

Martin Walter Seltmann

Of milquetoasts and daredevils

– Personalities in female eiders



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Martin Walter Seltmann

Environmental and Marine Biology
Department of Biosciences
Åbo Akademi University
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Supervisor

Markus Öst

ARONIA Coastal Zone Research Team

Åbo Akademi University & Novia University of Applied Sciences

Raseborgsvägen 9

10600 Ekenäs, Finland

Co-supervisor

Kim Jaatinen

ARONIA Coastal Zone Research Team

Åbo Akademi University & Novia University of Applied Sciences

Raseborgsvägen 9

10600 Ekenäs, Finland

Reviewer

Hannu Pöysä

Finnish Game and Fisheries Research Institute

Yliopistokatu 6

80100 Joensuu, Finland

Reviewer

Kees van Oers

Department of Animal Ecology

Netherlands Institute of Ecology

Droevendaalsesteeg 10

6708 PB Wageningen, The Netherlands

Opponent

Niels J. Dingemanse

Department of Biology II

Ludwig Maximilians University

Großhaderner Str. 2

82152 Planegg-Martinsried, Germany

Author's address

ARONIA Coastal Zone Research Team

Åbo Akademi University & Novia University of Applied Sciences

Raseborgsvägen 9

10600 Ekenäs, Finland

martin.w.seltmann@gmail.com

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“...gackgackgackgackgackgack...”

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Abstract

Traditionally biologists have often considered individual differences in behaviour or physiology as a nuisance when investigating a population of individuals. These differences have mostly been dismissed as measurement errors or as non-adaptive variation around an adaptive population mean. Recent research, however, challenges this view. While long acknowledged in human personality studies, the importance of individual variation has recently entered into ecological and evolutionary studies in the form of animal personality. The concept of animal personality focuses on consistent differences within and between individuals in behavioural and physiological traits across time and contexts and its ecological and evolutionary consequences. Nevertheless, a satisfactory explanation for the existence of personality is still lacking. Although there is a growing number of explanatory theoretical models, there is still a lack of empirical studies on wild populations showing how traditional life-history trade-offs can explain the maintenance of variation in personality traits.

In this thesis, I first investigate the validity of variation in allostatic load or baseline corticosterone (CORT) concentrations as a measure for differences in individual quality. The association between CORT and quality has recently been summarised under the “CORT-fitness hypothesis”, which states that a general negative relationship between baseline CORT and fitness exists. I then continue to apply the concept of animal personality to depict how the life-history trade-off between survival and fecundity is mediated in incubating female eiders (*Somateria mollissima*), thereby maintaining variation in behaviour and physiology. To this end, I investigated breeding female eiders from a wild population that breeds in the archipelago around Tvärminne Zoological Station, SW Finland. The field data used was collected from 2008 to 2012. The overall aim of the thesis was to show how differences in personality and stress responsiveness are linked to a life-history context. In the four chapters I examine how the life-history trade-off between survival and fecundity could be resolved depending on consistent individual differences in escape behaviour, stress physiology, individual quality and nest-site selection.

First, I corroborated the validity of the “CORT-fitness hypothesis”, by showing that reproductive success is generally negatively correlated with serum and faecal baseline CORT levels. The association between individual quality and baseline CORT is, however, context dependent. Poor body condition was associated with elevated serum baseline CORT only in older breeders, while a larger reproductive investment (clutch mass) was associated with elevated serum baseline CORT among females breeding late in the season. Interestingly, good body condition was associated with elevated faecal baseline CORT levels in late breeders. High faecal baseline CORT levels were positively related to high baseline body temperature, and breeders in poor condition showed an elevated baseline body temperature, but only on open islands. The relationship between

stress physiology and individual quality is modulated by breeding experience and breeding phenology. Consequently, the context dependency highlights that this relationship has to be interpreted cautiously.

Additionally, I verified if stress responsiveness is related to risk-taking behaviour. Females who took fewer risks (longer flight initiation distance) showed a stronger stress response (measured as an increase in CORT concentration after capture and handling of the bird). However, this association was modulated by breeding experience and body condition, with young breeders and those in poor body condition showing the strongest relationship between risk-taking and stress responsiveness. Shy females (longer flight initiation distance) also incubated their clutch for a shorter time. Additionally, I demonstrated that stress responsiveness and predation risk interact with maternal investment and reproductive success. Under high risk of predation, females that incubated a larger clutch showed a stronger stress response. Surprisingly, these females also exhibited higher reproductive success than females with a weaker stress response. Again, these context dependent results suggest that the relationship between stress responsiveness and risk-taking behaviour should not be studied in isolation from individual quality and that stress responsiveness may show adaptive plasticity when individuals are exposed to different predation regimes.

Finally, female risk-taking behaviour and stress coping styles were also related to nest-site choice. Less stress responsive females more frequently occupied nests with greater coverage that were farther away from the shoreline. Females nesting in nests with medium cover and farther from the shoreline had higher reproductive success. These results suggest that different personality types are distributed non-randomly in space.

In this thesis I was able to demonstrate that personalities and stress coping strategies are persistent individual characteristics, which express measurable effects on fitness. This suggests that those traits are exposed to natural selection and thereby can evolve. Furthermore, individual variation in personality and stress coping strategy is linked to the alternative ways in which animals resolve essential life-history trade-offs.

Sammanfattning (abstract in Swedish)

Biologer har traditionellt ansett individuell variation vara ett gissel då man vill undersöka en population av individer. Dessa skillnader har avfärdats antingen som mätfel eller som maladaptiv variation som omger populationens adaptiva medeltal. Nyare forskningsrön har utmanat denna uppfattning. Inom den mänskliga personlighetsforskningen har betydelsen av individuell variation erkänts sedan länge, men det är först nyligen som dess betydelse har uppmärksamats inom ekologiska och evolutionära studier i form av begreppet djurpersonlighet. Begreppet syftar på konsekventa skillnader i individers beteendemässiga och fysiologiska egenskaper som är stabila över tid och sammanhang och som kan ha viktiga ekologiska och evolutionära konsekvenser. Ännu saknas dock en tillfredsställande förklaring till uppkomsten av personlighet. Trots att det finns allt flera teoretiska förklaringsmodeller råder det fortfarande en brist på empiriska studier i naturpopulationer som undersökt ifall resursallokeringskonflikter mellan livshistoriefunktioner kunde förklara uppkomsten av personlighetsvariation.

I denna avhandling undersöker jag först ifall den allostatistiska belastningen, d.v.s. variation i grundnivån av stresshormonet kortikosteron, utgör ett mått på individens kvalitet. Den s.k. ”kortikosteron-fitness hypotesen” gör gällande att sambandet mellan grundnivån av kortikosteron och fitness förväntas vara negativt. I avhandlingens senare del tillämpar jag begreppet djurpersonlighet för att förklara hur ruvande ejderhonor (ådor) (*Somateria mollissima*) löser resursallokeringskonflikten mellan överlevnad och fekunditet, och hur ådornas individuella avvägningar avspeglas i variation i beteende och fysiologi. För detta ändamål undersökte jag häckande ådor från en population i närheten av Tvärminne zoologiska station i sydvästra Finland. Fältdatat insamlades mellan åren 2008 och 2012. Avhandlingens huvudsakliga målsättning var att visa hur individuella skillnader i personlighet och stressrespons är kopplade till livshistoriestrategier. I avhandlingens fyra delarbeten undersöker jag hur resursallokeringskonflikten mellan överlevnad och fekunditet kan lösas utgående från konsekventa individuella skillnader i flyktbeteende, stressfysiologi, individuell kvalitet och boplatsval.

I mitt första arbete kunde jag bekräfta ”kortikosteron-fitness hypotesen”, eftersom individer med höga grundnivåer av kortikosteron i serum och exkrementer i allmänhet hade lägre häckningsframgång. Däremot visade det sig att sambandet mellan individuell kvalitet och grundnivån av kortikosteron är starkt beroende av sammanhanget. Låg kroppskondition var förknippat med försämrad häckningsframgång bara bland äldre häckare, medan en större satsning på förökningen (kullvikt) var förknippad med förhöjda kortikosteronhalter i serum bland ådor som häckade sent på säsongen. Bland dessa sena häckare uppvisade ådor i bra kroppskondition förhöjda kortikosteronhalter i exkrementerna. Höga grundnivåer av kortikosteron i exkrementerna var också associerat

med en förhöjd kroppstemperatur under ruvningen, och ådor i dålig kroppskondition uppvisade en högre kroppstemperatur, men denna effekt kunde bara upptäckas på öppna häckningsholmar. Sambandet mellan stressfysiologi och individuell kvalitet beror alltså på häckningserfarenhet och häckningsfenologi och man bör därför vara försiktig med hur man tolkar sambandet.

Jag kunde också konstatera att stressresponsen är förknippad med individens risktagningsbenägenhet i närvaro av predatorer. Ådor som tog mindre risker (längre flyktavstånd från boet) uppvisade en högre stressrespons, mätt som ökningen av kortikosteronhalt i serum efter att vi fångat och behandlat fågeln. Detta samband var dock beroende av ådans häckningserfarenhet och kroppskondition, så att unga häckare och häckare i dålig kondition uppvisade det starkaste sambandet mellan risktagning och stressrespons. Skygga ådor (längre flyktavstånd) hade också en kortare ruvningstid. Jag visade också att graden av stressrespons och predationsrisken växelverkade med moderns förökningssatsning och förökningsframgång. Under år då predationsrisken var hög, uppvisade ådor med en större kull en högre stressrespons. Övåntat nog hade dessa ådor också bättre häckningsframgång under dessa farliga förhållanden. Mina resultat visar igen att sambandet mellan stressrespons och risktagningsbeteende formas av förhållandena och att sambandet därför inte bör studeras i isolation från individuell kvalitet, och att stressresponsen kan uppvisa adaptiv plasticitet då predationsrisken varierar.

Ådans risktagningsbenägenhet och stresshanteringsstrategi hade också ett samband med boplatstvalet. Ådor med lägre stressrespons häckade i bon som var mer skyddade för insyn av vegetation och i bon som befann sig lägre bort från strandlinjen. Kläckningsframgången var störst i bon som hade en intermediär täckningsgrad och kläckningsframgången var desto större ju längre bort från stranden boet befann sig. Dessa resultat antyder att den spatiella fördelningen av olika personlighetstyper inte är slumpmässig.

I denna avhandling kunde jag påvisa att personligheter och stresshanteringsstrategier är stabila individuella egenskaper som har mätbara effekter på fitness. Det här antyder i sin tur att dessa egenskaper är föremål för naturligt urval och kan därför formas av evolutionen. Jag kunde också visa att individuell variation i personligheter och stresshanteringsstrategier är förknippad med de alternativa sätt på vilka djur kan lösa grundläggande livshistorieallokeringskonflikter.

Contents

List of original papers

1. Introduction	11
1.1 What exactly is animal personality?	12
1.2 Ultimate explanations for the existence of consistent individual variation	12
1.3 Proximate mechanisms of consistent individual variation	14
2. Aim of the thesis	17
3. Materials and methods	19
3.1 Study species	19
3.2 Study area	19
3.3 Field methods	19
3.4 Laboratory methods	19
3.5 Data analyses	20
4. Main results and discussion	23
4.1 Female stress coping profiles and nest characteristics are repeatable	23
4.2 Baseline CORT as a context-dependent correlate of individual quality and fitness	27
4.3 Link between stress responsiveness and boldness is dependent on individual quality	29
4.4 Links between stress responsiveness, maternal investment and fitness are shaped by predation risk	32
4.5 Nest-site characteristics are associated with coping style and have fitness consequences	34
5. General conclusions and future directions	36
5.1 Unresolved issues	36
5.2 Future directions	37
5.3 Concluding remarks	39
6. Acknowledgements	41
7. Literature cited	43
Original papers	
Chapter I	57
Chapter II	67
Chapter III	77
Chapter IV	91

List of original papers

This thesis is based on the following papers, which will be referred to in the text by their Roman numerals:

- I** Jaatinen, K., Seltmann, M.W., Hollmén, T., Atkinson, S., Mashburn, K. & Öst, M. 2013. Context dependency of baseline glucocorticoids as indicators of individual quality in a capital breeder. *General and Comparative Endocrinology*, 191, 231–238.
- II** Seltmann, M.W., Öst, M., Jaatinen, K., Atkinson, S., Mashburn, K. & Hollmén, T. 2012. Stress responsiveness, age and body condition interactively affect flight initiation distance in breeding female eiders. *Animal Behaviour*, 84, 889–896.
- III** Jaatinen, K., Seltmann, M.W. & Öst, M. Context-dependent stress responses and their fitness consequences in a landscape of fear. Manuscript.
- IV** Seltmann, M.W., Jaatinen, K., Steele, B.B. & Öst, M. 2014. Boldness and stress responsiveness as drivers of nest-site selection in a ground-nesting bird. *Ethology*, 119, 1–13.

The original papers have been reprinted with the kind permission of Elsevier (paper **I** and **II**) and John Wiley and Sons (paper **IV**).

1. Introduction

Speaking about wild animals having personalities frequently creates confusion and misgivings among the general public, sometimes even among biologists. On the other hand, pet owners or people that work intensively with domesticated animals will happily tell you that those animals do show distinct behavioural patterns. However, it has been scientifically demonstrated that wild animals also possess distinct behavioural patterns or personalities. Interestingly, in bird studies, the term “personality” was first used as early as 1922 (Talbot 1922). When talking about animal personality nowadays, biologists refer to consistent individual variation in behavioural and physiological traits that is consistent over time and/or over contexts (Sih et al. 2004a, b, Réale et al. 2007, Coppens et al. 2010). Behavioural ecologists were curious about adaptive individual differences in behaviour and physiology in the second half of the last century (e.g., Huntingford 1976, Clark & Ehlinger 1987, Wilson et al. 1994). The criticism of falling for anthropomorphism, meaning the projection of human characteristics on animal traits, was however prevalent in those days. Hence only few behavioural biologists took an individual based approach for studying behaviour or physiology in the context of ecology and evolution. Variation in behaviour and physiology was regarded as non-adaptive “noise” around an adaptive population mean (Wilson 1998, Dall et al. 2004). Before the 1960’s it was

good practice to focus on differences between genera and higher level taxa. Since then there has been a slow shift in approaching adaptive variation in behaviour, with first comparing differences between species and then locally adapted populations of the same species. Only recently has there been a call for taking this development one step further by looking at adaptive individual differences of traits within single populations (Wilson 1998, Dall et al. 2004). Many behavioural ecologists heeded that call, which has resulted over the past decade in a growing body of theoretical and empirical research that tries to elucidate the existence of animal personalities. Personalities are found throughout a wide variety of taxa in the animal kingdom (Carere & Maestripieri 2013). Traits that are incorporated in personalities are e.g. exploration, aggressiveness, boldness, general activity, nesting behaviour, avoidance, sociability and stress-coping.

Animal personality research is probably the fastest growing field in behavioural ecology at the moment (Réale et al. 2010a). Evidence for consistent individual behaviour is found in new species at an increasing rate, and new theoretical models aimed at explaining the origin and the consequences of animal personality continue to emerge. Animal personalities have already been shown to have several important ecological and evolutionary consequences (Wolf & Weissing 2012) and also implications for animal welfare (Huntingford et al. 2013) and conservation (Smith & Blumstein 2013). Considering the

above, animal personality truly is a very exciting and auspicious field in current behavioural and physiological research. However, besides the efforts of some authors (Réale et al. 2007, Réale et al. 2010a, b, Carter et al. 2013) a unifying theory of animal personality has not yet emerged. Moreover, the acclaimed recent burgeoning theoretical development in the field is confronted with a lack of empirical studies on populations in the wild. Studying personality and its links with stress physiology in the wild and linking personality with traditional life-history and habitat selection are main issues in the field that are addressed in this thesis.

1.1 What exactly is animal personality?

The concept of animal personality encompasses the existence of consistent individual differences in behaviour and physiology. These differences are stable over time and across contexts (Réale et al. 2007). Throughout this thesis the broad-sense definition of personality is used. This definition does not restrict the kind of investigated behaviour, but rather looks at correlations of one behavioural trait between different environmental or temporal contexts or at correlations between two different behavioural traits (Réale et al. 2010a). Correlations between two or more behavioural or physiological traits are also called behavioural syndromes (Sih et al. 2004a, b) or coping styles (Koolhaas et al. 1999), respectively. A considerable body of studies has

shown that personalities and behavioural syndromes can evolve and be maintained by natural (Dingemanse et al. 2004, Wolf et al. 2007) and sexual (Réale et al. 2009, Schuett et al. 2010) selection. Behavioural ecologists have worked out several important axes of animal personality along which individuals can be placed: shyness – boldness, aggressiveness – cautiousness, fast and superficial explorers – slow and thorough explorers, proactive – reactive stress coping. Bold and fast explorers are considered to be more successful in constant environments with developing routine-like behaviours and shy and slow explorers are supposed to be more successful in changing environments, showing more flexible behaviour (Cockrem 2005). It is important to note that the concept of animal personality does not require that traits are rigorously fixed. Personality traits can vary according to an individual's state or its environment (e.g., Luttbegg & Sih 2010). However, individual rank orders are often maintained (Sih 2004a, b, Bell 2007). Furthermore, animal personality research has highlighted that variation is not only the raw material for natural selection to act on, but variation can also be the outcome of natural selection (Wilson et al. 1994).

1.2 Ultimate explanations for the existence of consistent individual variation

With the existence of personality traits several important questions arise: Why do we find consistent vari-

ation in animal behaviour in nature? Is individual variability maintained by natural selection and how does evolution maintain this variation, as one would perhaps expect natural selection to eliminate variation within populations? And why do we find consistent correlations between behavioural or physiological traits that seemingly reduce an animal's plasticity and therefore an optimal response to every situation?

During the last decade, many theoretical models have been proposed explaining how evolution can maintain variation in populations, thereby allowing different behavioural types to coexist. One explanation for the maintenance of behavioural variation within population is differences in individual state when behaviour is state dependent. At any given moment, two individuals of a population will differ in their state, e.g. in their energy reserves or regarding the environmental conditions they are facing. If behaviour is state-dependent and current state affects the costs and benefits of the behaviour, differences in original state can lead to adaptive differences in behaviour (Dall et al. 2004).

Even though individuals would not differ in their original state, negative frequency dependent selection can give rise to different behavioural types. For example, in foraging theory, individuals can adopt different behavioural strategies for acquiring food resources, with individuals being either "producers" or "scroungers" (Giraldeau & Beauchamp 1999). Furthermore, negative frequency depen-

dent selection can produce and maintain variation in behaviour where a mixture of responsive (e.g. eavesdropping) and unresponsive individuals are favoured (Dall et al. 2004, Wolf et al. 2008).

Environmental conditions vary in space and time. This circumstance has the potential to favour the coexistence of different behavioural types. Spatial variation in the environment could mean that a population distributes over more and less risky habitats. Depending on which habitat an individual is occupying, and considering that behavioural plasticity is costly, spatial variation can maintain the coexistence of more and less risk-taking individuals (Wilson 1998, Wolf & Weissing 2010). Temporally fluctuating environments can also lead to the coexistence of different behavioural types within a population. In great tits (*Parus major*), for example, selection favours different personality types in years that provided high or low food quality (Dingemanse et al. 2004). Hence, heterogeneous forms of selection can maintain variation in behaviour within populations (Dingemanse & Reale 2013).

A fourth potential adaptive explanation for personality traits is provided by social niche specialisation (Bergmüller & Taborsky 2010). This framework assumes that individuals choose different strategies to avoid social conflict, thereby increasing their fitness.

A fifth possibility for personality traits to arise is through coevolution with life history strategies, as previously proposed by a theoretical model

by Wolf and colleagues (2007). The model shows that the trade-off between current and future reproduction can lead to different consistent individual risk-taking strategies within a population, as predicted by life-history theory (Clark 1994). In two recent reviews (Stamps 2007, Biro & Stamps 2008) it has been shown that consistent individual differences in personality traits could be explained by individual differences in how animals resolve the allocation trade-off between growth and fecundity. Thus far, only few empirical studies performed on red squirrels *Tamiasciurus hudsonicus* (Boon et al. 2008) and on bighorn sheep *Ovis canadensis* (Réale et al. 2009) have highlighted the association between personality traits and life-history strategies. Female red squirrels that were more active showed a lower own overwinter survival, but an increased probability of offspring survival. Aggressive bighorn rams exhibited earlier reproduction and a shorter lifespan than docile rams.

The maintenance of consistent behaviour across time is more difficult to explain than the occurrence of variation in behavioural types. From a proximate point of view, the underlying architecture of behaviour provides adaptive explanations for consistent behavioural variation. This will be discussed in more detail in the next section. From an ultimate perspective, it can be costly for an individual to change the underlying mechanisms that produce behavioural consistency in time. One example is the hypothalamic-pituitary-

adrenal axis (HPA axis). It develops early in an animal's life and includes a series of complex connections between neurotransmitters, hormones, receptors and feedback mechanisms (e.g. von Holst 1998). The HPA axis is associated with numerous behavioural actions. Thus, it is conceivable that a fundamental change in that complex system would be very costly and hence an overall plastic response is not possible (Dall 2004). The evolution of a more flexible mechanism would require several steps, and intermediate forms of a new HPA axis might be rather unthrifty. The existence of an adaptive valley in the fitness landscape might prevent the evolutionary steps necessary to develop a more flexible architecture (Wolf et al. 2013). Furthermore, positive feedback mechanisms, like experience and skill improvement, can favour consistency in behaviour (Wolf et al. 2008). Related to this, winner-loser effects in competing individuals of a population can enhance consistency of behaviour (Dugatkin 1997).

1.3 Proximate mechanisms of consistent individual variation

The processes presented above may still not be strong enough to allow consistent personality traits to evolve without incorporating physiology, as shown by a recent theoretical model by Wolf and McNamara (2012). In their model, negative frequency dependent selection gave rise to variation in behaviour (see previous section). However, negative frequency dependent selection alone could

not generate individual consistency and correlations between traits. Only when physiology was included did the model generate extreme and consistent behavioural tendencies (Wolf & McNamara 2012). Hence, to fully understand the evolution and maintenance of personality traits, it is just as essential to explore the proximate mechanisms responsible for individual differences in behaviour so, as to understand the ultimate reasons why personality traits exist (cf. Tinbergen 1963).

Genes, physiology and neuroendocrine mechanisms form the underlying architecture of behaviour and reflect correlates of personality traits (Sih et al. 2004b). Genes can exert pleiotropic effects, meaning that one gene can influence the expression of two or more behavioural traits. Hence, genetic correlations provide a good explanation for consistency and correlations between behavioural traits. Furthermore, several studies illustrated that personality traits are heritable (van Oers et al. 2004, Quinn et al. 2009), a prerequisite for behavioural types to evolve. For example, through a candidate gene approach, studies have been able to link polymorphisms in the dopamine receptor D4 gene with exploratory behaviour (Fidler et al. 2007) and associate the gene for a serotonin transporter with aggressive and risk-taking behaviour (Champoux et al. 2002).

Like genes, hormones can also cause pleiotropic effects on different behaviours, thereby explaining why behaviours can correlate. Although pleiotropic effects of hormones might

be weaker than genetic correlations, they can still be very costly to uncouple (see previous section). Baseline concentrations of glucocorticoids (GCs), also called “stress hormones”, play an important role in daily energy balance by regulating resource acquisition (Sapolsky et al. 2000). Considering their major importance in controlling energetic demands, GCs are thought to have an orchestrating key role in mediating important life-history trade-offs, particularly between survival and reproduction (Zera & Harshman 2001, Ricklefs & Wikelski 2002). The link between neuroendocrine mechanisms and personality is especially well investigated in an individual’s response to stressful situations. Thus, stress-induced concentrations of GCs and HPA axis reactivity are of central interest. Individual consistencies in physiological and behavioural characteristics, that can be correlated, have been defined as coping styles (Koolhaas et al. 1999). Two distinct coping styles have been proposed which are closely related to personality types. Proactive stress coping is associated with highly aggressive behaviour, an active flight/fight response and a weak response of the HPA axis when in a threatening situation. Reactive stress coping includes low aggressive behaviour, freeze response and a weak response of the HPA axis when in a threatening situation (Koolhaas et al. 1999). It has been suggested that individuals with proactive coping styles show lower behavioural flexibility and fast reactions to environmental change, but the response can be inaccurate (Cop-

pens et al. 2010). Individuals that exert a proactive coping style rely on internal organizations of behaviour (Coppens et al. 2010). Reactive coping styles are associated with higher behavioural flexibility and slow reactions to environmental change. However, those changes are directed by environmental stimuli, showing that individuals with a reactive coping style can adapt better to environmental change (Coppens et al. 2010). The ability to cope with sudden or new environmental disturbances has considerable effects on life-history trade-off decisions, e.g. the reallocation of energy between immediate survival and long-term reproductive success (reviewed in Angelier & Wingfield 2013). Similar patterns in coping styles have been found in two selected lines of great tits (fast and slow exploration; Groothuis & Carere 2005) and in genetically selected lines of laboratory mice (*Mus domesticus*) (short and long attack latencies; Benus et al. 1991). When exposed to stress, fast exploring great tits as well as mice with short attack latency showed a weaker HPA axis response (Veene- ma et al. 2004, Carere et al. 2003). A recent study on great tits from the same selection lines (Groothuis & Carere 2005) has provided evidence for a genetic correlation between personality traits and stress physiology (Baugh et al. 2012). Individuals that were phenotypically selected for being fast-bold explorers exhibited

a weaker stress response than slow-shy explorers (Baugh et al. 2012) and slow explorers showed a faster increase in CORT and higher peak levels of CORT (Baugh et al. 2013). Interestingly, zebra finches (*Taenopygia guttata*) that were artificially selected for weak and strong stress responses also showed correlated behavioural patterns in exploration and risk-taking (Martins et al. 2007). However, zebra finches with higher CORT levels took more risks and were more explorative, an observation that is contradictory to the coping style literature (Koolhaas et al. 1999). Although contradictory, these results are nevertheless providing evidence that HPA axis reactivity and personality traits are closely linked.

Furthermore, differences in the structure of the hippocampus of an individual can be related to its coping style (Sluyter et al. 1994).

Some studies also suggest that differences in metabolic rate can promote differences in behaviour (Biro & Stamps 2010) and that incorporating metabolic variability can help in understanding why individuals behave consistently over time and across contexts (Careau et al. 2008). A promising approach for future personality research is the recently proposed pace-of-life syndrome (POLS; Réale et al. 2010b). The POLS integrates life-history, behaviour and physiology into a holistic framework, aiming to explain animal personalities.

2. Aim of the thesis

The overall aim of this thesis is to depict how the life-history trade-off between survival and fecundity is linked to consistent individual differences in incubating female eiders. Throughout the four chapters of this thesis, I investigate how this essential life-history trade-off could be resolved through individual differences in escape behaviour, stress physiology, individual quality and nest-site selection (Fig. 1). Of special interest is flight initiation distance (hereafter, FID) measured in a risky situation (a measure of boldness, *sensu* Réale et al. 2007). Moreover, I focused on physiological correlates of animal personalities, namely serum and faecal baseline CORT concentrations, serum stress-induced CORT concentrations and baseline and stress-induced body temperature. In a life-history context, boldness and stress responsiveness reflect the trade-off between investing in survival versus reproduction.

Repeatability is defined as the proportion of the total variance accounted for by differences among groups (Sokal & Rohlf 1995). It is essential for testing the reliability of multiple measurements through time or over contexts (Carter et al. 2013). Furthermore, for behavioural and physiological traits to be qualified as personality traits they have to be repeatable (Sih et al. 2004a, Reale et al. 2007). Repeatability of CORT is, furthermore, one of the underlying assumptions of the CORT-fitness hypothesis (Bonier et al. 2009a). In chapters **I**, **II** and **IV**

I estimated the repeatability of FID, physiological traits (CORT and body temperature) and nest-site characteristics (nest cover and nest distance to closest shoreline).

Chapter **I** focuses on elucidating the relationship between baseline corticosterone levels and fitness in the light of the CORT-fitness hypothesis. This hypothesis states that an elevated baseline concentration of CORT signals an impaired ability of an individual to cope with the prevailing environment, which can lead to low fitness. The study examines links between individual quality and baseline CORT levels in blood serum and faeces, explores whether the relationship between baseline body temperature and individual quality is modulated by nest-site habitat and determines the link between CORT and nest success, a correlate of fitness.

Chapter **II** explores how stress responsiveness is connected to boldness and individual quality. It also investigates how maternal stress coping is linked to incubation duration, a fitness component.

Chapter **III** continues in examining the adaptive potential of stress responsiveness by asking how predation risk modifies the relationship between stress responses and parental investment, and that between stress responsiveness and fitness (nest success).

Chapter **IV** investigates the association between stress coping styles and nest-site selection. Furthermore, I elucidate whether variation in boldness, stress responsiveness or

nest-site characteristics can explain component.
variation in nest success, a fitness

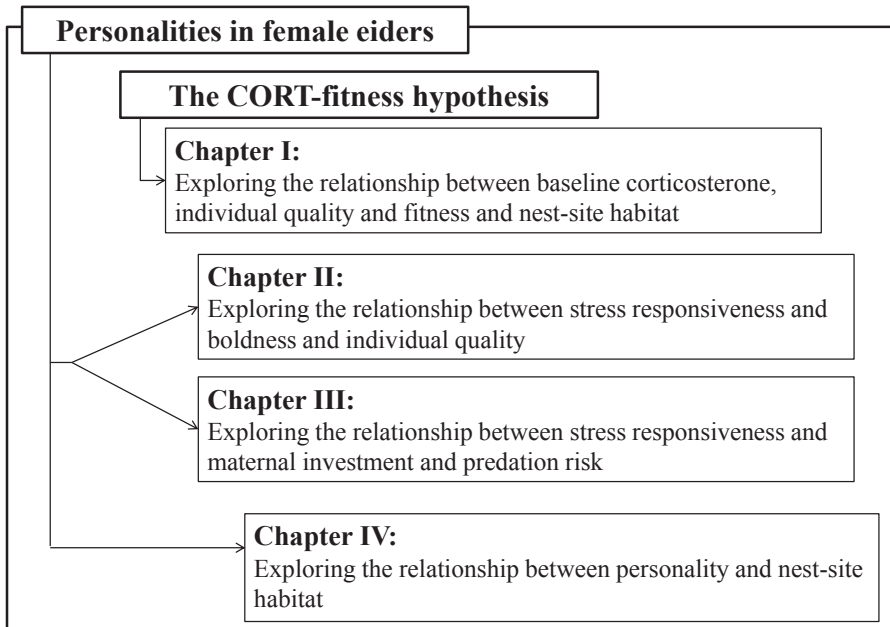


Figure 1. A conceptual outline of the thesis, visualizing the main functions of the four chapters.



Figure 2. Female eider, incubating in a nest with a decent roof (© Heikki Eriksson).

3. Materials and methods

3.1 Study species

All data for this thesis were collected on female eider ducks (*Somateria mollissima*) (Fig. 2). The eider is a long-lived ground-nesting seabird that breeds in the northern parts of Europe, North America and eastern Siberia. Females are the sole incubators and show high nest attentiveness (Bolduc & Guillemette 2003). They are capital precocial breeders, which rely almost entirely on bodily reserves during incubation, losing up to 40% of their pre-laying body weight (e.g., Parker & Holm, 1990). Females incubate their clutch for about 26 days, after which the hatched ducklings leave the nest within 24 hours. Both eggs (Öst et al. 2008a) and incubating females (Jaatinen et al. 2011, Ekroos et al. 2012) are subject to significant predation pressure. Eiders in this study population arrive at their breeding grounds in March and April and start incubating in the end of April – end of May.

3.2 Study area

All studies in this thesis were conducted on a well-studied eider population in the archipelago surrounding Tvärminne Zoological Station (59°50'N, 23°15'E), on the Baltic Sea in southwestern Finland (Fig. 3). Female eiders breed in two contrasting habitats: on small open granite islands, which are sparsely covered with patches of grasses, herbs or occasionally junipers (*Juniperus communis*) or on larger forested islands,

covered by closed stands of pine (*Pinus sylvestris*) and spruce (*Picea abies*) with an understory of juniper and other shrubs. Island area ranged from 0.05 ha to 10.49 ha (Lindström 2003). White-tailed sea eagle (*Haliaeetus albicilla*), eagle owl (*Bubo bubo*), American mink (*Neovison vison*) and raccoon dog (*Nyctereutes procyonoides*) are the main predators of incubating females, and hooded crows (*Corvus corone cornix*) and gulls (*Larus* spp.) the main egg predators. All study islands are protected by a prohibition on landing.

3.3 Field methods

We captured incubating females on their nests using hand nets. Trapping took place predominantly during the end of the incubation period in May or early June to minimize nest desertion. Trapped females were ringed with a standard metal ring, weighed on a spring scale and the length of the radius-ulna was recorded. An extensive overview on collected variables and techniques are to be found in Tables 1 and 2.

3.4 Laboratory methods

The identification of CORT concentrations of faecal and serum samples via radioimmunoassay (RIA) was carried out at the University of Fairbanks, School of Fisheries and Ocean Sciences, Juneau, AK, USA. A validation of the serum corticosterone RIA kit (ImmuChem™ Double Antibody, Corticosterone, 125I RIA Kit, MP Biomedicals, Orangeburg, NY) for eiders is provided by Nils-

son (2004). A double antibody RIA kit (ImmuChem™ Double Antibody, Corticosterone, 125I RIA Kit, MP Biomedicals, Orangeburg, NY) for corticosterone was validated for use with extracted faeces of European eiders (I).

3.5 Data analyses

All statistical analyses and graphs for the chapters of this thesis were performed with the statistical software R

that is freely available on the internet (R Core Team 2013). In this thesis generalized and linear mixed models were used to analyse the data. Repeatabilities and corresponding standard errors, confidence intervals and p-values (I, II, IV) were obtained by using the functions `rpt.remlLMM`, `rpt.binomGLMM.multi` and `rpt.remlLMM.adj` from the R software package `rptR` (Nakagawa & Schielzeth 2010).

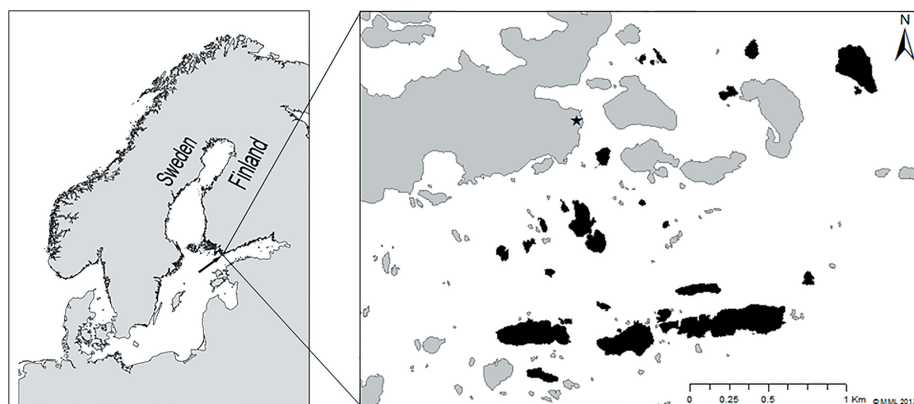


Figure 3. Map showing the archipelago around Tvärminne Zoological Station (star symbol on right map) at the entrance of the Gulf of Finland. Islands where females were trapped are marked in black, other islands are in grey.

Table 1. Summary of all variables collected and analysed in this thesis, with variable name, its function, its definition and the corresponding chapters of the thesis.

Variable	Function	Definition / method	Chapter
<i>Behaviour / female state</i>			
Flight initiation distance	Boldness	Distance between approaching researcher and female flushing off the nest	II, IV
Incubation onset	Competition for nest sites	Estimated via egg flotation	IV
Hatch date	Incubation timing	Estimated via egg flotation	I, II
Maternal experience	Age / experience	No. of years since bird was first ringed	I, II, IV
Body condition	Energy reserves	Log (weight at hatching) ~ log (radius-ulna)	I, II, IV
Clutch mass	Maternal investment	Total clutch mass corrected for incubation stage	I, III
<i>Physiology</i>			
Baseline corticosterone in serum	Health proxy	Blood sample within 3 min after trapping	I
Baseline corticosterone in faeces	Health proxy	Faeces sample from nest and/or female	I
Baseline body temperature	Homeostasis	Rectal temperature	I
Stress-induced corticosterone in serum	Stress responsiveness	Blood sample after handling	II, III, IV
Stress-induced body temperature	Stress responsiveness	Rectal temperature	IV
<i>Environment</i>			
Nest cover	Degree of concealment	Skywards photograph made with fisheye lens	III, IV
Nest distance to nearest shoreline	Distance to safety in water	GPS and ArcGIS	IV
Island-specific predation risk	Degree of risk	No. of killed females per censused nest per island	III
<i>Fitness</i>			
Incubation duration	Proxy for duckling condition	Time difference between real hatch date and estimated date of incubation onset	II
Probability of clutch hatching	Reproductive success	Successful if at least 1 duckling hatched	I
Viable proportion of the clutch	Reproductive success	Proportion of live ducklings to dead / unhatched ducklings	III, IV

Table 2. Summary of the control covariates included in different analyses, with the control covariate, its function, a definition and the corresponding chapters of the thesis.

Variable	Function	Chapter
<i>Control covariates</i>	<i>Potential effects on</i>	
Time of day	Daily rhythms in body temperature and corticosterone	II, IV
Year	Breeding phenology	II
Time to first blood sample	Baseline serum corticosterone / body temperature	I, III, IV
Time to second blood sample	Stress-induced serum corticosterone / body temperature	II, III, IV
Time after first trapping	Baseline serum corticosterone / body temperature	I
Island identity	Nest distance to nearest shoreline	IV
Incubation stage	Clutch mass	I, II, III, IV
Clutch size	Incubation duration	II

4. Main results and discussion

4.1 Female stress coping profiles and nest characteristics are repeatable

Significant repeatability suggests that a trait is to some extent genetically determined. Furthermore, repeatability estimates set an upper limit for heritability. In a recent review, Bell and colleagues (2009) demonstrated that behaviour in general is often repeatable. From the studies analysed for their review, they estimated an average value for repeatability of 0.37. This value actually fits well with the 3-year estimate of FID, being 0.37 (II), too. To date, no review on the repeatability of physiological traits has been published, although there is accumulating evidence for those traits being heritable and repeatable (e.g. Evans et al. 2006, Romero & Reed 2008). Female escape behaviour (FID), measures of baseline serum and faecal CORT (CORT0 and FC), baseline body temperature, measures of stress-induced CORT and body temperature were significantly repeatable over time (Tab. 3). Hence, these traits represent coherent and individually consistent coping styles. Furthermore, nest-site characteristics were significantly repeatable as well, but with estimates showing a low repeatability.

Estimates of repeatability ranged between slightly (0.13) and highly (0.80) repeatable (see Martin & Bateson (1986) for an interpretation of the strength of repeatability estimates).

In particular, the repeatability of FIDs (II) ranged from low (between three consecutive seasons) over moderate (between two consecutive seasons) to high (within each season). Variation in the repeatability of FID could be due to females changing their behaviour over time or due to different sample sizes within and between seasons. Within seasons, females do not change their behaviour strongly and multiple measurements of several females are available, resulting in higher and more reliable repeatability estimates. The lower repeatability estimate over several seasons could be caused by the inevitable fact that we cannot trap every female every year, leading to a much lower sample size for repeatability estimates over seasons. More importantly, however, annual variation in maternal investment could be responsible for the lower repeatability estimate over seasons, as clutch mass or clutch size can either positively (Osiejuk & Kuczyński 2007) or negatively (Albrecht & Klvaňa 2004) affect FID in birds.

Thus, these estimates might be less reliable or accurate than within-season estimates. Repeatability of most of our measured physiological traits is quite similar, and sample sizes are appropriate. Only FC exhibited lower repeatability than other physiological measures. A reason for this could be because CORT is extensively metabolized before excretion and reflects a longer-term measure of stress than baseline serum CORT. Despite high sample sizes and multiple repeated measures, it can prove

Table 3. Repeatability estimates for flight initiation distance FID (m), nest distance to shore (adjusted for island identity; m), proportional nest cover (%), stress-induced CORT concentration (ng/ml), stress-induced body temperature (°C), baseline serum CORT and faecal CORT concentration (ng/ml) and baseline body temperature (°C). Shown are the years of observation, the repeatabilities and their associated standard errors, 95% confidence intervals, P-values, and the number of observations and individuals (in parentheses) and the corresponding chapter of the thesis in which it was estimated.

Trait	Years	R	SE	CI	P	N	Chapter
FID	2009	0.80	0.04	0.73, 0.84	< 0.001	154 (65)	II
FID	2010	0.76	0.04	0.70, 0.81	< 0.001	166 (60)	II
FID	2011	0.76	0.04	0.67, 0.79	< 0.001	168 (66)	II
FID	2009–2010	0.69	0.06	0.57, 0.74	< 0.001	101 (26)	II
FID	2010–2011	0.54	0.12	0.32, 0.67	< 0.001	97 (22)	II
FID	2009–2011	0.37	0.14	0.15, 0.57	< 0.05	40 (7)	II
Nest distance to shore (adj)	2008–2012	0.20	0.04	0.11, 0.27	< 0.001	531 (213)	IV
Proportional nest cover	2008–2012	0.22	0.05	0.10, 0.24	< 0.05	620 (238)	IV
Stress-induced CORT	2009–2011	0.27	0.09	0.12, 0.42	< 0.05	240 (110)	IV
Stress-induced body temperature	2010–2012	0.25	0.07	0.09, 0.37	< 0.01	320 (147)	IV
Baseline serum corticosterone	2009–2011	0.27	0.08	0.11, 0.43	< 0.01	237 (108)	I
Faecal corticosterone	2008–2011	0.13	0.05	0.04, 0.26	< 0.05	415 (168)	I
Baseline body temperature	2009–2011	0.25	0.06	0.16, 0.37	< 0.001	371 (167)	I

difficult to find reliable repeatability estimates despite high sample sizes and multiple repeated measures.

It is rather unsurprising that nest-site characteristics are significantly repeatable, considering the high breeding philopatry in the investigated population (IV). The median breeding dispersal distance is 21 meters between seasons (Öst et al. 2011). Sometimes females use exactly the same nest-cup for many years in a row. However, repeatability estima-

tes of nest-site characteristics were still relatively low. A possible explanation is that we did not control for nest success in the analysis. Breeding dispersal increases after nest failure (Öst et al. 2011), which can potentially reduce the repeatability of nest-site characteristics between seasons.

Inter-individual variation in FID (II) or behaviour in general has several ecological and evolutionary consequences (reviewed in Wolf & Weissing 2012), e.g. differential

selection on personality types (cf. Biro & Post 2008). A strong individual component explaining variation in predator avoidance behaviour, as exemplified by FID, is seemingly a general phenomenon (birds: Carrete & Tella 2010; mammals: Malmkvist & Hansen 2002; fish: Coleman & Wilson 1998; reptiles: Carter et al. 2010). However, the relatively high consistency of individual FIDs does not mean that escape behaviours are strictly fixed. FIDs in female eiders still show plasticity and can be affected by a variety of factors such as maternal experience, predation risk (II) and probably also the nesting environment (IV).

The low but significant repeatability of baseline CORT concentrations in serum and faecal samples (I) is a prerequisite for the CORT-fitness hypothesis (Bonier et al. 2009a). The relative small intra-individual variation compared to inter-individual variation of CORT₀ and FC patterns allows inference about the fitness consequences of individual stress hormone profiles. Furthermore, the results (I) are in line with other studies that show repeatability of CORT₀ in other birds (great tits: Cockrem & Silverin 2002; black-browed albatrosses *Thalassarche melanophrys*: Angelier et al. 2010). Some previous studies have also shown that FC concentrations are repeatable (greylag geese *Anser anser*: Kralj-Fišer et al. 2007; upland geese *Chloephaga picta leucoptera*: Gladbach et al. 2011). These findings suggest that baseline CORT concentrations have a strong individual component, which should be considered

when investigating links between CORT concentrations, individual quality, environmental effects and fitness. Rensel and Schoech (2011) found repeatability of baseline CORT concentrations in Florida scrub-jays *Aphelocoma coerulescens*, which was mostly driven by correlations between baseline CORT concentrations in nestlings and yearlings. They suggest that the early environment is shaping the HPA axis of developing nestlings. This could certainly be the case, as the early environment can influence postnatal individual levels of CORT, as shown for some mammals (Hudson et al. 2011). Another explanation of repeatability of baseline CORT concentrations is maternal programming of the HPA axis at an early stage of development. In birds, maternal hormones are deposited in the egg yolk, affecting the HPA axis reactivity of nestlings (e.g., Love & Williams 2008). Since eiders are precocial breeders, with ducklings staying in the nest for only one day, the nest-site environment as such has probably little influence in shaping duckling HPA axis reactivity. Maternal programming may, therefore, be a promising mechanism that should be explored in future studies examining the repeatability of baseline CORT concentrations in female eiders.

The repeatability of baseline body temperature (I), together with its strongly positive correlation with baseline faecal CORT, demonstrates its use as a complementary indicator of stress. An elevated baseline body temperature seems to represent a long-lasting stress response, since fa-

ecal CORT concentrations represent a longer-term cumulative measure of stress (Möstl et al. 2005). In support of this concept are findings showing that changes in body temperature may be detectable for days after a single stressful event (Meerlo et al. 1996), just as for CORT concentrations (von Holst 1998). Females nesting on open islands showed higher baseline body temperature when in worse condition. Thus, high baseline body temperatures could generally indicate that individuals are facing a more challenging environment, as nesting on open islands is frequently accompanied by a more extreme thermal regime, higher predation risk by aerial predators or both.

In wild and laboratory birds, reported repeatability estimates for stress-induced CORT concentrations at 30 minutes of handling range from low to moderate (Kralj-Fišer et al. 2007, Cockrem et al. 2009). Our measure ($R = 0.27$, Tab. 3) of stress-induced CORT repeatability fell within this range (II). A consistent stress response in CORT towards disturbance seems to reflect individual sensitivity of the HPA axis, with animals having distinct coping styles (Koolhaas et al. 1999). CORT stress responsiveness appears to be generally repeatable in birds. Considering that consistency in bird FIDs is seemingly a general phenomenon too, both behavioural and physiological responses to stress could form a conjunct suit of traits determining an individual's performance in risky situations (II). Cockrem and Silverin (2002) suggest that

stress-induced CORT responsiveness is, in fact, a more stable individual trait than baseline CORT concentrations. This does not seem to be the case in female eiders, however, since the repeatability of both measurements was intriguingly similar ($R = 0.27$; I, IV).

Similar to stress-induced CORT concentrations, stress-induced body temperature (I) showed low but significant repeatability in female eiders. The repeatability of stress-induced body temperature has only been assessed once before in wild animals (Careau et al. 2012). In Eastern chipmunks (*Tamias striatus*) stress-induced rise of body temperature can be influenced by correlates of heat production and dissipation such as body mass or energy expenditure (Careau et al. 2012). Considering the manifold extrinsic and intrinsic factors affecting body temperature, it is highly interesting that we still find significant inter-individual variation in stress-induced body temperature just as in measures of baseline body temperature. It has been suggested that stress-induced rise in body temperature represents a controlled fever (Cabanac 2006) that might be involved in the "fight or flight" response and has adaptive value (Oka et al. 2001). Taken together, the repeatabilities of baseline and stress-induced body temperature strongly suggest that these variables provide two alternative stress indicators that complement the use of CORT measures when investigating stress coping styles in animals.

4.2 Baseline CORT as a context-dependent predictor of individual quality and fitness

Several studies have investigated the relationship between CORT₀ or FC, individual quality and fitness. Interestingly, the results are not consistent, as negative, positive and non-significant relationships between baseline CORT and fitness have been found (reviewed in Bonier et al. 2009a). Chapter I shows that, in female eiders, the relationship between baseline CORT and individual quality is context dependent (see also Angelier et al. 2010). Female body condition, an important correlate of individual quality, is generally negatively associated with CORT₀ and FC. However, this relationship is modulated by breeding experience and breeding phenology. This context-dependency accentuates the need for cautious interpretations of the relationship between CORT patterns and phenotypic quality (Fig. 4). The results support the CORT-fitness hypothesis, since CORT₀ tends to decrease with increasing body condition. However, younger breeders show almost no connection between CORT and body condition, whereas older breeders exhibit the steepest increase in serum CORT concentrations. This finding may indicate an age effect on stress tolerance, as aging often goes along with an increase in baseline CORT concentrations (Stein-Behrens & Sapolsky 1992, Purnell et al. 2004). It is conceivable that such effects of senescence on stress tolerance are exacerbated in birds in poor condition.

The interactive effect of timing of breeding and reproductive investment on CORT₀ and that of timing of breeding and body condition on FC suggest a common denominator linking these findings. The general increase in serum CORT levels with increasing reproductive investment (i.e. total clutch mass) was most pronounced in the late breeding season. Correspondingly, only late breeders showed an increase in FC with increasing body condition. There are at least three possibilities for explaining these common patterns. First, elevated CORT levels might reflect an intensified foraging effort, since producing larger clutches later in the season becomes more challenging for females. The CORT-adaptation hypothesis, which states that higher CORT levels facilitate foraging activity and parental care, supports this assumption (e.g., Crossin et al. 2012). The second explanation is based on the ‘preparative hypothesis’ (Romero 2002). Breeding late in the season might force the female to accelerate embryonic development of their clutch. This adaptive mechanism could be realized by mobilizing energy reserves which is mediated via higher CORT levels and only females in good body condition may be able to do so. Last, late-breeding females in good condition exhibiting increased CORT levels might just depict the efforts involved in gathering the required resources and this pattern might not bear an adaptive mechanism. For example, whereas female eiders laying large clutches generally show higher survival than those lay-

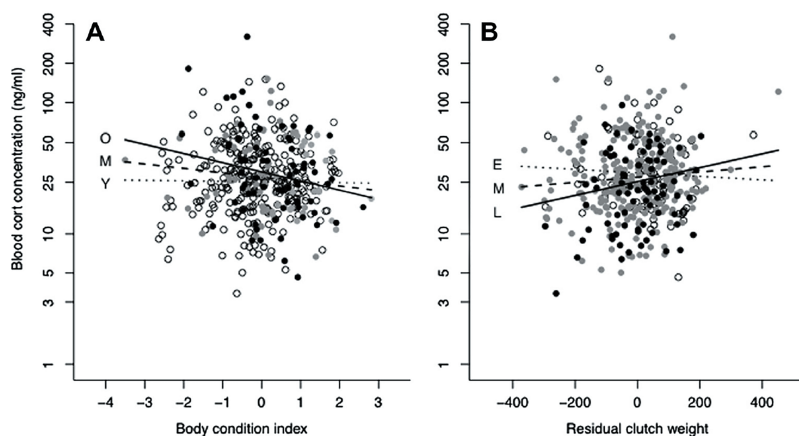


Figure 4. CORT0 levels decreased with increasing body condition (A). CORT0 of older females (solid line O, black filled dots) decreased more rapidly than those of intermediate-aged (dashed line M, gray filled dots) and young individuals (dotted line Y, open dots). CORT0 was also affected by reproductive investment (B). A negative association between reproductive investment and CORT0 was evident early in the breeding season (dotted line E, open dots), a positive association late in the season (solid line L, filled black dots), and essentially no association during the mid-season (dashed line M, filled grey dots).

ing smaller ones (Yoccoz et al. 2002), Descamps and colleagues (2009) showed that this pattern was actually reversed when there was heightened exposure to avian cholera. This result suggests that female eiders may only pay the fitness costs of high reproductive effort under unfavourable conditions.

Chapter I shows that the regulation of body temperature during incubation was affected by an interaction between individual quality and environmental harshness. An elevated body temperature was exhibited only by females in poor body condition on open islands. On those islands, the environmental conditions are more challenging, since incubating females are more exposed to harsh weather and direct sunlight than on forested islands where denser vegetation offers better protection from

the environment. In fact, the negative association between average ambient temperature and female body weight at hatching might suggest that nesting females in this population may be vulnerable to heat stress (Öst et al. 2008a). In addition, current research emphasizes the possibility that perceived risk of predation and predation pressure could explain the interrelationships between nesting habitat, individual quality and baseline body temperature (reviewed in Clinchy et al. 2013). The white-tailed sea eagle (*Haliaeetus albicilla*) poses a considerable threat to female survival, especially on open islands.

Finally, females with increased CORT levels in both their blood stream and their faeces suffered from lower hatching success (I), a result consistent with the CORT-fitness hypothesis. Elevated CORT concentra-

tions of females may per se provide an explanation for this observation. Maternal corticosterone can be passed from the mother to the eggs (e.g., Hayward & Wingfield 2004, Rubolini et al. 2005), and elevated CORT levels in ovo may both reduce hatching success and lead to worse conditioned offspring at hatching (e.g., Saino et al. 2005). Interestingly, CORT₀ as well as FC levels proved to be better predictors for nest success in eiders than body condition, which is an important determinant of nest success in this species (Lehikoinen et al. 2010).

The fact that CORT concentrations are negatively correlated with a suite of individual quality metrics and with a direct measure of fitness provides evidence that the CORT-fitness hypothesis holds for eiders and perhaps also for other capital breeders with a precocial mode of development. By highlighting the context dependency of the interrelationship between CORT secretion, individual quality and fitness, these results contribute to elucidating the seemingly contradictory views on these relationships (Bonier et al. 2009a, b, Dingemanse et al. 2010). The findings of chapter I particularly emphasize that differences between high- and low-quality individuals in their ability to cope with environmental stressors may only become apparent in the most challenging of environments.

4.3 Link between stress responsiveness and boldness is dependent on individual quality

In chapter II, I investigate the link between boldness (FID) and stress-induced CORT, since glucocorticoids are likely to be involved in educing consistent individual patterns in behaviour. Studies have shown that CORT is an important factor in mediating escape behaviours (Wingfield et al. 1998, Thaker et al. 2010, Atwell et al. 2012). Different mechanisms have been proposed in how CORT is involved in shaping behavioural stress responses (Carere et al. 2010): (a) Stress physiology determines behaviour, (b) additional factors jointly determine stress physiology and behaviour, and (c) behaviour determines physiology. While chapter II is unable to resolve this issue, it sheds light on the covariation of stress responsiveness and risk-taking behaviour in female eiders by placing it in a life-history context. This covariation is well-documented and forms the basis of consistent coping styles in animals (Koolhaas et al. 1999, Coppens et al. 2010). However, it has not been acknowledged that this link might be modulated or even controlled by individual state or status (Quinn & Cresswell 2005).

I found that in general, females with an elevated stress response had longer FIDs, i.e. they were less bold. This pattern appears to be a robust consequence of inherent differences in boldness rather than, e.g., differences in the time needed to detect and react to a predator, which also depends on nest concealment (IV). In-

terestingly, the link between boldness and stress responsiveness in female eiders runs opposite to the conventional definition of proactive and reactive stress coping styles. According to the prevailing view, proactive or bold individuals that are characterized by weak stress responsiveness show also an active fight/flight response. Reactive, shy individuals show strong stress responsiveness and respond to environmental risks with a freeze/hide reaction (e.g. Koolhaas et al. 1999; Schjolden et al. 2005).

Considering that individuals with slow reactions to disturbance are expected to show a reactive stress coping style associated with high stress responsiveness (cf. Quinn & Cresswell 2005), we actually found that bold females with short FIDs had a lower stress-induced stress response. Contradictory stress coping styles have also been found in greylag geese, where more aggressive individuals showed a positive correlation with stress-induced concentrations of faecal corticosterone (Kralj-Fišer et al. 2010). It is noteworthy that in our population of eiders a strong positive trend exists between female shyness, which is correlated with a higher concentration of stress-induced CORT and female aggression (Marin Seltmann, unpubl. data). This is in line with the results from greylag geese (Kralj-Fišer et al. 2010). One could speculate that coping styles in *Anseriformes* might show a different pattern than in mammal and bird (*Passeriformes* and *Galliformes*) model species (Koolhaas et al. 1999, Carere et al. 2003), because of different

life-histories. Kralj-Fišer and colleagues (2010) argue that modulatory factors of the dominance hierarchy could be responsible for this pattern. This might hold for female eiders, too, since females occupy consistent rank orders in brood rearing crèches. However, the simplest explanation for the apparently aberrant stress coping styles of female eiders may reflect their great reliance on crypsis during incubation, which may prevent the activation of the flight response in bold individuals. In contrast, most of the existing studies on proactive and reactive stress coping styles have been done either in mammals or in bird species not primarily relying on crypsis to avoid predation (Japanese quail *Coturnix coturnix japonica*, chicken *Gallus domesticus* and great tits) (reviewed in Koolhaas et al. 1999, Cockrem 2007).

Chapter II illustrates that despite the relative consistency of individual flight responses, FIDs can be flexible and modulated by stress-induced CORT concentrations, female breeding experience and body condition (Fig. 5). Young incubating females showed the expected increase in FIDs with increasing magnitude of the stress response, however, the direction of the relationship was reversed in the oldest breeders. We propose four not mutually exclusive explanations for the interactive effects of stress responsiveness and female breeding experience on boldness. First, this pattern may reflect a direct effect of senescence. Studies have indicated that the oldest individuals may be unable to dampen their physiological

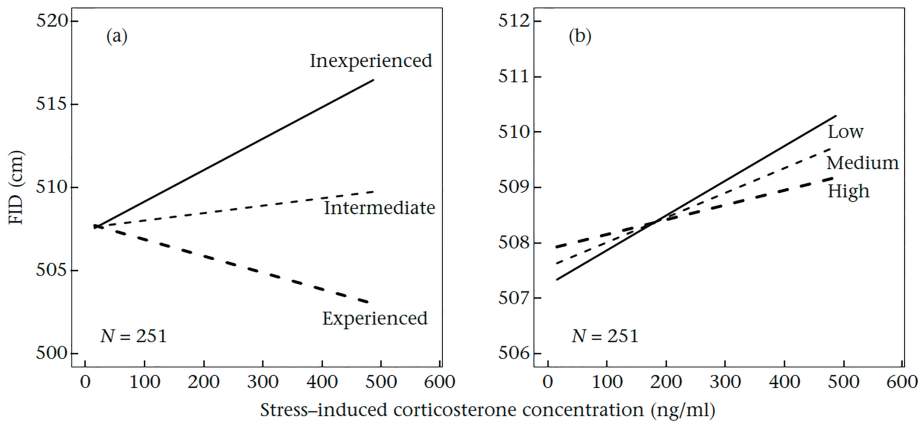


Figure 5. Stress-induced CORT concentrations and FIDs of female eiders in relation to (a) (minimum) years of breeding experience and (b) body condition. In panel (a), the solid line denotes females with little breeding experience, the dotted line females having intermediate breeding experience and the dashed line females with long previous breeding experience. In panel (b), the solid line denotes females in poor body condition, the dotted line females in intermediate body condition and the dashed line females in good body condition.

response to acute stressors (Goutte et al. 2010; Wilcoxon et al. 2011). However, we found no relationship between female breeding experience and stress-induced CORT concentrations (II) and this relative age-insensitivity of the CORT stress response agrees with studies conducted on other seabirds (e.g., Angelier et al. 2007a). Second, although stress may trigger the release of similar amounts of CORTs into the blood irrespective of female age, CORT receptors may be progressively down-regulated with advancing age (e.g., Stein-Behrens & Sapolsky 1992), and the concomitant attenuation of the stress response may facilitate an increase in reproductive performance with age (Heidinger et al. 2006). Third, CORT-mediated stress responses may be balanced or even overridden by the action of other hormones, particularly prolac-

tin. Its concentrations typically increase with advancing age in seabirds (e.g., Angelier et al. 2007a, b), and such interactive hormonal regulation may tend to inhibit flight reactions of incubating older females. Finally, female breeding experience may be correlated with the ability to assess local predation risk (Öst & Steele 2010), which may directly influence boldness. Stress physiology and boldness might become decoupled in older females through habituation of those individuals to their relatively 'safe' nest surroundings. This effect might even be enhanced by the females' social environment. Older birds are found in more centrally located nests on islands, where nest densities are higher (Öst & Steele 2010). Those females might be bolder, because boldness tends to increase in social situations (e.g., van Oers et al. 2005).

In addition, the relationship between CORT and FID was more pronounced in females with lower body condition than in females in good body condition. Following life-history theory, we might hypothesize that the expected fitness value of the current breeding attempt may be low for females in poor condition and thus they might rather prioritize their own than offspring survival (e.g., Stearns 1992). This view is supported by studies that show that hatching success is lower for female eiders in poor condition (Lehikoinen et al. 2010) and that the current brood is more often abandoned by those females shortly after hatching (Bustnes & Erikstad 1991, Kilpi et al. 2001). As individual body condition shows high annual repeatability (Jaatinen & Öst 2011), it seems likely that individual boldness in eiders is influenced by body condition (cf. Luttbeg & Sih 2010).

Both body condition as well as FID affected incubation duration, a fitness proxy in eiders. Females in poor body condition had a shorter incubation period, which accords with the notion that such females can reduce mass loss by keeping their incubation time short (Hanssen et al. 2002). On the contrary, females in good condition may be capable of bearing the costs of mass loss that result from a longer incubation time, thereby facilitating offspring quality (Hanssen et al. 2002). Furthermore, females with longer FIDs had an abbreviated incubation period. This agrees with our hypothesis that shy individuals should incubate faster when predation pressure on incubating females is

the highest (Ekroos et al. 2012). Shy individuals may put a higher emphasis on their own survival during incubation, and reducing incubation constancy is one way to achieve that aim (cf. Martin & Schwabl 2008).

To conclude, the results of chapter II help to explain why stress responsiveness may correlate with survival (e.g., Angelier et al. 2009), as the tendency to take risks by less stress responsive individuals may place them at greater risk of predation. I also demonstrate that the effects of individual quality and stress physiology on personality traits should not be studied in isolation, because their effects are likely to be intertwined.

4.4 Links between stress responsiveness, maternal investment and fitness are shaped by predation risk

Chapter II demonstrated the link between stress responsiveness and risk-taking behaviour. In chapter III, I elaborate on these findings, by exploring how the value of current reproduction and predation risk, both of which are closely linked to risk taking, interactively modify the acute stress reactivity. Under low predation risk, females exhibited a weaker stress response when they had invested more in current reproduction, whereas under high predation risk, this pattern was reversed. The stress response was weaker for females nesting in more covered nests and it was also negatively associated with the viable proportion of the clutch. Once more, the relationship was context-dependent: reproductive success decreased

with increasing CORT reactivity under low predation risk, but increased under high predation risk. This context dependency of CORT reactivity is similar to the findings on baseline CORT of chapter I.

When future fitness expectations are high, individuals should be less willing to take risks (Clark 1994, Wolf et al. 2007, Nicolaus et al. 2012). Nevertheless, the results are contradictory. Larger clutch size has been associated with greater risk taking (Forbes et al. 1994, Albrecht & Klvaňa 2004) and attenuated stress responses (Lendvai et al. 2007). In contrast, larger clutches have also been linked with risk averseness (Osiejuk & Kuszyński 2007) and stronger stress responses (Crisuolo et al. 2006). In eiders, it has been argued that the increased costs of incubating enlarged clutches lead to potentiated stress reactivity (Crisuolo et al. 2006). We suggest that these apparent contradictions can be resolved by considering the intensity of predation risk and the species-specific emphasis on current versus future fitness. Reduced stress responsiveness is related to shorter FIDs (II), and this association may ensure breeding constancy (Lendvai et al. 2007) under low predation risk and/or low future fitness expectations. However, under high risk of predation preparing for potential attacks elevated stress responsiveness may be adaptive, particularly in long-lived species (Romero 2002, Bókony et al. 2009). In female eiders, body condition at hatching is positively linked to clutch size (Öst et al. 2008b). Better body condition (Ekroos et al. 2012)

as well as larger clutches (Yoccoz et al. 2002) are generally associated with higher survival. Considerable costs for producing larger clutches may arise merely under challenging conditions, such as during disease outbreaks (Descamps et al. 2009) or under elevated predation risk (III). When breeding conditions deteriorate, increased adrenocortical sensitivity can depict such costs (Crisuolo et al. 2006).

Females in covered nests showed attenuated stress reactivity. We suggest three different explanations as to why this pattern exists. First, females nesting in covered nests may show decreased stress reactivity, because they are more confident in escaping detection. In ground-nesting birds, nest cover has been related to postponed flight behaviour (Albrecht & Klvaňa 2004) and increased trappability (Öst & Steele 2010). Second, in open nests, frequent exposure to aerial predators might come along with increased stress reactivity. Finally, females nesting in covered nests may be generally less responsive to environmental stressors (IV).

An immediate increase in CORT levels should facilitate survival at the expense of current reproduction (Breuner et al. 2008). Surprisingly, female eiders showed a positive relationship between increasing CORT levels and reproductive success. The CORT adaptation hypothesis provides a possible explanation, as it links reproductive effort with elevated baseline CORT levels and reproductive success (Bonier et al. 2009a). Under high predation risk,

an increase in CORT secretion could promote clutch survival. Higher maternal CORT levels speed up the rate of embryonic development (Schmidt et al. 2009). This mechanism might help to keep the incubation period short, as long incubation periods can increase the risk of female and clutch predation (Martin & Schwabl 2008). Similarly, shy eider females with longer FIDs had a shortened incubation period (II).

4.5 Nest-site characteristics are associated with coping style and have fitness consequences

In chapter IV, I investigated if boldness (FID) and stress responsiveness (stress-induced CORT and stress-induced body temperature) are associated with nest-site selection. I characterised nests by their amount of cover and their distance to the closest shoreline. Furthermore, I explored if female and nest characteristics were related to the viable proportion of the clutch, a fitness component.

As the influence of personality traits on habitat selection has been highlighted as one of the major themes in personality research (Wolf & Weissing 2012), I hypothesised that the boldness and stress responsiveness of female eiders would play an important role in determining their nest-site selection. This hypothesis was supported by my results. Accordingly, bolder and less stress responsive individuals occupied more concealed nests farther from the shoreline.

Different personalities may co-

exist if proactive and reactive coping styles show differential adaptive values depending on the environmental context (Cockrem 2005, Blas et al. 2007, Breuner et al. 2008). Particularly, proactive individuals might perform better in constant environments, whereas reactive individuals are more successful in variable environments (Cockrem 2005). In eiders, this argumentation seems plausible. The amount of environmental variation increases the more nest cover and nest distance to shore decrease. Incubating in open nests exposes females to more direct solar radiation, wind and rain, which may cause heat stress (Fast et al. 2007, Öst et al. 2008a) or increase heat loss (Kilpi & Lindström 1997). In addition, nests located closer to the shoreline are more likely to be affected by flooding (cf. Van de Pol et al. 2010), which may be responsible for the lower hatchability of eggs in such nests. Especially in open nests, partial clutch predation on early-laid eggs is high. Nesting close to the shore increases the likelihood of detection by particularly aerial predators and hence increases clutch predation rates at habitat edges (cf. Lloyd et al. 2005). In fact, the mere presence of predators can induce continuous psychological stress, which is related to higher stress responsiveness (Clinchy et al. 2013) and body temperature (Campeau et al. 2008) and can reduce the proportion of eggs hatching successfully (Zanette et al. 2011). Choosing an open nest close to the shore seems to be rather counterproductive for current reproduction. However, short-term repro-

ductive success is only one component of fitness.

Consistent differences in personality traits can arise when those traits are linked to consistent differences in how individuals resolve life-history trade-off between reproduction and survival (e.g. Stamps 2007, Wolf et al. 2007). Productivity and survival cannot be maximized at the same time and indeed, empirical evidence suggests that proactive individuals give emphasis to higher productivity with a concomitantly potential reduction in survival rates (reviewed in Smith & Blumstein 2008). Probably in line with this trade-off hypothesis is the observed association between differences in nest-site characteristics and consistent differences in boldness and stress responsiveness in female eiders. By nesting in covered nests farther from the shore, bold individuals (shorter FIDs, attenuated stress response) may emphasize clutch survival, however, simultaneously expose themselves to higher predation risk. More cover can compromise the chances of predator detection (cf. Schneider & Griesser 2013) and also reduce escape opportunities. Female eiders nesting in concealed nests are more easily caught by us (Öst & Steele 2010), presumably indicating their greater susceptibility to real predation. In shorebirds, higher predation mortality in concealed nests has been reported before (Amat & Maserro 2004). Furthermore, shy females (longer FIDs, strong stress responses) nesting closer to the shore can increase their survival rate by escaping faster to the water (Bentzen et al. 2009)

or benefit from lower (mammalian) predation pressure (Spencer 2002).

Nest-site selection had fitness consequences which originated from differences in nest-site characteristics rather from differences in personality traits or state of the females. Accordingly, nests further away from the shoreline and with intermediate cover had a higher viable proportion of the clutch. The latter finding indicates the possibility of stabilizing selection acting on nest concealment. But why did most females nest in sites offering either very little or high concealment considering that nests with intermediate cover actually produced the highest proportion of hatched young? One simple explanation could be that selection for intermediate nest cover was rather weak. Furthermore, the timing of incubation onset was not associated with the measured habitat characteristics (IV), which suggests that females do not compete for any special nesting habitat type (cf. Öst et al. 2008a, Öst & Steele 2010, Ekroos et al. 2012).

The results of chapter IV demonstrate that personality and stress coping styles are related to nest-site choice and that this relationship seems to be in line with the trade-off hypothesis for the evolution of personality (e.g. Wolf et al. 2007). Furthermore, individual differences in personality and stress coping style may affect fitness indirectly by breeding habitat selection. Personality types are distributed non-randomly and therefore it is possible that differential selection acts on these types (cf. Wolf & Weissing 2012).

5. General conclusions and future directions

5.1 Unresolved issues

When measuring their stress-induced CORT concentration of female eiders (**II**, **III** and **IV**), we were not able to follow the standard procedure established by von Holst (1986) and Wingfield and colleagues (1992). Based on the nature of our study – particularly due to ethical considerations – it was unfortunately not possible to wait 30 minutes after each bird is caught to obtain maximum stress-induced CORT concentrations. Blood samples at, e.g., 0, 5, 10, 15 and 30 minutes per bird would provide a detailed stress response curve until its potential maximum at 30 minutes. However, the timing of the CORT stress response plateau has not yet been investigated in wild female eiders and hence we cannot say at which time the plateau is reached. The CORT concentrations of the second blood samples were affected by the time elapsed until the second sample, suggesting that the plateau was not yet reached. I am nonetheless confident that the inclusion of the covariate ‘time elapsed from trapping until the second blood sample’ in the statistical analysis (**II**, **III** and **IV**) effectively removed the influence of variable sampling times of females on our results. While it would be highly interesting to define the CORT plateau of female eiders, the inclusion of absolute maximum CORT concentrations would unlikely affect the results or conclusions drawn in my work.

Another methodological issue is that the studies included in this thesis possibly suffer from a trapping bias. It has been suggested that the existence of personality leads to a bias in trapping individuals that are overly bold (Biro & Dingemanse 2009, Garamszegi & Török 2009). The shyest individuals might not be caught at all, and thereby studies are at risk of missing the characterization of the least bold fraction of the population. This is potentially a problem in our study population of eiders, where trapping success can never be perfect. By catching the missing proportion of the population, the results of this thesis may indeed change. However, because the omission of the least bold fraction of the population actually tends to make the current results conservative and we were still able to find links between personality and e.g. nest-site choice and fitness, the effect of this sampling bias would be to underestimate the differences we observed.

A more serious shortcoming of our data is the question about cause and effect when investigating nest cover and personality (especially FID). Nest cover might influence FID or boldness, but it is also conceivable that different personalities select different nest sites (**IV**). The two mechanisms might not be mutually exclusive and actually reflect a positive feedback between environment and behaviour. Without experimental manipulations of nest characteristics, this explanation remains speculative and it is not possible to infer causality between female and nest-site charac-

teristics. Some support for the idea that females with different stress-coping styles may differ regarding their nest-site selection stems from the fact that the stress response measures were determined after removing the female from her nest. Furthermore, the experimental work by D'Alba and colleagues (2011) indicate that female characteristics may be more likely to determine the characteristics of the nest site rather than the other way round. Through conducting experiments in which the amount of nest cover is experimentally reduced or enlarged, it should be possible to reveal causal relationships between female and nest-site characteristics.

Related to this issue is the lacking survival analysis of female eiders occupying different nest sites. This would be crucial to finally determine the validity of the trade-off hypothesis explaining personalities (IV). However, with only 2 years of overlapping data on FID, stress-induced CORT and stress-induced body temperature, such a survival analysis would be weak and of little value.

Interestingly, the findings of chapter II demonstrate that the link between boldness and stress responsiveness in female eiders runs opposite to the conventional definition of proactive and reactive stress coping styles (Koolhaas et al. 1999). Additionally to the HPA axis activity one would need to identify the sympatho-adrenomedullary (SAM) activity by measuring the strength of the increase of catecholamines to ultimately define the coping style of eiders and verify boldness and shyness.

Finally, as pointed out in chapter I and III, we considered clutch mass as a good measurement of reproductive investment in female eiders because all eggs are produced from stored reserves and conspecific brood parasitism (CBP) is relatively infrequent in our study population. However, this last assertion can be challenged. Although only 6% of all eggs in our study population are of non-natal origin, the fact that 20-22% of clutches in this population are parasitized (Waldeck et al. 2004) means that the proportion of parasitic eggs is considerably higher than 6% in those nests that do get parasitized. Assuming that brood parasites target hosts randomly with respect to their personality and stress coping style, the occurrence of CBP should not bias our results. However, as suggested in a recent review (Avilés & Parejo 2011), personality could amongst others be related to the risk of brood parasitism. We also found that the length of the incubation period was affected by female boldness (FID) (II). Investigating whether the time period between laying of the first egg and incubation onset - the time window when CBP is most likely possible because of the host's absence from the nest - may depend on the host's personality traits is therefore an interesting question for further research.

5.2 Future directions

Several behaviours maybe modulated by CORT. Pleiotropic effects of hormones are a common mechanism, and thus the inclusion of other

behaviours besides boldness such as aggression, dispersal or general activity could bear valuable insights into the architecture of personality traits in female eiders. Furthermore, it would be highly interesting to measure the boldness of females in a context other than reproductive behaviour. One could then evaluate if these personality traits are consistent not only across time (II), but also across contexts. From a physiological perspective, studies investigating the potentially interactive effects of different hormonal control mechanisms on boldness would be especially desirable. As mentioned above, catecholamines should be measured to determine eider stress coping styles, since they seem to run opposite to the conventional definition of proactive and reactive stress coping styles. Catecholamines (e.g., adrenalin and noradrenalin), released by the SAM system, are involved in the stress reaction of an animal and are released into the blood stream even before GCs. When confronted with a stressor, reactive and bold individuals show a high sympathetic reactivity (noradrenaline) and a low parasympathetic reactivity (adrenalin), whereas in reactive and shy individuals this pattern is reversed (reviewed in Koolhaas et al. 1999, Cockrem 2007).

Additionally it is an unresolved problem how survival and breeding success, and ultimately lifetime reproductive success, is shaped by potential interactions between the preferred breeding habitat and stress coping style (IV). The study population of eiders investigated in this thesis

may offer particularly exciting possibilities to evaluate the adaptive value of contrasting stress coping styles in different environments, as female survival on open islands is lower than on forested islands (Ekroos et al. 2012). In order to adequately evaluate the long-term relationship between personality, adult survival and offspring production, one would also need to analyse how female survival depends on nest-site characteristics. With additional years of data available, it should be possible to pursue this question in the future.

Other exciting unexplored avenues for further research are the potential link between personality and sociability and that between personality and juvenile survival. Are bold or shy females more or less likely to merge with other brood-rearing females, affecting the preferred number of coalition partners in brood-rearing coalitions? Female group size, in turn, may demonstrably affect the per capita survival rate of eider ducklings (Öst et al. 2008b). Or is duckling survival directly dependent on maternal personality? And do bold females prefer bold or shy partners when forming brood-rearing coalitions? The mixture of personality types among cooperating individuals may be an important determinant of reproductive success, as shown in, e.g., great tits (Both et al. 2005). The eider study system in Tvärminne provides an excellent, and perhaps even unique, opportunity to address these questions. After hatching of the clutch, the females leave with their ducklings to the sea. Unlike most other eider po-

pulations outside the Baltic Sea, where females and their newly-hatched broods immediately disperse long distances from their breeding colonies to feed (Gorman & Milne 1972, Bustness & Erikstad 1993), females at Tvärminne stay close to the breeding islands during most of the post-hatch brood-rearing period (Öst & Kilpi 2000). This makes females and their clutch relatively easy to observe for most of the brood-rearing period and thereby provides opportunities to address the open questions mentioned above.

On a more general note, researchers should finally agree on one common framework and a common nomenclature in the near future, in order for animal personality research to continue to thrive as a top branch of ecological and evolutionary research. Several frameworks have been proposed recently (e.g. Réale et al. 2007, Réale et al. 2010a, b, Carter et al. 2013). However, a common framework of animal personality is still not implemented, which often makes it difficult to compare studies that supposedly measure the same personality trait, but actually assess different behaviours (Carter et al. 2012). Likewise, McNamara and Houston (2009) have recently proposed that a common framework that integrates function and mechanisms is elementary for the future progress of personality research in behavioural ecology. Although the review by Wolf and Weissing (2012) presented 14 important consequences that consistent individual behaviour has on ecology and evolution, many of the-

se consequences have only received rudimentary attention so far. Their review however showed that “personality differences matter” and that they form an “important third dimension of ecologically and evolutionarily relevant intraspecific variation” (Wolf & Weissing 2012). Applying the concept of animal personality for addressing practical issues in conservation biology (Smith & Blumstein 2013) and animal welfare (Huntingford et al. 2013) would be particularly welcome, as empirical research is still lagging behind the expectations expressed.

5.3 Concluding remarks

The findings of chapter **I** and **III** show that serum and faecal baseline CORT as well as the acute CORT reactivity are related to fitness in female eiders. Importantly, these relationships were always context dependent. CORT-fitness relationships were modulated by internal individual quality and by external environmental stimuli. This context dependency might be an explanation why earlier studies have found positive, negative or neutral associations between CORT and fitness. The results highlight the significance of scrutinizing the degree of environmental challenge and thereby contribute to bridging the gap between the sometimes incongruent views on these important but elusive relationships. The repeatability of baseline CORT (**I**) showed that the CORT-fitness hypothesis was generally supported in female eiders. In chapter **II** I illustrated that CORT

stress responsiveness and boldness (FID) correlate in female eiders. The correlational nature of FID and stress-induced CORT has been shown before in other species (e.g., Thaker et al. 2010, Atwell et al. 2012). However, in this thesis, I emphasize the interactive nature of this correlation showing that it can be modulated by individual quality such as maternal experience and body condition.

The effects of personality traits on habitat selection have been highlighted as one of the major themes in per-

sonality research (Wolf & Weissing 2012). In chapter IV, I provided one of the first demonstrations that maternal boldness and stress responsiveness are associated with, and possibly even responsible for, variation in nest-site selection. Perhaps the greatest novelty value of the study lies in illustrating how personality and coping style can explain variation in nest-site choice in the context of the trade-off hypothesis for the evolution of personality (Wolf et al. 2007).

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Martin Walter Seltmann

Of milquetoasts and daredevils – Personalities in female eiders

This thesis describes how the life-history trade-off between survival and fecundity in female eiders (*Somateria mollissima*) could be resolved depending on consistent individual differences in escape behaviour, stress physiology, individual quality and nest-site selection. It demonstrates that these differences, termed personalities and stress coping strategies, are persistent individual characteristics with measurable effects on fitness. It suggests that these traits are subject to natural selection and thereby can evolve. Furthermore, this thesis demonstrates that individual differences in stress physiology are related to individual quality in female eiders.

The Author

Martin graduated from Stiffland Gymnasium Tirschenreuth in 2001. He received his Master of Science degree in Ecology and Organismic Biology from University of Bayreuth in 2008. Since 2009, he has been working as a PhD student in the eider research group in the Aronia Coastal Zone Research Team, Åbo Akademi & Novia University of Applied Sciences.

