0,61	74	1,24494
82-7	1	3,35	10,00	0,56	87	0,18636
82-8	1	8,14	10,00	0,55	113	0,96765
82-10	1	3,71	10,00	0,63	117	0,24508
82-11	2	2,21	3,24	0,45	111	-1,23384
82-12	1	10,00	10,00	0,62	100	1,27103
24-1	1	6,37	10,00	0,66	83	0,67895
24-2	1	10,00	10,00	0,63	95	1,27103
24-3	1	10,00	10,00	0,49	134	1,27103
24-4	1	7,03	10,00	0,61	90	0,7866
24-5	2	4,45	10,00	0,56	80	0,36578
24-6	1	2,28	10,00	0,58	83	0,01183
24-7	2	10,00	10,00	0,51	99	1,27103

24-8	1	10,00	10,00	0,64	133	1,27103
24-9	1	4,85	10,00	0,67	115	0,43102
24-10	2	3,44	10,00	0,57	97	0,20104
24-11	1	0,77	10,00	0,62	126	-0,23447
24-12	2	1,07	8,17	0,58	78	-0,51966
173-1	1	4,47	8,76	0,64	111	0,14264
173-2	1	7,91	10,00	0,63	92	0,93013
173-3	2	3,92	4,45	0,65	97	-0,734
173-4	2	2,21	4,09	0,62	114	-1,07864
173-5	2	6,66	8,58	0,64	108	0,46698
173-6	1	7,13	10,00	0,70	99	0,80291
173-7	1	1,86	10,00	0,76	91	-0,05668
173-8	2	0,24	10,00	0,66	106	-0,32091
173-9	1	10,00	10,00	0,63	105	1,27103
173-10	2	5,20	5,37	0,61	99	-0,35724
173-11	2	0,27	0,69	0,59	70	-2,01585
173-12	1	5,27	10,00	0,72	110	0,49953
149-1	2	2,40	2,66	0,65	126	-1,30874
149-2	2	4,03	4,49	0,50	126	-0,70875
149-3	1	9,51	10,00	0,58	73	1,19111
149-4	2	10,00	10,00	0,60	107	1,27103
149-5	2	7,27	10,00	0,46	94	0,82574
149-6	1	10,00	10,00	0,43	38	1,27103
149-7	2	5,37	10,00	0,70	71	0,51584
149-8	2	3,19	10,00	0,70	94	0,16026
149-9	1	2,38	9,45	0,51	85	-0,07228
149-10	2	0,13	0,24	0,68	126	-2,12085
149-11	2	1,60	1,67	0,46	102	-1,61999
149-12	1	4,49	4,68	0,47	95	-0,59903
94-7	1	7,98	9,32	0,62	126	0,8174
94-11	1	1,25	2,51	0,49	114	-1,52371
177-2	1	10,00	10,00	0,82	123	1,27103
177-3	1	3,57	5,02	0,67	120	-0,68701
177-4	1	0,84	4,39	0,62	118	-1,24733
177-7	1	4,17	9,14	0,69	118	0,16309
177-9	1	2,88	4,60	0,60	126	-0,87624
177-12	1	0,31	0,47	0,66	121	-2,04949
156-2	1	6,06	7,19	0,53	103	0,11533
156-3	1	0,43	6,34	0,56	116	-0,95817
257-1	1	7,23	7,58	0,65	110	0,37737
257-3	2	0,85	1,24	0,66	123	-1,82083
257-4	1	6,23	7,86	0,63	121	0,26539
257-5	1	4,09	6,47	0,62	127	-0,33745
257-6	1	3,75	10,00	0,69	105	0,2516
257-7	1	4,11	5,48	0,63	106	-0,51495
257-8	2	1,02	2,04	0,61	120	-1,64703
257-9	1	0,72	7,62	0,69	110	-0,67716
257-10	2	10,00	10,00	0,71	126	1,27103
257-12	1	9,41	10,00	0,74	113	1,1748

Dataset of parent generation (males) – aggression data

ind	fights	mountings	mass	move	out	age	PC exploration
164	1	10	10	71	0,64	0,39	0
3	1	0,25	0,43	67	0,69	0,44	0,64
1	1	1,84	2,02	80	0,74	0,14	0,72
87	1	10	10	7	0,6	0,19	0,33
274	1	10	10	76	0,8	0,64	0,69
210	1	10	10	77	0,66	0,33	0,94
32	1	0,8	4,4	78	0,68	0,5	0,75
309	1	2,79	5,14	89	0,64	0,33	0,31
200	1	8,09	8,39	91	0,58	0,48	0,7
197	1	0,17	5,17	95	0,64	0,47	0,57
306	1	5,07	7,01	96	0,72	1	0,75
167	1	9,72	10	101	0,64	0,17	0,08

Dataset of offspring generation – aggression data

ind	fights	mountings	mass	move	out	age	PC exploration
12-1	0,21	0,47	0,52	0,96	2,31	98	-1,43869
12-4	0,37	0,33	0,54	4,12	4,68	80	-,50460
12-6	0,5	0,7	0,52	9,27	10	94	1,27616
12-7	1	0,67	0,45	1,06	1,46	82	-1,57315
300-12	0,39	0,6	0,72	1,17	10	75	-,04098
300-8	0,32	0	0,63	1,3	10	91	-,01984
31-1	0	0,79	0,63	0,44	10	89	-,15969
31-12	0,73	0,17	0,55	2,59	7,14	92	-,31720
31-2	0,5	0,33	0,64	7,77	10	79	1,03225
31-4	0,67	0,53	0,55	1,63	3,04	112	-1,20030
31-8	0,22	0,56	0,56	9,12	10	89	1,25177
124-12	0,67	0,54	0,7	0,85	7,34	89	-,56468
124-2	0	0	0,63	0,31	7,95	96	-,54433
124-5	0,67	0	0,63	2,98	6,02	109	-,45237
279-1	0	0,56	0,52	4,06	10	68	,42896
279-10	0	0,64	0,54	0,24	10	101	-,19221
279-3	0,05	0,29	0,64	0,26	10	85	-,18896
279-6	0	0,67	0,64	5,61	10	90	,68101
175-11	0,42	0,33	0,64	7,07	7,65	138	,50173
243-3	0,33	0,4	0,5	2,53	2,85	130	-1,08764
243-9	0,67	0,75	0,41	0,38	10	106	-,16945
33-13	0,42	0,52	0,62	10	10	136	1,39487
135-1	0,45	0,44	0,61	0,19	1,61	96	-1,68802
135-5	0,04	0,33	0,65	3,65	3,95	90	-,71047
135-7	0,52	0,28	0,72	10	10	89	1,39487
161-4	0,33	0,28	0,68	2,71	10	88	,20944
161-7	0,71	0,67	0,67	10	10	94	1,39487
191-2	0,11	0,79	0,56	0,75	3,37	107	-1,28488
191-3	0,67	0,83	0,54	2,53	2,84	129	-1,08941
55-3	0,36	0	0,7	0,33	10	100	-,17758
r30-3	0,67	0,6	0,51	0,37	5,51	135	-,96722
r30-5	1	0,72	0,63	0,2	10	110	-,19872

R30-8	0,33	0,76	0,47	4,63	5,46	117	-,28336
105-12	0,2	0,47	0,65	10	10	73	1,39487
105-8	0,33	0,22	0,55	1,3	2,86	110	-1,28588
77-10	0,33	0,5	0,5	10	10	89	1,39487
77-3	1	0,5	0,48	10	10	128	1,39487
184-10	0,49	0,7	0,61	0,58	10	94	-,13692
184-5	0,82	0	0,61	10	10	108	1,39487
202-11	0,33	0,21	0,63	2,8	3,02	137	-1,01359
202-8	0,08	0,33	0,65	2	2,47	109	-1,24120
202-9	0,46	0,51	0,61	8,32	10	91	1,12168
216-6	0,5	0,47	0,7	3,45	10	105	,32977
216-7	0,06	0,5	0,55	1,31	10	71	-,01822
206-1	0,92	0,33	0,57	0,4	4,81	141	-1,08646
206-12	0,67	0,33	0,66	1,02	4,05	128	-1,12040
206-6	1	0,33	0,48	0,11	0,27	159	-1,93863
180-1	0	0,69	0,58	6,24	10	99	,78345
180-12	0	0,29	0,72	10	10	72	1,39487
180-7	1	0,19	0,63	3,27	10	134	,30050
180-8	0,67	0,5	0,7	10	10	74	1,39487
229-3	0,67	0,61	0,64	6,77	10	97	,86964
312-2	0	0,22	0,57	10	10	106	1,39487
312-5	0,5	0,58	0,66	3,2	10	94	,28912
312-7	0	0,5	0,58	1,36	2,74	93	-1,29740
296-4	0,39	0,74	0,6	0,6	2,77	78	-1,41566
296-6	0,17	0,11	0,58	0,58	10	97	-,13692
305-11	0,71	0,4	0,57	3,16	3,6	101	-,85221
305-5	0	0,24	0,55	10	10	101	1,39487
305-6	0,42	0,22	0,63	0,27	1,12	99	-1,76190
315-9	0,11	0,81	0,51	4,17	10	100	,44685
119-11	0,33	0,47	0,61	4,8	9,67	99	,49078
119-2	0,33	0,22	0,6	4,95	10	115	,57369
119-3	0,67	0,08	0,52	2,6	4,01	130	-,87057
119-7	0,33	0,33	0,63	6,36	10	145	,80297
295-1	0	0,6	0,61	8	10	79	1,06965
295-3	0,67	0,67	0,64	2,23	2,61	107	-1,17898
r23-10	0,42	0	0,59	4,18	10	91	,44848
r23-12	0,67	0,82	0,58	3,59	6,68	107	-,23615
r23-7	0,67	0,33	0,58	10	10	91	1,39487
r23-8	0	0,65	0,59	3,18	7,73	101	-,11664
188-8	0,13	0	0,59	7,05	10	89	,91517

Principle component analysis

PC exploration output – exploration dataset (both generations)

Deskriptive Statistiken

	Mittelwert	Standardabweichung	Analyse N
out	7,7988	3,12868	586
move	4,6379	3,49601	586

Korrelationsmatrix

		out	move
Korrelation	out	1,000	,540
	move	,540	1,000
Signifikanz (1-seitig)	out		,000
	move	,000	

Inverse Korrelationsmatrix

	out	move
out	1,412	-,763
move	-,763	1,412

KMO- und Bartlett-Test

Maß der Stichprobeneignung nach Kaiser-Meyer-Olkin.		,500
Bartlett-Test auf Sphärizität	Ungefähres Chi-Quadrat	201,481
	df	1
	Signifikanz nach Bartlett	,000

Kommunalitäten

	Anfänglich	Extraktion
out	1,000	,770
move	1,000	,770

Extraktionsmethode:
Hauptkomponentenanalyse.

Erklärte Gesamtvarianz

Kompo nente	Anfängliche Eigenwerte			Summen von quadrierten Faktorladungen für Extraktion		
	Gesamt	% der Varianz	Kumulierte %	Gesamt	% der Varianz	Kumulierte %
1	1,540	77,018	77,018	1,540	77,018	77,018
2	,460	22,982	100,000			

Extraktionsmethode: Hauptkomponentenanalyse.

Komponentenmatrix[a]

| | Komponente |
	1
out	,878
move	,878

Extraktionsmethode:

Hauptkomponentenanalyse.

a. 1 Komponenten extrahiert

PC exploration output – exploration dataset (offspring generation)

Deskriptive Statistiken

	Mittelwert	Standardabweichung	Analyse N
out	7,8482	3,13269	510
move	4,6161	3,50667	510

Korrelationsmatrix

		out	move
Korrelation	out	1,000	,528
	move	,528	1,000
Signifikanz (1-seitig)	out		,000
	move	,000	

Inverse Korrelationsmatrix

	out	move
out	1,387	-,733
move	-,733	1,387

KMO- und Bartlett-Test

Maß der Stichprobeneignung nach Kaiser-Meyer-Olkin.		,500
Bartlett-Test auf Sphärizität	Ungefähres Chi-Quadrat	166,120
	df	1
	Signifikanz nach Bartlett	,000

Kommunalitäten

	Anfänglich	Extraktion
out	1,000	,764
move	1,000	,764

Extraktionsmethode:
Hauptkomponentenanalyse.

Erklärte Gesamtvarianz

Kompo nente	Anfängliche Eigenwerte			Summen von quadrierten Faktorladungen für Extraktion		
	Gesamt	% der Varianz	Kumulierte %	Gesamt	% der Varianz	Kumulierte %
1	1,528	76,417	76,417	1,528	76,417	76,417
2	,472	23,583	100,000			

Extraktionsmethode: Hauptkomponentenanalyse.

Komponentenmatrix[a]

	Komponente
	1
out	,874
move	,874

Extraktionsmethode:
Hauptkomponentenanalyse.

a. 1 Komponenten extrahiert

PC exploration output – aggression dataset (both generations)

Deskriptive Statistiken

	Mittelwert	Standardabweichung	Analyse N
move	4,3589	3,67191	84
out	7,4169	3,26143	84

Korrelationsmatrix

		move	out
Korrelation	move	1,000	,560
	out	,560	1,000
Signifikanz (1-seitig)	move		,000
	out	,000	

KMO- und Bartlett-Test

Maß der Stichprobeneignung nach Kaiser-Meyer-Olkin.		,500
Bartlett-Test auf Sphärizität	Ungefähres Chi-Quadrat	30,726
	df	1
	Signifikanz nach Bartlett	,000

Kommunalitäten

	Anfänglich	Extraktion
move	1,000	,780
out	1,000	,780

Extraktionsmethode:
Hauptkomponentenanalyse.

Erklärte Gesamtvarianz

Komponente	Anfängliche Eigenwerte			Summen von quadrierten Faktorladungen für Extraktion		
	Gesamt	% der Varianz	Kumulierte %	Gesamt	% der Varianz	Kumulierte %
1	1,560	78,022	78,022	1,560	78,022	78,022
2	,440	21,978	100,000			

Extraktionsmethode: Hauptkomponentenanalyse.

Komponentenmatrix[a]

	Komponente
	1
move	,883
out	,883

Extraktionsmethode: Hauptkomponentenanalyse.

a. 1 Komponenten extrahiert

Complete output of the heritability estimates derived from "AV Bio-Statistics 4.9 Prof."

PC exploration

=== Estimation of heritability, half sib - full sib design, Lynch & Walsh method ===

Number of lines in the data file :	510
Number of sires :	19
Mean number of dams per sire :	3
Mean number of offspring per dam :	894.737
Total number of individuals, T :	510
Overall mean trait value :	-0.0176471
SS(Sires) :	206.418
SS(Dams(sires)) :	274.621
SS(Sibs(dams)) :	216.737
SS(total) :	264.841
k1 (in table 18.3, page 574) :	867.319
k2 (in table 18.3, page 574) :	94.773
k3 (in table 18.3, page 574) :	-135.029
N(sires, check) :	19
N(dams, check) :	3
N(Total - T, check) :	510

========= Variance components - Lynch & Walsh ===========

Source	d.f.	SS	MS
Sires	18	206.418	114.677
Dams(sires)	38	274.621	0.722688
Sibs(dams)	453	216.737	0.478449
Total	509	264.841	0.520317
Var(s)	-0.0297295		
Var(d)	0.0281603		
Var(e)	0.478449		
Var(z)	0.476879		

Difference between var(s) and var(d) is 194.722 % (large values indicate strong dominance and maternal effects)

Given that the difference is small, the h2, is (var(s)/var(z)*4 =-0.00658099

Otherwise, the estimate of heritability, h2, is -0.249367 +/- 0.0668993 (SE)

Test for the sire effects in balanced set-up
$F_{(18, 38)} = 1.58681$
$P = 0.113957$

Test for the dam effects
$F_{(38, 453)} = 1.51048$
$P = 0.0290827$

Test for the presence of additive genetic variance
$F_{(19.4183, 38)} = 1.50834$
$P = 0.137934$

Test for the equality of var(s) and vad (d)
$F_{(2.68586, 38)} = -1.33037$
$P = 1$

Latency to become active

=== Estimation of heritability, half sib - full sib design, Lynch & Walsh method ===

Number of lines in the data file :   510
Number of sires   :   19
Mean number of dams per sire   :   3
Mean number of offspring per dam :   894.737
Total number of individuals, T   :   510
Overall mean trait value   :   461.612
SS(Sires)   :   441.406
SS(Dams(sires))   :   597.318
SS(Sibs(dams))   :   5.220
SS(total)   :   6259.04
k1 (in table 18.3, page 574)   :   867.319
k2 (in table 18.3, page 574)   :   94.773
k3 (in table 18.3, page 574)   :   -135.029
N(sires, check)   :   19
N(dams, check)   :   3
N(Total - T, check)   :   510

========= Variance components - Lynch & Walsh ===========

Source	d.f.	SS	MS
Sires	18	441.406	245.225
Dams(sires)	38	597.318	157.189
Sibs(dams)	453	5.220	115.239
Total	509	6.259	122.967
Var(s)	-0.623177		
Var(d)	0.483676		
Var(e)	115.239		
Var(z)	113.844		

Difference between var(s) and var(d) is 177.615 % (large values indicate strong dominance and maternal effects)

Given that the difference is small, the h2, is (var(s)/var(z)*4 =-0.0245075

Otherwise, the estimate of heritability, h2, is -0.218959 +/- 0.0614925 (SE)

Test for the sire effects in balanced set-up
$F(18, 38) = 1.56007$
$P = 0.122549$

Test for the dam effects
$F(38, 453) = 1.36403$
$P = 0.0774025$

Test for the presence of additive genetic variance
$F(19.6012, 38) = 1.4899$
$P = 0.145059$

Test for the equality of var(s) and var(d)
$F(1.71933, 38) = -1.04853$
$P = 1$

Latency to emerge

=== Estimation of heritability, half sib - full sib design, Lynch & Walsh method ===

Number of lines in the data file :   510
Number of sires   :   19
Mean number of dams per sire   :   3
Mean number of offspring per dam :   894.737
Total number of individuals, T   :   510
Overall mean trait value   :   784.824
SS(Sires)   :   460.873
SS(Dams(sires))   :   495.091
SS(Sibs(dams))   :   4039.24
SS(total)   :   4995.2
k1 (in table 18.3, page 574)   :   867.319
k2 (in table 18.3, page 574)   :   94.773
k3 (in table 18.3, page 574)   :   -135.029
N(sires, check)   :   19
N(dams, check)   :   3
N(Total - T, check)   :   510

========= Variance components - Lynch & Walsh ===========

Source	d.f.	SS	MS
Sires	18	460.873	256.041
Dams(sires)	38	495.091	130.287
Sibs(dams)	453	4039.24	891.664
Total	509	4.995	981.376
Var(s)	-0.903073		
Var(d)	0.474112		
Var(e)	891.664		
Var(z)	848.768		

Difference between var(s) and var(d) is 152.5 % (large values indicate strong dominance and maternal effects)
Given that the difference is small, the h2, is (var(s)/var(z)*4 =-0.101078
Otherwise, the estimate of heritability, h2, is -0.425592 +/- 0.0965748 (SE)

Test for the sire effects in balanced set-up
$F_{(18, 38)}$ = 1.9652
P = 0.0395642

Test for the dam effects
$F_{(38, 453)}$ = 1.46117
P = 0.0409775

Test for the presence of additive genetic variance
$F_{(19.1803, 38)}$ = 1.85653
P = 0.0515829

Test for the equality of var(s) and vad (d)
$F_{(4.27953, 38)}$ = -2.07514
P = 0

Mean latency to become active and latency to emerge

=== Estimation of heritability, half sib - full sib design, Lynch & Walsh method ===

Number of lines in the data file :   510
Number of sires   :   19
Mean number of dams per sire   :   3
Mean number of offspring per dam :   894.737
Total number of individuals, T   :   510
Overall mean trait value   :   623.208
SS(Sires)   :   365.568
SS(Dams(sires))   :   431.952
SS(Sibs(dams))   :   3493.3
SS(total)   :   4290.82
k1 (in table 18.3, page 574)   :   867.319
k2 (in table 18.3, page 574)   :   94.773
k3 (in table 18.3, page 574)   :   -135.029
N(sires, check)   :   19
N(dams, check)   :   3
N(Total - T, check)   :   510

========= Variance components - Lynch & Walsh ===========

Source	d.f.	SS	MS
Sires	18	365.568	203.093
Dams(sires)	38	431.952	113.672
Sibs(dams)	453	3493.3	771.149
Total	509	4290.82	842.991
Var(s)	-0.63714		
Var(d)	0.421491		
Var(e)	771.149		
Var(z)	749.584		

Difference between var(s) and var(d) is 166.154 % (large values indicate strong dominance and maternal effects)

Given that the difference is small, the h2, is (var(s)/var(z)*4 =-0.0575384

Otherwise, the estimate of heritability, h2, is -0.339997 +/- 0.0764042 (SE)

Test for the sire effects in balanced set-up
F(18, 38) = 1.78667
P = 0.0655145

Test for the dam effects
F(38, 453) = 1.47405
P = 0.037512

Test for the presence of additive genetic variance
F(19.2887, 38) = 1.69264
P = 0.0824653

Test for the equality of var(s) and var(d)
F(3.50637, 38) = -1.70936
P = 1

Zusammenfassung

Es ist allgemein bekannt, dass Individuen einer Population, desselben Geschlechts oder gar derselben Größe oft unterschiedliche Verhaltensmuster aufweisen, wobei diese Variationen nicht unbedingt willkürlich bzw. ziellos sein müssen. Tiere haben demnach, genau wie Menschen, individuelle Persönlichkeiten bzw. sogenannte Verhaltenssyndrome. Die individuelle Persönlichkeit äußert sich in den beständigen Unterschieden im Verhalten zwischen Individuen, die innerhalb eines Kontexts wiederholt auftreten. Verhaltenssyndrome werden als konstante, korrelierende Verhaltensweisen definiert, die auch unabhängig von der Situation und Zeit bestehen bleiben. Eines der interessantesten Syndrome ist dabei das Aggressions-/Aktivitätssyndrome. Die Ergebnisse von Kortet and Hedrick (2007) sprechen für eines dieser Verhaltenskorrelationen bei *G. integer,* wobei aggressivere Männchen generell aktiver und gegenüber Prädatoren weniger vorsichtig sind als weniger offensive. Neueste Erkenntnisse deuten außerdem darauf hin, dass Verhaltenssyndrome erbliche Komponenten aufweisen.

In meiner Diplomarbeit untersuchte ich die individuelle Verhaltensvariation und deren erbliche Komponenten bei adulten Feldgrillen (*G. integer*). Ich prüfte, ob intrasexuelle Aggression mit der generellen Aktivität in einem unbekannten, möglicherweise sogar gefährlichen Umfeld korreliert. Um die individuelle Bereitschaft eine unbekannte, möglicherweise gefährliche Umgebung zu erkunden, wurden die Latenzzeiten der ersten Bewegung sowie des Verlassens eines sicheren Versteckes gemessen. Die Männchen wurden außerdem einem intrasexellen Aggressionstest unterzogen, wobei die Anzahl der gewonnenen Kämpfe sowie die Kopulationsversuche notiert wurden. Um anschließend die Heritabilität („Erblichkeit"), die ein Maß für die genetische Variabilität eines Merkmals in einer Population ist, zu ermitteln, wurden zwei Generationen den genannten Versuchen unterzogen und anschließend miteinander verglichen bzw. die Resultate der Nachkommen einer Varianzanalyse unterzogen. Zusätzlich prüfte ich die Beziehungen zwischen einigen "life-history" Merkmalen (Gewicht, Alter der Geschlechtsreife und Paarungsversuche) und Verhaltenstypen.

Ich konnte, wie erwartet, eine signifikante Korrelation zwischen den Latenzzeiten der ersten Bewegung und des Verlassens des sicheren Refugiums nachweisen, welche gemeinsam die Erkundungsaktivität widerspiegeln. Entgegen meiner Erwartungen konnte ich allerdings kein Verhaltenssyndrom nachweisen, da ich keine signifikante Korrelation zwischen dem Erkundungsverhalten und der intrasexuellen Aggressionsvariable feststellen konnte. Dies sollte allerdings nicht als eine schlechte Nachricht interpretiert werden, da immer noch wenig

Theorie existiert, um das Auftreten dieser Syndrome ausreichend zu erklären. Mögliche Erklärungen für die Abwesenheit des Syndroms können z.B. das Fehlen von Prädatoren, das Nahrungsüberangebot und die über mehrere Generationen bestehende Laborhaltung sein.

Des weiteren konnte ich meinen Daten entnehmen, dass mutige bzw. erkundungsfreudige Individuen ein geringeres Körpergewicht und dabei zudem eine längere Entwicklung bis zur Geschlechtsreife aufweisen. Weniger offensive Individuen waren im Vergleich zu Erkundungsfreudigen schwerer und entwickelten sich darüber hinaus schneller zu adulten Tieren.

Außerdem konnten aggressive, intrasexuell dominante Männchen gegenüber weniger aggressiven, nicht mehr Kopulationsversuche erzielen, in der Tat wurden kleinere Männchen von den Weibchen bevorzugt, wobei es allerdings keinen Zusammenhang zwischen Größe und Kampfkraft gab.

Im Gegensatz zu der Verwandtschaftsanalyse, die nur negative Schätzungen der Heritabilität ergab, konnte ich geringe erbliche Komponenten mittels Eltern-Nachkommen-Regression ermitteln. Schätzungen der Heritabilität ergaben für die Erkundungsbereitschaft Werte von 0,03 bis 0,13. Und auch für die Kampfkraft konnte mittels Vater-Sohn-Regression die Heritabilität geschätzt werden ($h^2 = 0,23 \pm 0,40$). Da die gemessenen Merkmale geringe erbliche Komponenten aufweisen, können sie sich im Laufe eines Evolutionsprozesses verändern und somit können Anpassungen (Adaptionen) an die Umwelt entstehen. Aussagekräftige Ergebnisse zur Heritabilität können allerdings nur mit einer größeren Stichprobenzahl erzielt werden.

Curriculum vitae

Personal details

Full name	Christina Gruber
Marital status	single
Date of birth	9. May 1985
Nationality	Austrian

Education

1999-2004	higher-level secondary commercial college (Zwettl, Austria)
2004 - Dez. 2009	University of Vienna: Biology (Vienna, Austria)
Sept. - Dez. 2008	Erasmus Exchange: University of Oulu (Finland)
April 2009-Dez. 2009	Diploma Thesis:

Behavioural variation in the field cricket (*Gryllus integer*); what is the role of heritable components?

Supervisor in Austria: Prof. Dr. Hannes Paulus

Supervisor in Oulu: Prof. Dr. Raine Kortet

Practical experience

2000 – 2007	office/clerical worker at Lagerhaus TechnikCenter Zwettl, Zwettl, Lower Austria (at least one month per year)
Nov. – Dez. 2007	student assistant in "clever dog lab" project, Department for Neurobiology and Cognition Research, University of Vienna. Supervisor: Friederike Range & Ludwig Huber
Sept. – Dez. 2008	student laboratory researcher in crayfish project (Emil Aaltonen foundation funded, 3-years-project), Department of Biology, University of Oulu. Supervisor: Raine Kortet

Publication list

Range F., Heucke S. L., <u>Gruber C</u>., Konz A., Huber A., Virányi Z. (2009): The effect of ostensive cues on dogs' performance in a manipulative social learning task. *Applied Animal Behaviour Science* 120, 170-178