PETRI T. NIEMELÄ

Associations and basis of personality, life-history and social interactions

Academic Dissertation

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Department of Biology

Author's address: University of Eastern Finland
                         Department of Biology
                         P.O.Box 1111
                         80101 JOENSUU
                         FINLAND
                         email: petri.niemela@uef.fi

Supervisors: Professor Raine Kortet,
                         University of Eastern Finland
                         Department of Biology
                         P.O.Box 111
                         80101 JOENSUU
                         FINLAND
                         email: raine.kortet@uef.fi

                         Assistant Professor Anssi Vainikka,
                         University of Eastern Finland
                         Department of Biology
                         P.O.Box 111
                         80101 JOENSUU
                         FINLAND
                         email: anssi.vainikka@uef.fi

                         Docent Heikki Hirvonen,
                         University of Helsinki
                         Department of Biology
                         P.O.Box 65
                         5602 Helsinki
                         FINLAND
                         email: heikki.hirvonen@helsinki.fi

Reviewers: Professor Indrikis Krams,
                         University of Tartu
                         Institute of Ecology and Earth Sciences
                         50090 Tartu
                         Estonia
                         email: indrikis.krams@biology.lv

                         Assistant Professor Gábor Herczeg,
                         Eötvös Loránd University
                         Department of Systematic Zoology and Ecology
                         1053 Budapest
                         Hungary
                         email: gaborherczeg@caesar.elte.hu

Opponent: Professor Veijo Jormalainen,
                         University of Turku
                         Department of Biology
                         FIN-20014 Turku
                         FINLAND
                         email: veijo.jormalainen@utu.fi

ABSTRACT

During recent years, studies of animal personalities and behavioural syndromes have received a wide attention among behavioural ecologists. One of the key aims of the field has been to understand the emergence and maintenance of animal personalities in independent populations. Animal personality is defined as consistent between-individual differences in behaviour across time and / or across contexts. Association between two or more behaviours is defined as behavioural syndrome. Hypothesized integration between animal personality and life-history has created a need to understand the evolutionary aspects of the potential integration structures. For this thesis, I studied 1) whether the key behavioural traits (i.e. boldness and aggression) can be considered as personality traits in our study populations and if behaviours integrate into behavioural syndromes in our model organism Western stutter-trilling cricket, *Gryllus integer*, 2) whether certain life-history traits (cellular immune defence, maturation time and body mass) would be associated with personality. I also examined 3) the nature of these associations (i.e. phenotypic or genetic) and 4) if social environment has an impact on personality or behavioural syndromes. Thus, I studied both ecological and evolutionary aspects of these associations. Finally, I build 5) a conceptual framework to understand the evolutionary potential of behavioural plasticity, emergence of personalities and coexistence of different behavioural types. My results indicate that there are stable between-individual differences in boldness in our study population and therefore, animal personalities. Boldness and immunity were associated phenotypically, but not genetically. Moreover, boldness and life-history were not associated. Maturation time, body mass and encapsulation were all associated phenotypically. These phenotypic correlations were partly underpinned by relatively tight genetic correlations. Thus, it is possible that these tight, genetic associations between the traits may limit the evolutionary potential of individual traits. Moreover, social interactions induced by variations in population density during ontogeny can generate a behavioural syndrome between two distinct behaviours (aggression and boldness). Repetitive aggressive encounters do not affect the individual level of boldness, but dominant individuals are consistently bolder compared to subordinant. Environmental variation may affect the emergence of consistency in behaviour so that animal personalities may be most likely present in environments with little variation or with high amount of variation.

TIIVISTELMÄ

Viime vuosina eläinten persoonallisuustutkimus on saanut paljon huomiota käyttäytymisekologien keskuudessa ja tarve selittää persoonallisuutta ilmiönä populaatiotasolla on kasvanut. Persoonallisuus on määritelty yksilöiden välisen käyttäytymisen ajallisena ja tilanteesta riippumattomana stabiilisuutena. Käyttäytymissyndrooma puolestaan määritetään kahden tai useamman käyttäytymisen toisiinsa kytkeytymisenä. Elinkiertopiirteiden ja persoonallisuuden kytkeytyminen toisiinsa luo tarpeen ymmärtää ilmiön ekologista ja evolutiivista perustaa. Väitöskirjassani tutkin, 1) esiintyykö mallilajillamme, Kalifornialaisella kenttäsirkalla, *Gryllus integer*, persoonallisuuspiirteitä keskittymällä yleisesti tunnistettuihin persoonallisuuspiirteisiin; rohkeuteen uudessa ympäristössä ja aggressiivisuuteen sekä, ovatko kyseiset käyttäytymispiirteet kytkeytyneet toisiinsa muodostaen käyttäytymissyndrooman. Lisäksi tutkin 2) onko rohkeus kytkeytynyt elinkiertopiirteiden (immuunipuolustuksen taso, kehitysaika ja koko) kanssa, sekä 3) tämän mahdollisen kytkeytymisen luonnetta (fenotyyppinen vs. geneettinen kytkeytyminen). Tutkin myös 4) sosiaalisen ympäristön vaikutuksia persoonallisuuden ja käyttäytymissyndroomien ilmentymiseen. Lopuksi, 5) muodostin käsitteellisen mallin joka hahmottaa käyttäytymisen plastisuuden evolutiivista potentiaalia, persoonallisuuden muodostumisen edellytyksiä ja eri käyttäytymistyyppien samanaikaista esiintymistä. Tutkimusteni mukaan mallilajini tutkimuspopulaatiosta on löydettävissä pysyviä eroja käyttäytymisessä yksilöiden välillä (persoonallisuuksia). Persoonallisuus ja immuunipuolustus olivat kytkeytyneet toisiinsa fenotyyppisesti, mutta eivät geneettisesti. Persoonallisuuden ja elinkiertopiirteiden välillä ei ollut yhteyttä mutta kehitysaika, massa ja immuunipuolustus olivat kaikki fenotyyppisesti kytkeytyneet. Fenotyyppisen kytkeytymisen selittivät osittain tiukat geneettiset korrelaatiot piirteiden välillä, jotka voivat rajoittaa yksittäisen piirteen evolutiivista kehitystä. Yksilön kokema sosiaalinen ympäristö voi saada aikaan käyttäytymisten kytkeytymistä toisiinsa (käyttäytymissyndrooma) mutta, vaikka dominantit yksilöt olivat rohkeampia verrattuna alisteisiin, toistuvat aggressiiviset interaktiot yksilöiden välillä eivät vaikuttaneet rohkeuden tasoon tai toistettavuuteen. Ympäristön vaihtelevuus voi vaikuttaa persoonallisuuksien esiintymiseen luonnon populaatioissa siten, että persoonallisuuksia esiintyy todennäköisimmin kun ympäristössä ei ole suurta vaihtelua tai kun vaihtelua on paljon.

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LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following articles, which are referred to in the text by their Roman numerals I–V.

I Niemelä P T, Vainikka A, Hedrick A V and Kortet R. Integrating behaviour with life history: boldness of the field cricket, *Gryllus integer*, during ontogeny. *Functional Ecology* 26, 450-456. 2012.

II Niemelä P T, Dingemanse N J, Alioravainen N, Vainikka A and Kortet R. Genetic associations between immune defense, personality and life-history. Manuscript, submitted to *Behavioral Ecology*.

III Niemelä P T, Lahdenperä S, Vainikka A and Kortet R. Nymphal density, behavioral development and life-history in a field cricket. *Behavioral Ecology and Sociobiology* 66, 645-652. 2012.

IV Niemelä P T, Martinez G, Vainikka A, Kortet R. Consistent differences in boldness between winning and losing individuals. Manuscript, *submitted*.

V Niemelä P T, Vainikka A, Forsman J, Loukola O and Kortet R. How does variation in the environment and costs of individual cognition explain the existence of consistent behavioural differences? Manuscript, submitted to *Ecology and Evolution*.

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AUTHOR´S CONTRIBUTION

In all the papers (I, II, III, IV and V), I had the principal responsibility for writing, data collection, and final data analysis. For study II, N. Alioravainen collected about half of the data. For study III, S. Lahdenperä collected important part of the data. For study IV, G. Martinez helped in data collection. All the study designs and statistical analyses were planned together with Anssi Vainikka and Raine Kortet. All the co-authors in each paper contributed to manuscript writing and finalization.

Contents

1. Introduction

Traditionally, animal behaviour has been studied inside separate ecological contexts and the overall adaptive value of variance in behaviour among individuals has been often neglected as uninformative noise around a mean. In contrast, animal personality research focuses on within- and between-individual variation in behaviour. Studies of stable behavioural differences among individuals across time and contexts are relative new phenomenon in the field of behavioural ecology. At the early 21st century, personality studies expanded to behavioural ecology from human sciences such as psychology (Gosling & John 1999, Gosling 2001). Since then, theoretical studies and conceptual reviews concerning the existence of animal personalities, stability of behavioural differences, and plasticity of behaviour have gained broad attention (Sih et al. 2004a,b, Biro & Stamps 2008, Wolf et al. 2008, Dingemanse et al. 2010, Dingemanse & Wolf 2010, Réale et al. 2010, Stamps & Groothuis 2010, Wolf & Weissing 2010) and animal personalities have been found in numerous species from different taxa (Sih et al. 2003, Dingemanse et al. 2002, Boon et al. 2007, Dingemanse et al. 2007, Vainikka et al. 2010, Wilson et al. 2010). Personality approach has opened new, more holistic insights to the field, compared to traditional behavioural ecology, which viewed different behaviours as independent traits with optimal value for every context and situation.

Recently, the studies of animal personalities have taken even more integrative approaches and aimed at comprehensive understanding of associations between personality and life-history traits (Stamps 2007, Biro & Stamps 2008, Barber & Dingemanse 2010, Kortet et al. 2010, Réale et al. 2010, Sih et al. 2012). According to verbal and formal models, life-history trade-offs might generate and maintain personality differences between individuals and generate associations between distinct behaviours by setting different fitness expectations for different behaviours (Stamps 2007, Wolf et al. 2007a, Biro & Stamps 2008). Due to variance in their states, individuals differ in their future fitness expectations, which generate stable between-individual differences in behaviour. Because personalities must have an adaptive basis to evolve, it is important to be able to explain the mutual within-population existence of different stable behavioural strategies (Dingemanse & Wolf 2010, Wolf & Weissing 2010). Moreover, since personality is potentially associated with life-history for the abovementioned reasons, there is a need to understand the ecological and evolutionary mechanisms that produce and maintain these often co-varying structures in nature (Réale et al. 2007, Biro & Stamps 2008, Réale et al. 2010, Sih et al. 2012).

1.1. ANIMAL PERSONALITY AND BEHAVIOURAL SYNDROME

1.1.1. Definitions

Animal personality studies have adopted many of the definitions from personality studies in human psychology (Gosling & John 1999, Gosling 2001). Animal personalities are defined as consistent between-individual differences in behaviour across time and / or across contexts (for example in mating and feeding contexts) (Réale 2007, Stamps & Groothuis 2010). Behaviours may also be associated with each other and form behavioural syndromes (for example the well-known coupling between aggression and boldness) (Stamps & Groothuis 2010). To still represent personality, behaviour can be plastic as long as individuals shift their behaviour in same direction so that between-individual relative differences remain constant (Sih et al. 2004b, Réale et al. 2007). Different behaviours may become associated with each other tightly, for example, by hormonal or genetical mechanisms (Figure 1). Tight associations between behaviours may limit the independent variation of single behaviour, cause behavioural plasticity to be limited and thus also explain maladaptive behaviour (Sih et al. 2004a and references therein). For example, in fishing spiders, aggressive females have short latencies to attack and kill prey items. Aggressive females expressed unnecessary carryover aggressiveness in mating context by killing courting males before copulation leading to low reproductive success (Arnqvist & Henriksson 1997, Johnson & Sih 2005).
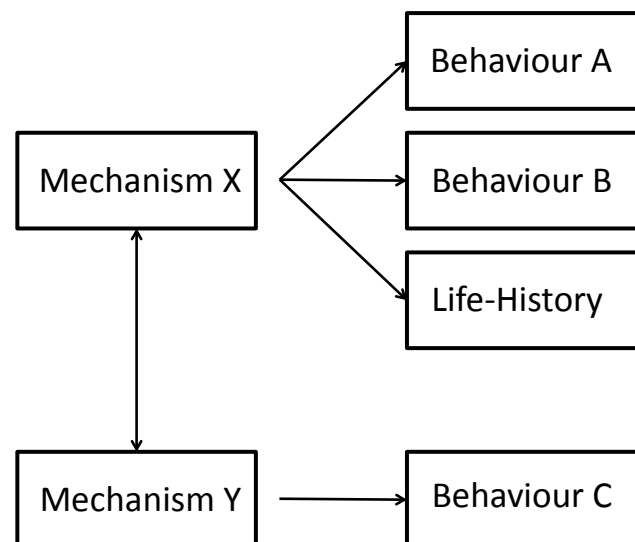

Figure 1. Behavioural and life-historical traits can become associated with each other through common mechanisms (Modified from Sih et al. 2004a).

1.1.2. Behavioural types

Because within- and between-individual differences in behaviour are often consistent, individuals can be divided to different, stable, behavioural types (Sih et al. 2004b). Consistent between-individual differences in behaviour can be found at three different levels; differences within a single behaviour (for example within aggression or boldness), differences in suites of functionally distinct behaviours (some are consistently more bold and aggressive across time and contexts compared to others) and differences in behavioural plasticity (Dingemanse & Wolf 2010). Since different behaviours may share a common mechanism, the plasticity of behaviours may be limited (Sih et al. 2004a). Limited plasticity means that individuals are not free to express optimal behaviour across time or context but rather follow their individual, relatively stable, behavioural style. The lack of optimal plasticity leads to context-dependent fitness/survival trade-offs, where individual has high fitness/survival in one context, but low fitness/survival in other context (Stamps 2007). For example, in streamside salamander larvae, *Ambystoma barbouri*, individuals that spent less time in their refuge in predator free environment, were also more exposed in environments where predators were present. This led to higher mortality compared to more cautious individuals (Sih et al. 2003).

At the early days of animal personality research, behaviour was thought to be restricted and non-plastic. However, recent theoretical studies suggest that behavioural plasticity and between-individual differences in plasticity are important part of animal personality concept, which technically, can be represented as a behavioural reaction norm having both intercept (mean level of behaviour) and slope (change in behaviour according to gradient) (Dingemanse et al. 2010). The level of behavioural plasticity may depend on behavioural type. For example, "slow" (i.e. shy, non-aggressive) behavioural types may express higher level of plasticity compared to "fast" behavioural types (i.e. aggressive, bold) (Koolhaas et al. 1999, Wolf et al. 2008, Dingemanse et al. 2010, Stamps & Groothuis 2010). Behavioural type-dependent plasticity in behaviour can potentially be explained by physiological differences between-individuals (Coppens et al. 2010).

1.1.3. Coexistence of behavioural types/personality differences

If tight associations between behavioural traits lead to non-optimal plasticity and maladaptive behaviour in some situations, why behaviours have not been evolved towards high plasticity leading to optimal behavioural response in every context and situation? Phenotypic plasticity *per se* can be costly in terms of energy, time or other resources leading to selection against optimal response in every situation (DeWitt et al. 1998, Auld et al. 2010). There may be genetic restrictions, which limit the evolutionary potential of traits (Sih et al. 2004a), or environmental charachteristics, which select against plastic behaviour (c.f. V). However, several ecological and evolutionary explanations for the coexistence of stable between-individual differences in behaviours have been suggested (Dingemanse & Wolf 2010, Wolf & Weissing 2010).

Growth-survival trade-offs have been used to explain the coexistence of different behavioural types (Stamps 2007). "Fast" (aggressive, bold, active)) individuals may be overall superior competitors compared to "slow" (non-aggressive, shy) individuals and may therefore have fitness benefit if all the other fitness aspects are equal (Sih et al. 2004b, Smith & Blumstein 2008). However, because limited across context plasticity, "fast" phenotypes may express unnecessary "spillover" aggressiveness in other contexts and, because of unnecessary boldness, be more susceptible to predators (see above) leading to equal fitness of two extreme behavioural types (e.g. Sih et al. 2004b). In general, "fast" individuals can have higher reproductive success but lower survival in other contexts (i.e. context-dependent survival trade-off) balance this fitness benefit gained from higher fecundity (Smith & Blumstein 2008). Moreover, general mechanisms known to support diversity, such as dynamic, spatiotemporal variation in selection pressures may be one of the main reasons to maintain the coexistence of behavioural types in nature (Dingemanse & Réale 2005). Environmental selection pressures are variable across time selecting against "fast" types in certain years and "slow" types in other years leading to dynamic coexistence of different types (Dingemanse & Réale 2005).

Between-individual differences in state (physiological, morpholocigal) are a potential answer to explain consistent differences in behaviours. Behaviour may be functionally associated with stable state variables leading to a situation where also behavior is relatively stable in time. Also, state can affect multiple behaviours at the same time explaining the correlations between multiple behaviours (Dingemanse & Wolf 2010). Potential state differences explaining differences in behaviour include energy reserves, body size, reproductive value, productivity or metabolic rate (Dingemanse & Wolf 2010). Between-individual differences in state can erode with time by negative feedback mechanisms (Luttbeg & Sih 2010): individuals that start with high assets (i.e. high state: high energy reserves, high reproductive value) should be cautious and unaggressive, which will cause their assets to erode and finally equal with individuals having initially low but continuously increasing assets over time (Luttbeg & Sih 2010, however, see Wolf et al. 2007b). Therefore, negative feedback loops are unlikely to explain long term behavioral differences between individuals (Luttbeg & Sih 2010). Instead, positive feedback of individual behavior on state can explain the maintenance of long-term differences in individual behavior by reinforcing originally small differences in assets (McElreath et al 2007, Luttbeg & Sih 2010). For example, individuals with high assets (e.g. large size) are often bold and aggressive, and thus gain more assets leading to state-dependent (e.g. size-dependent) safety from predators and helping them to win fights, which in turn leads to positive feedback to their state and further enforces the behavioural differences between the individuals and tightens the associations between behaviours (McElreath et al. 2007, Luttbeg and Sih 2010). Differences in initial assets may arise, for example, due to variation in growth rate due to innate and / or environmental differences (Arendt 1997, Luttbeg & Sih 2010). One of the proposed ultimate mechanisms for initial asset differences is the co-evolutionary arms-race between parasites and hosts,

which induce innate differences in immune functions leading to inherent state differences between individuals (Kortet et al. 2010).

1.1.4. Ecological impact of animal personalities

Animal personalities can be found in individual, population and species level and, since individual behavioural type affects individual's fitness, personalities likely have major implications to all ecological phenomena in nature (Réale et al. 2007, Biro & Stamps 2008, Sih et al. 2012). Animal personalities may affect, for example, species distribution and abundance, migration, species interactions, population dynamics, ecological invasions, susceptibility to harvesting and recovery from human disturbance (e.g. Sih et al. 2012). Behavioural type of a population or species may have great impacts on population dynamics. Since intimidation effects of predators can be considered ecologically equally important as direct predation effects (Preisser et al. 2005), individual differences in susceptibility to intimidation effects could have large scale ecological implications on functional responses and food web dynamics. For example, an introduced predator can cause a patch to become extinct relatively easily, if patch includes mainly bold, aggressive and exploratory individuals with carryover behavioural effects (Sih et al. 2003). Clearly, the behavioural types of both predator and prey, have impact on species interactions and communities. Aggressive predators (individuals or species) consume more prey and have wider selection of prey species compared to less aggressive predators, and correspondingly bold and aggressive prey get eaten more often compared to shy and less aggressive prey species / or individuals (Sih et al. 2012). Inability to react to environmental change, to respond to environmental cues or to adopt novel survival strategies by some individuals, populations or species (i.e. proactive types: aggressive, bold) may cause those populations to be unable to survive if environment is changing rapidly. Rapid changes to environments can be found especially in human disturbed landscapes (Sih et al. 2012), and because of behavioural type related restrictions to respond, different species or populations are not in the same level of tolerance to environmental change. Interestingly, shy bird species have been found to be more susceptible to human disturbance and more likely to express declining population sizes (Moller 2008). Species with broad range of variation in behavioural types can manage to succeed in broader range of spatial or temporal variation (Sih et al. 2012), and thus have greater distribution compared to more type-restricted species. Therefore, the studies of animal personalities are crucial to comprehensively understand the ecological patterns like population dynamics, species distributions and the effects of human activity to populations or species in nature.

1.2. ASSOCIATION BETWEEN BEHAVIOUR AND LIFE-HISTORY

1.2.1. Personality life-history axis

Recent theoretical studies suggest that behavioural traits and personality are potentially associated with several life-history traits (Stamps 2007, Biro & Stamps

2008, Barber & Dingemanse 2010, Kortet et al. 2010, Réale et al. 2010) (Figure 1). Examples of such life-history traits are growth rate, metabolic rate and immune defence (Stamps 2007, Biro & Stamps 2008, Kortet et al. 2010, Barber & Dingemanse 2010, Luttbeg & Sih 2010). To maintain high growth rate individuals need consistently high energy intake rates, which can be acquired only by being bold, aggressive and active (Stamps 2007). Deviations from constant growth rate have been found to contribute negatively, for example, to lifespan/survival, dominance rank, fecundity, adult morphology, adult body size, offspring size and offspring acquisition of breeding territory, lower offspring survival and low quality (Dewitt et al 1998, Metcalfe & Monaghan 2001) and therefore, differences in life-history traits like growth rate, can promote stable behavioural differences. Moreover, aggression or activity may lead to higher predator-based mortality favoring faster maturation of individuals with such behavioural types (Stamps 2007, Biro & Stamps 2008).

Strength of immune defence is one of the most important life-history traits that have been suggested to co-vary with personality (Barber & Dingemanse 2010, Kortet et al. 2010, Luttbeg & Sih 2010). Parasitism is likely linked to activity and exploration of the host (Wilson et al. 1993, Barber & Dingemanse 2010, Boyer et al. 2010), which forms an adaptive basis for linkage between immune defence potential and personality. Parasites often manipulate hosts´ traits (also behavioural) (Seppälä et al 2004, Thomas et al. 2005, Seppälä et al. 2008, c.f. Barber & Dingemanse 2010, Kortet et al. 2010). Parasitism may affect behavioural traits indirectly by affecting hosts´ state leading to population specific behavioural expression if populations include endemic parasites altering the state of hosts by different, population related, magnitudes (Barber & Dingemanse 2010). Also, different behavioural types may also be susceptible to different parasites (Wilson et al. 1993), which may lead to a situation, where different behavioural types invest in immune defence in different ways (Koprivnikar et al 2011, I, II).

1.2.2. Pace-of-life syndrome (POLS)

Environmental and ecological aspects shape the evolution of life-histories (Stearns 1992), and may cause traits to be associated in the certain manner because of energetic or recourse based trade-offs. According to POLS-framework, the underlying reason for the multi-trait associative system can be found in historical, adaptive organization of physiological control mechanisms. This organization is caused by environmental selection pressures which constrains the individual variation of traits and binds certain trait combinations together in predictable manner in population and species level (Ricklefs & Wikelski 2002, see also Reznick et al. 2002 for r- and K-selection strategies). Because physiology of the species binds its trait expressions to confronted environment, populations or species can produce only a limited set of trait combinations due to genetic constrains of physiological response mechanisms or allocation of limited resources (Ricklefs & Wikelski 2002, Wikelski et al. 2003). According to POLS hypothesis, species or populations can be divided to a "fast-slow" (in this context, not related to behavioral strategies) continuum where several traits

are associated predictably according to ecological conditions of the environment. Along this "fast-slow" continuum, "fast" (fast maturation, short developmental time, short lifespan) types and "slow" (long maturation time, short developmental time, long lifespan) types can be found (Ricklefs & Wikelski 2002, Wikelski 2003, Wiersma et al. 2007). Tropical birds, for example, have been characterised to "slow" end of the POLS continuum with slow basal metabolic rates, long lifespan and late maturation while bird species from the temperate region are often found to express "fast" type characteristics, such as high metabolic rate, short lifespan and fast maturation (Wiersma et al. 2007 and references therein). Immune defence is one of the traits hypothesized to be part of POLS-syndrome (Ricklefs & Wikelski 2002). "Slow", long living, types should invest more resources to a rapid, strong immune response to protect future reproductive success in the cost of present reproduction, compared to "fast", short-living types investing the present reproduction at the expense of longevity (Ricklefs & Wikelski 2002, Tieleman et al. 2005). In real life, life-history states are dynamic and can be altered, at least temporally, due to, for example, stress reactions. In stress response individuals can jump from a physiological state to another due to adjustment of the endocrine system and enhance survival at the expense of other functions (Wingfield et al. 1998). If an alternative state is sustained for long periods, it may even alter the apparent life-history strategy of an individual (Ricklefs & Wikelski 2002).

Recently, integration of animal personalities and life-history has opened new insights for the study of "personality-life-history syndromes" (personality-POLS) (Réale et al. 2010). "Personality life-history" syndrome theory is similar compared to "pace-of-life" syndrome (POLS) hypothesis with the addition of behavioural traits to life-history associative structure. Also, traditional POLS studies have been conducted mainly between population and species level compared to personality-POLS hypothesis, which works also within population and individual level (Wikelski et al. 2003, Tieleman et al. 2005, Sparkman & Palacios 2009, Réale et al. 2010). Behavioural traits may be under the same physiological control mechanisms than other life-history traits (Sih et al. 2004a). Also, behaviour of an individual potentially affects the organism-environment interaction generating the functional relationship between personality and life-history (Ricklefs & Wikelski 2002). More aggressive, bold and exploratory individuals may, for example, have an access to greater amount of recourses compared to shy, non-aggressive individuals. According to personality-POLS framework, "fast" individuals with short lifespan, fast growth and high reproduction tend to be more active, exploratory and aggressive compared to "slow" individuals. Personality-POLS and personality-life-history axis show remarkable similarities in their hypothesized associative structures between behavioural and life-historical traits (Stamps 2007, Biro & Stamps 2008, Réale et al. 2010), and in personality-POLS hypothesis by Réale et al. (2010) recognize that there already are existing theories between this associative structure. However, the personality-POLS hypothesis gives first, fully integrative framework between personality and other traits. So far, there are only a handful of empirical phenotypic and, virtually no

quantitative genetic evidence for associations between life-history and animal personality.

1.2.3. Evolutionary potential of covariation between personality and life-history

Phenotypic covariation between traits can arise from both environmentally induced and genetic mechanisms (Sih et al. 2004b, Biro & Stamps 2008). Evolvability of a trait depends on both the environmental selection pressures and the heritability (i.e. amount of phenotypic variation (V_P) explained by genetic variation (V_a)) of the trait (Falconer & MacKay 1996). The selection pressure defines the direction of evolution and amount of evolutionary pressure while heritability defines the amount of genetic variation the selection can work on. Phenotypic co-variation between traits does not necessarily indicate the presence of genetic association unless the heritability of the traits is high (Hadfield et al. 2007, MCGuigan & Blows 2007, Dingemanse et al. 2012). Therefore, by studying only phenotypic expression of behaviour, life-history and immunology we cannot reliably predict responses to selection and evaluate the evolutionary potential and stability of associative structure between traits (Raucher 1992, Dochtermann & Roff 2010, Dingemanse et al. 2012). Potential associations between the life-history, immune function and behaviour are not well-known (Réale et al. 2010). Also, we do not know whether these connections between traits have a genetic basis and thus, how to place the associative structure between traits in an evolutionary framework. Hence, one of the main future aims of the field is to quantify the nature of associations between life-history, immune function and personality.

1.4. PERSONALITY AND SOCIAL INTERACTIONS

Interactions with conspecifics are an important factor for generating the social hierarchy and defining the individuals´ position in social continuum (Francis 1988, Huber & Kravitz 1995, Neat et al. 1998, Obermeier and Schmitz 2003, Delgado-Morales et al. 2004, Wong & Candolin 2005, Schwartz et al. 2007, Hock & Huber 2007). In our model species, *Gryllus integer*, dominance is achieved by aggressive encounters (Kortet & Hedrick 2007). Population's social structure and individuals' social positions in a group affect the fitness pay-offs of certain behaviours since group size defines the patters of social interactions (Webster & Ward 2010). Therefore, an individual´s social status may explain its fitness value and position in behavioural continuum. For example, in our model species, individuals that are more aggressive and win more aggressive interactions, achieve higher status in population (Kortet & Hedrick 2007), which in turn may help individuals to achieve better territories or more copulations compared to less aggressive ones (Leonard & Hedrick 2009). Moreover, similarly to some other taxa, aggressiveness is associated with boldness (Kortet & Hedrick 2007), and has also been found to be generally associated with

dominance (Francis 1988, Vrontou et al. 2006). Thus, individual´s social status may explain other, associated behaviours.

Potential mechanisms affecting behaviour in social environments are conformity or social facilitation (Webster & Ward 2010). Conformity is frequency-dependent phenomenon, where individuals perform the behaviour of the majority of the social group (Webster & Ward 2010). In social facilitation, presence of a social group makes individual performs behaviours in a way they would not have done without a presence of conspecifics (Webster & Ward 2010). The ecological mechanisms for such behavioural shifts include reduced risk of predation and increased levels of competition for resources according to group size (Webster & Ward 2010), which in turn affect the payoffs of different behaviours. Group size may, for example, affect the resource intake rates and aggression so that in high density *per capita* resource intake rates are reduced, which may cause the number of aggressive encounters and aggressive behaviours to rise. Moreover, boldness may be changed if aggression is associated with boldness.

1.5. COGNITION, BEHAVIOURAL PLASTICITY AND ENVIRONMENTAL VARIATION

To be able to collect and process and use complex information from the environment, individuals need efficient information processing machinery, cognition (Heyes & Huber 2000, van Horik & Emery 2011). Environments express substantial spatiotemporal variation (Ruokolainen et al. 2009, García-Carreras & Reuman 2011, Bezault et al. 2011). Cognitive learning is a common phenomenon in nature (Papini 2002), helping individuals to adapt behaviourally to confronted, variable, environments. Cognition is expensive in terms of time and energy, since neuronal tissue needed for efficient cognition is one of the most expensive tissue types (Armstrong 1983, Laughlin et al. 1998, Purdon & Rapoport 1998, Isler & Van Schaik 2009a, Isler & Van Schaik 2009b) and information acquisition is costly in terms of time, reliability and predation costs (DeWitt et al 1998). Therefore, cognitive abilities, and thus, behavioural plasticity is presumably expressed only in environments, where fitness benefits of cognition exceeds the cost. Spatiotemporal variation of the environment defines the amount and complexity of the information individual needs to deal with when making fitness decisions and thus, defines the selective regime for cognition. The evolution of plasticity is generally favored in variable environments, where information from the environmental variation is not hidden (low noise) (Relyea 2002, McElreath & Strimling 2006). Accordingly, high cognitive ability is also favoured in variable environments (Bergman & Feldman 1995, Heyes & Huber 2000, Godfrey-Smith 2002, Mery & Kawecki 2002, Kerr & Feldman 2003). However, when environmental variability is too high, cognition is selected against (Bergman & Feldman 1995, Kerr & Feldman 2003).

The differences in responsivity (cognition) between behavioural types may be caused by underlying differences in their physiology (Coppens et al. 2010). Some may be able to harvest reliable information from the environment more efficiently

(responsive individuals) compared to others (stereotypic individuals) because of their superior cognitive abilities (Sol et al. 2005). Therefore, different behavioural types may be favoured in different kinds of environments. Stereotypic individuals have advantage in environments selecting against cognition and responsive individuals in environments selecting for cognition (stable or highly variable and variable environments, respectively). Moreover, between the environments where responsive or stereotypic individuals are favored, there are environments, where both types express equal fitness and thus, are likely able to coexist (V, Figure 2). The ability to plastic behavioural responses enables optimal behavioural responses according to context and may thus limit the existence or expression of animal personalities and behavioural syndromes.
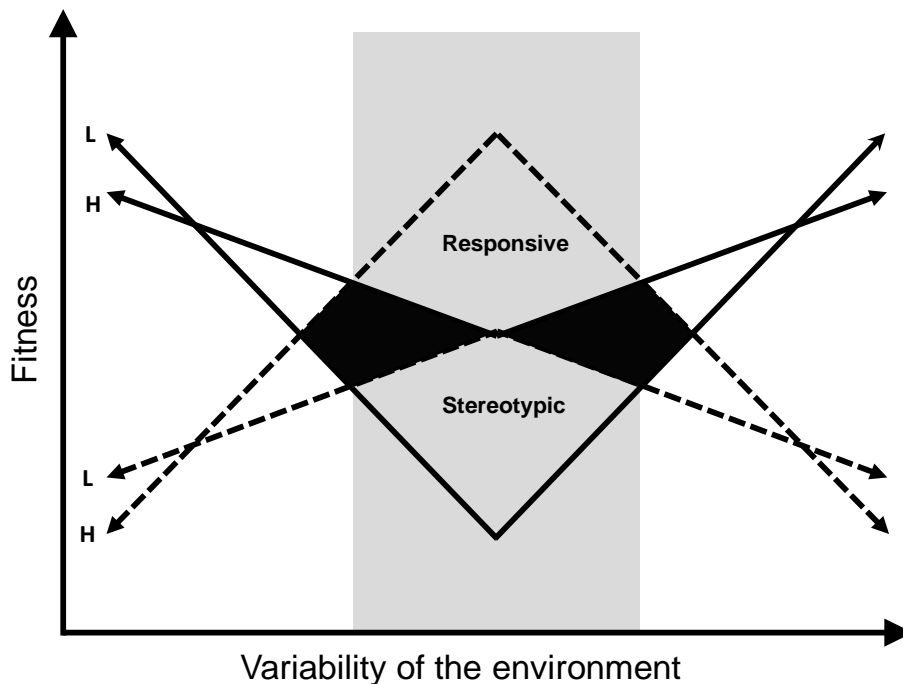
Figure 2. Behavioural type-dependent fitness benefits of information usage within and between behavioral types in environments with different environmental variability. In grey area the benefits of cognition exceeds its energetic costs. Therefore, responsive behavioral types (dashed line) with high (H) and low (L) cognitive abilities dominate in these kinds of environments, compared to stereotypic behavioral types (solid lines) that instead dominate in invariable or highly variable environments (i.e. outside grey area). Variation in cognitive abilities within and between behavioral types leads to environment - dependent coexistence of different behavioural types (black area). In the grey area, the high plasticity in behaviour potentially restricts the consistency in behaviours and therefore may limit the abundance of animal personalities or behavioural syndromes.

1.6. OBJECTIVES OF THE STUDY

The present thesis focuses on the emergence of animal personality and behavioural syndromes, associations between life-history and personality and plasticity of behaviour. In this thesis I study if stable behavioural differences (i.e. animal personalities) and associations between behaviours exist in the study population of our model species, the Western stutter-trilling cricket, *Gryllus integer*. Moreover, I study, if personality, immune defence, maturation time and body mass are associated with each other and if phenotypic associations have a genetic basis (i.e. reveal the evolutionary potential of this association). I examine how social interactions affect the emergence of animal personalities and life-history and how environmental information usage, combined with environmental variability, form an evolutionary framework explaining personality differences and behavioural plasticity. I use *G. integer* as a model species in all the experiments of this thesis, except in work V, which is purely conceptual.

The specific aims of the thesis are:

- To investigate whether the key behavioural traits (i.e. boldness and aggression) can be considered as *personality traits* and whether there can be found *behavioural syndromes* in our study populations (I, III, IV).

- To examine the phenotypic associations between life-history and behaviour and stability of behaviour through ontogeny (I).

- To study the heritability and genetic associations between behaviour and life-history (II).

- To find out if individuals' social environment as an ecological factor affect the expression, associations and stability of behaviours (III, IV).

- To evaluate the environmental conditions and individual level characteristics that are required for behavioural plasticity and formation of animal personalities in population level (V).

2. Materials and methods

2.1. STUDY MODEL: Western stutter-trilling cricket, G. integer

I used *G. integer* as main model organism. This cricket species has been used widely in behavioural, mate choice and life-historical studies (Wiegmann 1999, Gray & Cade 1999, Bertram 2000, Martin et al. 2000, Kortet et al. 2007). Recently it has been included also as a model species in animal personality research (Kortet and Hedrick 2007, Hedrick & Kortet 2012). Male *G. integer* are territorial possessing a small area where they call to attract reproductive females and which they defend against other males (Hedrick 2000). Within a territory there is a small burrow in the ground, which is sometimes surrounded by protective cover, which also works as a shelter against predators (Hedrick 2000). In nature, crickets are predated by several predators including mice, birds and toads (Hedrick 2000, Hedrick & Kortet 2006). *G. integer* natural distribution covers a continuum from southern Texas, Arizona and Utah to California and southern Oregon (Walker 2012). Our study population (20 subpopulations), originating from Davis, Central California, was established in 2008. The size of our population was all the time at least 800-1500 individuals. Offspring from a subpopulation was mixed randomly with offspring from other subpopulations to maintain genetic diversity. Also, our laboratory population was supplemented with offspring of wild individuals from Davis, California in 2010 (n = 50)

2.2. GENERAL STUDY DESIGN

All the experiments presented in this thesis were conducted in laboratory facilities of University of Oulu between 2009-2011 (Table 1).

Table 1. *Summary of the experimental designs of the studies in the thesis.*

Main research topic	Description of the work	Measured traits
Paper I: Is behaviour consistent trough ontogeny and is life-history associated with personality?	Correlative design to study consistency of behaviour across ontogeny and phenotypic associations between traits.	Boldness and body mass repeatedly across ontogeny, Body size*, growth rate and encapsulation response.
Paper II: Are personality and life-history heritable and are there genetic associations between traits?	Nested maternal half-sib, full-sib experimental design to study heritability of and genetic correlations between traits.	Boldness, body mass, developmental time and encapsulation response.
Paper III: Does social environment during ontogeny affect the association of behaviours or life-history and behaviour?	Study with three different levels (treatments) of sociality; solitary grown individuals, groups of four individuals and group of ten individuals.	Boldness, aggression, body mass, developmental time and encapsulation response.
Paper IV: Do enforcement of dominance status alter the level of boldness or break up personalities?	Study with two different levels of dominance (dominant and subdominant) and one control level. Repeatedly manipulate individuals either to win or lose in dominance trials and observe if boldness change accordingly.	Boldness repeatedly, dominance and body mass
Paper V Define the evolutionary emergence and coexistence of behavioural types.	Conseptual framework: How environmental variation induced differences in cognition cause differences in behavioural plasticity leading to environmental gradient -dependent expression of personalities?	no measurements

 * Body size include the measurements of total body length and pronotum width

2.2.1. Behavioural and dominance measurements

We measured boldness, aggression and dominance (defined here as social status). Boldness was measured using previously standardized methods modified from the studies by Ann Hedrick and Raine Kortet (Hedrick 2000, Hedrick & Kortet 2006, Kortet & Hedrick 2007). In behavioural experiments, we measured boldness in a novel environment. As a proxy for boldness, we used latency times to become active (early boldness in I and IV, de-freezing in II) and latency to emerge from a shelter (late boldness in I and IV, overall boldness in II) after disturbance in a novel environment. This kind of behavioural measurement method has been previously used also with other taxa such as mammals (Boissy 1995). Boldness is defined as

activity in potentially dangerous environment (Réale et al. 2007). "Freezing" is a behavioural antipredator response used by invertebrates against threatening situations (Chelini et al. 2009). As our crickets expressed "freezing" when placed inside our experimental setup, our experimental environment expressed itself as "potentially dangerous" to our experimental animals.

Aggression and dominance was measured in males against a weight-matched random conspecific. Measurement of aggression was done by following roughly the methods previously used by Kortet and Hedrick (2007). In our experiment, individuals gained points according to different aggressive postures against conspecific (III). In work IV, we judged dominance by observing the winning and losing individuals and gave dominance status for the individual that was clearly dominant by the end of the trial. Therefore, in this work, I do not treat dominance as a behavioural trait, but rather as social status.

2.2.2. Immunological studies

We measured encapsulation response against novel object as a proxy for cellular immune response. Encapsulation response against novel antigen has been previously used for measuring the level of cellular immune defence in insects (Gillespie et al. 1997, Rantala & Roff 2005). Hemocytes circulating in hemolymph recognise foreing objects like bacteria or parasitoid eggs (Lavine & Strand 2002) and aggregate on the surface of the novel objects. In the encapsulation process, prophenoloxidase (ProPO) is activated to phenoloxidase (PO), which forms quinones with oxygen and phenols, leading to the formation of melanin on the capsule formed by the hemocytes (Cerenius & Söderhäll 2004, Jiang 2008). This melanin capsule suppresses the intruder and makes it unable to function. Nylon monofilament capsule has been previously used successfully as foreign intruder to activate the cellular immune defence cascade in invertebrates (Rantala & Roff 2005). Here, we used 2 mm long, 0.16 mm thick nylon monofilament (Stroft GTM, Germany) roughened with sandpaper to activate and measure the level of cellular immune defence (i.e. encapsulation response). Implants were set inside CO_2 anesthetized crickets abdomen for 24 hours. The level of encapsulation was measured as the grey value of the photographed implant (see more specific methods from I, II, III).

2.2.3. Other measurements

As a proxy for body size, we used the measurements of body length and the width of the pronotum which have been used earlier as a proxy for body size (e.g. Zuk 1988, Hunt et al. 2004). Body measurements were taken from CO_2-anesthetized crickets. To create one variable describing general body size, we combined these two variables using Principal Component Analysis (PCA) (Jolliffe 2002). Body mass was measured to the nearest 0.001g. Developmental time was calculated as time in days from hatching to maturation.

3. Results and discussion

3.1 ANIMAL PERSONALITIES AND LIFE-HISTORY (I, II)

One of the main findings of my thesis was the detection of stable between-individual behavioural differences (i.e. animal personalities) in boldness in our study population (I, IV, See also Niemelä et al. 2012). Even though field crickets were bolder in juvenile stages compared to adult stages, stable between-individual differences were present both, across ontogeny and after sexual maturation. Across ontogeny only late boldness was repeatable, but after sexual maturation differences in both early and late boldness were consistent between individuals (I, IV, Niemelä et al. 2012). Our team has been the first to find stable behavioural differences (i.e. personalities) in widely use model species, *G. integer*.

We found both, phenotypic and genetic support for within population level POLS hypothesis. According to POLS, population and species level trait associations can be divided to "fast"- and "slow" continuum where "fast" types have fast maturation, low body mass and low immune defence potential (Wikelski et al. 2003, Wiersma et al. 2007). Our results revealed a positive phenotypic association between maturation time, body mass and immunity within population, therefore supporting the predictions of POLS hypothesis in our study population. Phenotypic associations were underpinned by genetic correlations between maturation time and body mass and maturation time and encapsulation. Overall, however, the personality-POLS hypothesis did not get full phenotypic and no genetic support from our results (I, II). According our results only encapsulation response was associated phenotypically with personality so that bold individuals had higher encapsulation responses compared to shy conspecifics (II). However, individuals that were shy in early juvenile stage, had higher encapsulation response after maturation (I), indicating dynamic nature of trait associative structure across ontogeny. Maturation time and boldness and body mass and boldness were not associated either phenotypically or genetically. The phenotypic association between encapsulation response and boldness as adults was opposite compared to what Réale et al. (2010) suggested in his conceptual POLS framework. Building up, maintaining and using of immune system imposes high energetic costs (Armitage et al. 2003, Freitak et al. 2003, Schmid-Hempel 2003). Thus, like growth rate, it requires high energy intake rates which are supported by bold and exploratory behaviours. Therefore, an alternative, resource based hypothesis for the phenotypic association between immunity and personality suggested by Kortet et al. (2010) may explain the positive association between encapsulation response and boldness. Bold and aggressive individuals, who are able to collect lot of energy from the environment, are able to build up and maintain high immunity.

Ecologically, the higher immune defence potential for bold individuals is an interesting phenomenon, since parasites often affect the morphology, physiology or manipulate the behaviour of the host (Thomas et al. 2005, Rolff & Reynolds 2009), and have great impact of the host´s fitness through infections or other physiological mechanisms (Rolff & Reynolds 2009). Boldness and activity most likely elevate the risk of parasitism and lead to infections by more diverse selection of pathogens compared to shy and less bold individuals and therefore, these behaviours affect negatively to fitness in parasitism-context (Wilson et al. 1993, Barber & Dingemanse 2010, Boyer et al. 2010). Bold individuals can compensate their potentially higher susceptibility for parasitic infections by their higher cellular immunity potential and be able to resist the behavioural manipulation and other negative effect of parasitism more efficiently compared to shy conspecifics (Kortet et al. 2010).

The fact that all life-history traits were heritable (i.e. there is high additive genetic variation in our study population), means that selection can act on these traits (i.e. they have high evolutionary potential). However, despite the high heritability of life-history traits, genetic linkage between traits may also limit the evolvability of an individual trait (Rolff & Reynolds 2009). If traits are associated via linkage disequilibrium, association structure can be uncoupled by natural selection relatively easily and traits become free to evolve independently. On the other hand, if traits are associated via genetic pleiotropy, the association of traits is difficult to uncouple by selection and independent evolution of traits is limited (Rolff & Reynolds 2009).

Phenotypic expressions of traits depend on confronted environment and within population selection pressures (Gotthard & Nylin 1995, Wikelski et al. 2003, Kraft et al. 2006, Wiersma et al. 2007, McCairns & Bernatchez 2012, work III). For example, in our study species, individuals have been found to differ in their boldness according to the level of predation pressure (Hedrick & Kortet 2006, Niemelä et al. 2012). The amount of measurable genetic variation and heritabilities (i.e. amount of phenotypic variation (V_P) explained by genetic variation (V_a)) of traits most likely depends on environmental characteristics (Dingemanse et al. 2009), since environmental variation affects the amount of V_P (Hoffman & Merilä 1999). Realized selection pressures have most likely affected the genetic associative structures of traits over evolutionary time. Therefore, the associative structure suggested by personality-POLS may not be applicable to all populations, but rather a subset of populations with certain environmental characteristics. According to my results, personality-POLS hypothesis cannot fully be applied in our study population (I, II). Also, personality and life-historical traits may have different responses to change in environmental gradient, since these traits are not coupled genetically (II). This was supported by my results, where population density, as an environmental variable, shaped the expression of several life-history traits but behavioural traits remained unchanged (III). However, even when personality is not associated genetically with life-history, behaviours may still be associated phenotypically with life-history in some environments. This is if those environments cause plastic responses individually to behaviour and life-history generating phenotypic covariation between the two. It is clear that more empirical

studies from multiple populations with different selection pressures are needed to reveal the most general associative structures between personality and other traits.

3.2 SOCIAL INTERACTIONS, BEHAVIOUR AND LIFE-HISTORY (III, IV)

The role of social interactions during ontogeny has been so far neglected from the studies of animal personalities and behavioural syndromes. Social interactions are important forces balancing the dynamics of a population by creating a social dominance structures and therefore, reducing the amount of aggressive encounters (Obermeier & Schmitz 2003, Delgado-Morales et al. 2004, Wong & Candolin 2005, Schwartz et al. 2007, Hock & Huber 2007). Since social interactions define the position of an individual within population, they also have potential to shape behaviour of an individual. My results of the association between aggression and boldness in highest population density indicate that social interactions during ontogeny may generate behavioural syndromes (III). In high population densities, boldness and aggression were negatively associated so that aggressive individuals expressed low boldness. However, the level of expression of individual behavioural traits did not depend of the confronted social environment (III). Moreover, we found that dominant individuals were consistently bolder compared to subordinant or control individuals (i.e. dominance-boldness syndrome) (IV). This is interesting, since our results suggest a behavioural type dependent resource holding potential (Ranta & Lindström 1993, Vainikka et al. 2011), and thus a behavioural type-dependent reproduction potential in our study population. In reality, higher fitness potential of bold individuals may be balanced by other factors like higher predation rate or wounding potential of aggressive encounters against conspecifics in bold individuals (Dingemanse & Wolf 2010, Wolf & Weissing 2010).

Kortet & Hedrick (2007) found activity in novel environment and aggression to be positively associated among the solitary grown offspring from wild derived mothers. In our studies, dominant were bolder compared to subordinant, but aggression was not related to boldness in solitary grown individuals (III, IV). Instead, aggression was negatively associated with boldness in high population density (III, IV). Our finding of the negative association between these behavioural traits contrasts the association that is usually hypothesized between these traits (i.e. positive association) (Kortet & Hedrick 2007, Stamps 2007, Biro & Stamps 2008). This may be because environmental characteristics favoured plastic, negative association between these behaviours. Negative association can be explained by higher resource holding potential by aggressive males (Ranta & Lindström 1993, Vainikka et al. 2011). Aggressive males may have thought our experimental boldness vial to be defendable resource and may have thus stayed there longer. Dynamic nature between aggression and boldness enforces the assumption that these behaviours are expressed independently with each other and may be associated through phenotypic plasticity because of correlative ecological pressure for these traits.

The causality between sociality and animal personalities is not clear; does achieved social status define personality or does personality define social status of an individual? Since boldness was consistent through ontogeny (I), it seems that individual level behavioural trajectories may be defined during early ontogeny and are not affected so strongly by social interactions later in life. However, the behavioural syndrome between two different, repeatable personality traits, aggression and boldness (Niemelä et al. unpublished data for repeatability of aggression), may be generated by social interactions during ontogeny, which imply plastic associations between these traits. In a previous study conducted in crickets derived from the wild I found that change in predation pressure potential can break up animal personalities (i.e. the consistency of behaviour) (Niemelä et al. 2012). However, social status of an individual or enforcement of social status did not affect the consistency of boldness or induced change in boldness (IV). It seems that the consistency of behaviour may broke apart and associations between behaviours may be maintained by some ecological gradients. This suggests that individuals are able to adjust individual behaviours or associations between distinct behaviours according to context (i.e. context dependence) thus being capable of producing behaviourally plastic responses (Niemelä et al. 2012, III). Since behaviours were not associated in all treatments (III), aggression and boldness are not likely to be associated through tight genetic mechanisms but rather correlative plasticity for behavioural traits according to environmental variation. The absence of covariation between aggression and boldness in solitary grown individuals and groups of four individuals suggests that there is some threshold group size above which the two measured behavioural traits are likely associated. Thus, in nature, population density may be important environmental factor generating associations between different behaviours through phenotypic plasticity (i.e. behavioural syndromes).

Despite the costs of phenotypic plasticity (DeWitt et al. 1998, Auld et al. 2010), traits can be affected by environmental gradients relatively easily (III, Stearns 1989, Gotthard & Nylin 1995, Edler 1995, Applebaum & Heifetz 1999, McCairns & Bernatchez 2012). This was also supported by our results. Encapsulation response, maturation time and body mass expressed different values in different population densities. The strength of cellular immunity has been found to be density dependent in several insect species (Reeson et al. 1998, Barnes & Siva-Jothy 2000, Wilson et al. 2001, 2002, 2003). The phenomenon of increasing investments in the immune system with increasing population density is known as adaptive prophylaxis (Wilson & Reeson 1998, Barnes & Siva-Jothy 2000). The strength of the encapsulation response is mainly determined by the number of haemocytes and phenoloxidase (PO), triggering melanin production (Lavine & Strand 2002, Wilson et al. 2002, Ling & Yu 2005, Carton et al. 2008, Strand 2008). Haemocytes are believed to be somewhat similar in all insects (Carton et al. 2008). There is evidence that the number of haemocytes and number of haemocytes with surface POs can change in response to stress, wounds or infection (Ling & Yu 2005, Markus et al. 2005, Strand 2008), which may be triggered by high population density. High population density potentially exposes individuals

to higher parasitism and thus allocation to higher encapsulation response in high population density seems beneficial. The allocation to encapsulation response may cause trade-offs with other fitness related traits like body mass, which was lowest in highest density treatment. Moreover, body mass, encapsulation response and maturation time was found to be genetically associated (II). Thus, change in one trait may cause correlative changes in other, genetically related traits. Since behaviour was not genetically associated with life-history (II), the changes in behaviour are not necessary expressed according to changes in life-history (III).

3.3 EMERGENCE AND COEXISTENCE OF ANIMAL PERSONALITIES (V)

In my conceptual framework, I search for environmental and individual level characteristics that define the existence of consistent behavioural differences, i.e. animal personalities. Explaining the emergence and coexistence of different behavioural types has been under wide interest among theoretical personality researchers and several different explanations have been introduced to solve this problem (Wolf et al. 2007a, Wolf et al. 2008, Dingemanse & Wolf 2010, Wolf & Weissing 2010). There is, however, potentially unrealistic, common trend in models explaining coexistence of different behavioural types: in nature different behavioral types do not necessary coexist in all populations or metapopulations. It may well be that in one environment there may be only genotypes from the other end of the personality continuum expressing consistency in different ways compared to other environments.

Cognition is favored in variable environments (Bergman & Feldman 1995, Heyes & Huber 2000, Godfrey-Smith 2002, Mery & Kawecki 2002, Kerr & Feldman 2003). However, when environmental variability is too high, cognition is selected against (Bergman & Feldman 1995, Kerr & Feldman 2003). In such environments adaptation to cues may no longer be beneficial since cognitive machinery needed for accurate predictions for the future phenomena is too expensive to be supported. Also, stable environments may select against cognition, since expensive cognitive machinery is an energetic cost in such environments. Since behavioural flexibility is most likely involved with cognitive abilities, non-flexible behaviours may be expressed in environments, where cognition is selected against and flexible behavioural responses expressed in environments, where cognition is selected for (Figure 2 and V). Therefore, consistent differences in behaviour are most likely favoured in environments selecting against cognition. As responsive behavioural types are more flexible, moderately variable environments should favour more behavioural plasticity than invariable or highly variable environments, and thus finding statistically consistent behaviours in those environments could be more difficult when compared to environments, which favour high individual consistency in behaviour. However, plasticity is not necessarily always beneficial, since in some cases, it would be more adaptive for an individual to express strictly consistent behaviour. In these cases, also responsive individuals may express limited flexibility and potential for plasticity may

therefore remain hidden. Our framework does not only explain mutual existence to different behavioural types, but also when only genotypes from the one end of the personality continuum should exist. Our framework may also explain the existence of consistent differences between several behaviours, i.e. behavioural syndromes (Garamszegi et al. 2012) in some environments. There are several studies where behavioural syndromes are not found in predictable way (Bell 2005, Bell & Sih 2007, Dingemanse et al. 2007). This may well be because environments supporting responsive behavioural types, individual behaviours can be optimized individually according to ecological context or situation so, that positive or negative correlation between behaviours is absent.

4. Conclusions and future prospects

Studies conducted for this thesis present ecological, phenotypic and genetic view to the associations between personality and life-historical traits. My study is the first one to reveal empirically, if the most important suggested life-history traits (i.e. immune defence and maturation time) to generate personalities are associated genetically with consistent behaviour. Life-history traits were found to be genetically linked. Despite the high heritabilities of these traits, the genetic associations have potential to limit the evolvability of individual traits. According my studies animal personality and life-history does not have common genetic background (II) since immunity was associated with personality only phenotypically, and thus, our results do not (fully) support the personality-POLS hypothesis. However, positive association between life-history and immunity support the predictions of within population POLS-hypothesis (I, II).

It seems that associative structure between traits may vary according to environmental selection pressures (Dingemanse et al. 2007, Réale et al. 2010). Moreover, the expression of traits is dependent on the confronted environment (Hoffman & Merilä 1999), as also suggested by our life-history results in different population densities (III). However, since individual behavioural traits were not affected by differences in social environment (III, IV), it seems that behavioural traits do either express almost immediate plastic responses or they are defined at the very early stage at individuals ontogeny (canalization). Since my results suggests that ecological gradients can affect the formation of behavioural syndromes (III) and break up animal personalitites (Niemelä et al. 2012), it seems that animal personalities, in general, do not limit the expression of behaviours in our study population.

The associations between life-historical and behavioural traits have been repeatedly suggested to explain the existence of stable between-individual differences in behaviour (Stamps 2007, Biro & Stamps 2008). However, my results do not give much support to those hypotheses (I, II). In future, more holistic approaches should be taken to study integratively ecologically relevant functions that have been traditionally studied independently. Moreover, these studies should be made between-population level to reveal environmental selection pressures which generate the stable associations between traits. Also, animal personalities should be studied across wide range of environmental gradients to reveal the realistic nature of consistency of behaviours and amount of behavioural plasticity.

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