**Bertille Mohring**

# Breeding During a Predation Regime Shift

## Behavioural and physiological responses of female common eiders facing the recovery of their native predator

Åbo Akademi
University

## Bertille Mohring

Born 1995

Previous studies and degrees

Master, AgroParisTech, France, 2019

Cover picture: Bertille Mohring

# Breeding During a Predation Regime Shift

## Behavioural and physiological responses of female common eiders facing the recovery of their native predator

Bertille Mohring

Environmental and Marine Biology
Faculty of Science and Engineering
Åbo Akademi University

Centre d´Etudes Biologiques de Chizé
UMR 7372 CNRS–La Rochelle
Université

Åbo, Finland, 2023

**Supervised by:**

Dr Markus Öst
Environmental and Marine Biology
Åbo Akademi University
Turku, Finland

Dr Kim Jaatinen
Nature and Game Management Trust Finland
Degerby, Finland

Dr Frédéric Angelier
Centre d’Etudes Biologiques de Chizé, UMR 7372 CNRS–La Rochelle Université
Villiers-en-Bois, France

**Reviewed by:**

Associate Professor Kimberley Mathot
Department of Biological Sciences,
University of Alberta,
Edmonton, Alberta, Canada

Professor Michaela Hau
Max Planck Institute for Biological Intelligence
Seewiesen, Germany

**Faculty opponents:**

Assistant Professor Suvi Ruuskanen
Department of Biological and Environmental Science
University of Jyväskylä
Jyvaskyla, Finland

Professor Jon Brommer
Department of Biology
University of Turku,
Turku, Finland

**Author’s address:**

Bertille Mohring
Environmental and Marine Biology
Åbo Akademi University
Aurum, Henrikinkatu 2
20500 Turku Finland

email: bertille.mh@gmail.com

ISBN paperback: 978-952-12-4329-5
ISBN electronic: 978-952-12-4330-1

Painosalama, Åbo, 2023

# Abstract

Predation is a key selective force driving prey trait evolution. Yet, the extent to which predator-consumptive and predation risk effects shape phenotypes is still poorly understood. Since predation risk increases the cost of current reproduction, long-lived prey are predicted to prioritize survival and future reproduction by reducing reproductive investment under high predation risk (e.g., through changes in life-history, behaviour, physiology or morphology). However, the relative roles played by adaptive plastic responses (i.e., within-individual phenotypic variation) and selective processes (i.e., among-individual phenotypic variation) in allowing populations and individuals to persist under fluctuating predation threat in the wild have been overlooked.

In my thesis, I shed light on these knowledge gaps by evaluating the responses of a sea duck species, the common eider *Somateria mollissima*, to fluctuating predation risk from their native predator, the white-tailed eagle *Haliaeetus albicilla*. I focused on adjustments of behavioural and physiological traits to the recovery of white-tailed eagles in southwestern Finland. As a long-lived species characterised by energetically-costly fasting during incubation and frequent intermittent breeding, common eiders are ideal for studying the life-history trade-off between reproduction and survival. I relied on a long-term individual-based monitoring of breeding females (> 2500 breeding attempts from > 1000 individuals in 2008-2022) to explore variations in risk-taking behaviour (measured by flight initiation distance) and physiological proxies of energy allocation (baseline corticosterone levels) and parental effort (baseline prolactin levels) in response to temporally and spatially variable predation risk. The longitudinal data collection was not restricted to the focal variables, but also integrated a monitoring of female characteristics (e.g., age, body condition and clutch size) and parameters such as nesting microhabitat and fine- and large-scale predation risk indices, allowing a good understanding of concurrent changes occurring in the population.

First, in agreement with the prediction that long-lived prey should reduce parental investment under elevated predation threat, I found that increasing predation threat was associated with longer flight initiation distances (i.e., reduced risk-taking) over breeding attempts. Importantly, this response was explained by a plastic adjustment of flight initiation distance to the risk of predation on breeding females, but also by the selective disappearance of risk-taking phenotypes from islands characterised by high nest predation risk. Supporting the latter notion, I showed that risk-taking strategies affected fitness (including survival, breeding propensity and hatching success), especially under elevated predation risk. My results thus provide among the first evidence that the target of predation (adults or offspring) determines the mechanisms driving adjustment of risk-taking propensity to perceived predation risk. In risky environments, females were also more likely to rely on prior experience with a threat to dampen their flight response when repeatedly confronted with a harmless stimulus (here, a human approach over consecutive days). Such short-term habituation to non-life-threatening stimuli is likely adaptive and could limit the reproductive costs of an overreaction to benign stimuli.

Second, I found that baseline corticosterone levels were positively associated with reproductive investment. In addition, baseline corticosterone levels were downregulated when incubating under high predator activity, again reflecting decreased energetic reproductive investment under threat of predation. Additionally, this physiological adjustment was habitat-dependent, as females downregulated baseline corticosterone levels under higher predation risk on themselves on open islands (associated with lower adult survival) but not on forested islands where nests are visually concealed from predators. Last, while I predicted that incubating females would display lower baseline prolactin levels – mediating reduced parental effort – under high predation threat, this prediction was not directly supported by my results. However, elevated baseline prolactin levels were still found to be indirectly related to predation pressure. Indeed, elevated prolactin levels seemed to promote hatching success in years characterised by elevated predation pressure. Overall, high prolactin levels favoured hatching success under constraining extrinsic (e.g., poor climatic conditions) or intrinsic conditions (e.g., when incubating a large clutch).

Thus, the results drawn from my thesis provide valuable insight into the short- and long-term responses of prey individuals and populations to a changing predation regime. Interestingly, most of the observed responses seemed to be driven by within-individual adjustments of behaviour or physiology to perceived predation threat, supporting the idea that predation risk effect may be more important in explaining prey trait evolution than predator-consumptive effects. However, even though longitudinal studies carried out in the wild have the advantage of encompassing the complexity of natural processes by integrating concomitant changes in intrinsic or extrinsic factors, these studies remain correlational, and further experimental work is needed to assess the causal links between predation risk and prey responses. Nevertheless, my results have far-reaching implications for conservation, by improving the knowledge on seabird responses to fluctuating predation risk from a native avian predator.

**Keywords**: corticosterone; flight initiation distance; incubation; parental investment; physiology; predation risk; predator-prey interactions; prolactin; reproduction; selection; *Somateria mollissima*.

# Sammanfattning (abstract in Swedish)

Predationen driver evolutionen av bytesdjurs egenskaper, men de direkta och indirekta predationseffekternas roll är omdebatterad. Eftersom predationsrisken ökar kostnaden för nuvarande reproduktion, förväntas långlivade bytesdjur prioritera överlevnad och framtida reproduktion genom minskad reproduktiv investering under hög predationsrisk (via förändringar i livshistoria, beteende, fysiologi eller morfologi). Dock är den relativa betydelsen av adaptiva plastiska reaktioner (inom-individuell fenotypisk variation) och selektion (fenotypisk variation mellan individer) föga kända vid anpassningen till varierande predationstryck.

Jag fyller dessa kunskapsluckor genom att utvärdera hurdana beteendemässiga och fysiologiska responser ejdern *Somateria mollissima* uppvisar på fluktuerande predationsrisk från sin naturliga predator, havsörnen *Haliaeetus albicilla*, vars population snabbt återhämtat sig i sydvästra Finland. Eftersom ejdern är långlivad, genomgår en energimässigt påfrestande ruvning och regelbundet avstår från häckning, är den idealisk för att studera livshistorieavvägningen mellan reproduktion och överlevnad. Min avhandling bygger på en individuell långtidsuppföljning av häckande ådor (> 2500 häckningsförsök; > 1000 individer; t2008-2022) och m.h.a. dessa data undersökte jag hur risktagningsbenägenheten (flyktavstånd från boet), energiallokeringen (grundnivån av kortikosteron) och investeringen i omvårdnad av avkomman (grundnivån av prolaktin) beror på temporärt och rumsligt varierande predationsrisk. Data omfattade även andra individuella egenskaper (t.ex. ålder, kroppskondition och kullstorlek), häckningsmikrohabitat och fin- och storskaliga predationsriskindex, för att kunna följa upp andra förändringar som skett i populationen.

Långlivade bytesdjur förväntas minska investeringen i reproduktion under förhöjt predationshot, och i enlighet med detta fann jag att ett ökat predationshot var förknippat med längre flyktavstånd från boet (minskat risktagande) mellan upprepade häckningsförsök. Detta förklarades av en plastisk justering av flyktavståndet till predationsrisk riktad mot häckaren själv, men också av ett selektivt bortfall av risktagande fenotyper på öar med hög bopredationsrisk. Sammantaget påverkade risktagningsstrategierna fitness (överlevnad, häckningsbenägenhet och häckningsutfall), i synnerhet då predationsrisken var hög. Dessa resultat utgör ett av de första bevisen på att målet för predation (vuxna individen eller avkomman) formar de mekanismer som driver anpassningen av risktagningsbenägenhet till predationsrisk. I farliga miljöer var ådorna också mer benägna att förlita sig på tidigare erfarenhet av predationshot, vilket dämpade flyktresponsen under upprepade konfrontationer med ett ofarligt stimulus (människa) under samma häckning. Kortvarig habituering till icke-livshotande stimuli är adaptivt ifall det minskar de reproduktiva kostnaderna för att överreagera på godartade stimuli.

Grundnivån av kortikosteron var positivt associerad med reproduktiv investering. Kortikosteronnivåerna minskade då rovdjursaktiviteten var hög, vilket återspeglar minskad energetisk reproduktiv investering under predationshot. Denna fysiologiska justering berodde på livsmiljön – ådorna hade en lägre kortikosteronnivå då de utsattes för ett predationshot på öppna öar (lägre vuxenöverlevnad) – men inte på skogsklädda öar, som erbjuder ett bättre skydd från rovdjur. Jag förutspådde att ruvande ådor skulle uppvisa lägre grundnivåer av prolaktin under högt predationshot – eftersom detta kunde styra en minskad satsning på omvårdnad av avkomman – en prediktion som inte stöddes av mina resultat. Prolaktinnivåerna visade sig dock vara indirekt relaterad till predationstrycket, eftersom en hög nivå främjade kläckningsframgången då predationstrycket var högt. Sammantaget gynnade höga prolaktinnivåer kläckningsframgången under krävande yttre (dåliga klimatförhållanden) eller inre förhållanden (stor kull).

Mina resultat belyser hur bytesindivider och -populationer på kort och lång sikt reagerar på en förändrad predationsregim. De flesta responser berodde på inom-individuella anpassningar av beteende eller fysiologi till predationshot; alltså kan predationsrisken vara viktigare för att förklara evolutionen av bytesdjurs egenskaper än den direkta dödligheten. Trots att longitudinella studier tar hänsyn till komplexiteten i naturliga processer genom att integrera förändringar i inre eller yttre faktorer, är de ofta korrelativa. Därför behövs experiment för att identifiera kausaliteten mellan predationsrisk och bytesdjurens responser. Det oaktat är mina resultat bevarandebiologiskt värdefulla, genom att de förbättrar kunskapen om sjöfåglars responser på fluktuerande predationsrisk från en naturligt förekommande fågelpredator.

**Nyckelord**: Beteende, ejder, fysiologi, föräldrainvestering, livshistorieteori, naturligt urval, plasticitet, predator-bytesinteraktioner, reproduktion, stresshanteringsstrategier, *Somateria mollissima*

# Résumé (abstract in French)

La prédation agit comme une force de sélection majeure faisant évoluer les phénotypes des proies. Cependant, la mesure dans laquelle la consommation directe de proies par les prédateurs et le risque de prédation façonnent ces traits est encore méconnue. Etant donné que le risque de prédation augmente le coût de la reproduction, les espèces longévives devraient prioriser leur survie et leur reproduction future en réduisant leur investissement reproducteur lorsque le risque de prédation est élevé (par exemple en modifiant leurs traits d'histoires de vie, comportement, physiologie ou morphologie). Cependant, le rôle de la plasticité et de la sélection dans la capacité des populations et des individus à faire face à un risque de prédation fluctuant a été peu étudiée dans un contexte naturel.

Dans ma thèse, j'ai mis ces mécanismes en lumière en évaluant les réponses d'un oiseau marin, l'eider à duvet *Somateria mollissima*, face au retour de son prédateur, le pygargue à queue blanche *Haliaeetus albicilla*. Cette espèce est idéale pour étudier les compromis entre reproduction et survie, notamment en raison de sa longue durée de vie et de sa capacité à jeûner durant l'incubation et à se reproduire de manière intermittente. A travers un suivi à long terme (2008-2022) j'ai exploré les modifications de comportement de prise de risque (mesurée à travers la distance de fuite) et d'indicateurs physiologiques d'allocation énergétique (évaluée *via* les niveaux basaux de corticostérone) et d'effort parental (mesuré *via* les niveaux basaux de prolactine) en réponse à une variation spatio-temporelle de la prédation. Ce jeu de données n'est pas restreint au suivi des variables d'intérêt mais inclut également les caractéristiques des individus (par exemple leur âge, condition corporelle ou taille de ponte), de leur nid, ou le risque de prédation à fine et large échelles, permettant de comprendre les divers changements se produisant simultanément dans la population.

Tout d'abord, en accord avec la prédiction selon laquelle les proies longévives devraient réduire leur investissement parental lorsque la prédation est forte, j'ai montré qu'une augmentation de la prédation était associée à un allongement de la distance de fuite, indiquant une réduction de la prise de risque. Cette réponse est liée à une modification plastique (intra-individuelle) de la distance de fuite au risque de prédation des adultes, à laquelle s'ajoute une disparition sélective (inter-individuelle) des phénotypes associés à une forte prise de risque sur les îles où la prédation des nids est forte. En accord avec cette idée, j'ai mis en évidence un lien entre stratégie de prises de risque traits démographiques (survie, probabilité de se reproduire et succès à l'éclosion), en particulier lorsque la prédation est élevée. Mes résultats sont parmi les premiers à montrer que les mécanismes (plasticité ou sélection) façonnant les ajustements de prise de risque des individus dépendent de la cible des prédateurs (parents ou progéniture). A l'échelle intra-annuelle, les femelles nichant sur des îles où la predation est forte étaient, au contraire, plus susceptibles de réduire leur distance de fuite lorsqu'elles étaient confrontées de manière répétée à une tentative de prédation (une approche humaine répétée pendant plusieurs jours consécutifs). Cette habituation à court terme pourrait limiter les coûts reproductifs associés à l'expression d'une surréaction face à des stimuli stressants mais bénins.

De plus, j'ai montré que les niveaux basaux de corticostérone étaient reliés positivement à l'investissement reproducteur. Les femelles incubant sous fort risque de prédation présentaient des niveaux plus faibles, reflétant de nouveau une réduction de l'investissement énergétique dans la reproduction. Cet ajustement physiologique dépendait de l'habitat, les femelles réduisant leurs niveaux basaux de corticostérone en cas de risque élevé de prédation sur elles-mêmes sur les îles ouvertes (associées à une survie adulte plus faible), mais pas sur les îles boisées où les nids sont dissimulés sous la végétation. Enfin, alors que j'avais prédit que les femelles présenteraient des niveaux basaux de prolactine plus bas (médiant une réduction de l'effort parental) en cas de risque de prédation élevé, aucune relation directe entre la prolactine et la prédation n'a été mise en évidence par mes résultats. Néanmoins, j'ai montré l'existence d'une relation indirecte entre les niveaux basaux de prolactine et la prédation. En effet, maintenir des niveaux basaux élevées de prolactine pendant l'incubation semble favoriser le succès à l'éclosion lorsque les conditions extrinsèques ou intrinsèques sont contraignantes. Cela inclut un risque de prédation élevé, de mauvaises conditions nutritives avant la reproduction, ou encore le fait d'incuber un grand nombre d'œufs.

Les résultats de ma thèse permettent ainsi de mieux comprendre les réponses à court et long terme des proies face à un changement de régime de prédation. Ces réponses semblent principalement résulter d'ajustements intra-individuels, soutenant l'idée selon laquelle le risque de prédation pourrait mieux prédire les évolutions des phénotypes que la consommation directe des proies par les prédateurs. Cependant, même si les études basées sur des suivis long-terme en milieu naturel ont l'avantage de prendre en compte la complexité des processus naturels, elles restent corrélationnelles, et des travaux expérimentaux sont maintenant nécessaires afin d'identifier les liens de cause à effet entre le risque de prédation et les réponses des proies. Mes résultats ont néanmoins des implications pour la conservation, en approfondissant les connaissances sur les réponses des oiseaux marins à une prédation fluctuante de la part d'un prédateur indigène.

**Mots clefs**: comportement ; corticostérone : distance de fuite ; incubation ; investissement parental ; plasticité ; prolactine ; selection ; *Somateria mollissima* ; théorie des traits d'histoire de vie.

# Table of contents

# 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 | **Mohring, B.**, Angelier, F., Jaatinen, K., Steele, B., Lönnberg, E., & Öst, M. (2022). Drivers of within- and among-individual variation in risk-taking behaviour during reproduction in a long-lived bird. *Proceedings of the Royal Society B, 289*(20221338).<br>doi: 10.1098/rspb.2022.1338 |
| II | **Mohring, B.**, Angelier, F., Jaatinen, K., Steele, B., & Öst, M. Habituation or sensitization? Predation risk and breeding investment drive short-term adjustment of flight initiation distance in incubating common eiders. *Manuscript.* |
| III | **Mohring, B.,** Angelier, F., Jaatinen, K., Barbraud, C., Steele, B., & Öst, M. Fitness consequences of risk-taking strategies under increasing predation pressure: a study of flight initiation distance in incubating common eiders. *Manuscript.* |
| IV | **Mohring, B.**, Angelier, F., Jaatinen, K., Parenteau, C., & Öst, M. (2021). Parental investment under predation threat in incubating common eiders (*Somateria mollissima*): a hormonal perspective. *Frontiers in Ecology and Evolution, 9*(637561).<br>doi: 10.3389/fevo.2021.637561 |
| V | **Mohring, B.**, Öst, M., Jaatinen, K., Parenteau, C., Grimaud, E., & Angelier, F. (2023). Breeding under pressure: corticosterone is associated with reproductive investment under fluctuating predation risk in a long-lived sea duck. *Functional Ecology, 37*(11), 2868-2882.<br>doi: 10.1111/1365-2435.14435 |
| VI | **Mohring, B.**, Öst, M., Jaatinen, K., Parenteau, C., Pallud, M., & Angelier, F. Parenting in a changing environment: a long-term study of prolactin, internal state and reproductive success in common eiders. *Manuscript.* |

Author contributions to the individual papers:

| | Paper I | Paper II | Paper III |
|---|---|---|---|
| **Study design & methods** | BM, MÖ, FA, KJ | BM, FA, MÖ, KJ | BM, CB, FA, MÖ, KJ |
| **Data collection** | MÖ, KJ, BS, EL | MÖ, KJ, BS | MÖ, KJ, BM |
| **Data analysis** | BM, FA, MÖ, KJ | BM, FA, MÖ, KJ | BM, CB, FA, MÖ, KJ |
| **Manuscript preparation** | BM, FA, MÖ, KJ, BS, EL | BM, MÖ, FA, KJ, BS | BM, FA, CB, MÖ, KJ |

| | Paper IV | Paper V | Paper VI |
|---|---|---|---|
| **Study design & methods** | BM, MÖ, FA, KJ | BM, FA, MÖ, KJ | BM, FA, MÖ, KJ |
| **Data collection** | MÖ, KJ | MÖ, KJ, BM | MÖ, KJ, BM |
| **Laboratory analyses** | CP, BM | EG, CP, BM | MP, CP, BM |
| **Data analysis** | BM, FA, MÖ, KJ | BM, FA, MÖ, KJ | BM, FA, MÖ, KJ |
| **Manuscript preparation** | BM, FA, MÖ, KJ, CP | BM, FA, MÖ, KJ, CP, EG | BM, FA, MÖ, KJ, CP, MP |

BM: Bertille Mohring; BS: Ben Steele; CB: Christophe Barbraud; CP: Charline Parenteau; EG: Emmanuelle Grimaud; EL: Elin Lönnberg; FA: Frédéric Angelier; KJ: Kim Jaatinen; MP: Marie Pallud; MÖ: Markus Öst.

The original publications have been reproduced with the permission of the copyright holders.

**Copyrights:**

# 1. Introduction

In a context of global change and biodiversity crisis (Ceballos et al., 2010, 2015), individuals and populations may have to face rapid changes in their ecosystems, that can even occur during an individual's lifetime. Such pressures include climate changes (e.g., temperature, rainfall), anthropogenic alterations of ecosystems (e.g., urbanisation, habitat fragmentation), or changes in predation regime (e.g., introduction of invasive alien predators or recovery of native predators) (Dias et al., 2019). The relative importance of these abiotic and biotic pressures differs between systems, and, within the scope of my thesis, I am interested in a system primarily shaped by a change in predation regime.

## 1.1. Predator-prey interactions

Interactions between predators and prey have been at the centre of scientists' attention for centuries. Historically, predator-prey interaction studies have mainly focused on the consumptive effect of predators on prey, i.e., the removal of prey individuals from the ecosystem by direct killing (Lima, 1998a; Zanette & Clinchy, 2017). Predators were thus described as exerting top-down control on prey population density through consumption. Later emerged the concepts of bottom-up control of predator density by food supply and of cyclicity of predator-prey population dynamics, following the idea that food limitation – associated with reduced prey density – may, in turn, affect predator populations.

A classic textbook example of cyclicity in predator-prey interactions is the cycle of Canada lynx *Lynx canadensis* and snowshoe hare *Lepus americanus* populations in the boreal forests of North America (Peckarsky et al., 2008). There, snowshoe hare populations follow regular density-dependent 9- to 11-year cycles (Krebs et al., 1995, 2001). These cycles have for long been presented as shaped by consumptive mechanisms (Krebs et al., 1995). To sum up, under low predator abundance, prey density increases. As prey density, i.e., food resources, increase, predator density also rises. Through consumption, high predator density drives down prey numbers, and when predators reach and exceed carrying capacity, the prey population collapses. The rarefication of prey is followed by a crash of the predator population, and with low predator abundance, the cycle repeats itself.

Importantly, consumptive mechanisms do not only shape prey density, but also act as a central driver of phenotypic selection (Relyea, 2002). Predators thus often target prey characterised by specific traits. Accordingly, predators may preferentially prey upon young, sick or weak individuals (Genovart et al., 2010), or exert selective pressure on prey morphology such as prey size (Karanth & Sunquist, 1995; Quinn & Kinnison, 1999) or colour (Husak et al., 2006; Palleroni et al., 2005; Stimson & Berman, 1990). As an example, higher predation of conspicuous orange-winged morphs of monarch butterflies

*Danaus plexippus* by two introduced bulbul species (red-whiskered bulbuls *Pycnonotus jacosu* and red-vented bulbuls *Pycnonotus cafe*) is thought to explain the predominance of white-winged monarch butterfly morphs on the island of Oahu, in Hawaii (Stimson & Berman, 1990).

In addition to predator-consumptive effects, growing evidence highlight the importance of also considering the non-consumptive effects of predators on prey individuals and populations (Lima, 1998a; Zanette & Clinchy, 2017), referred to as predation risk effects (Box 1; Peacor et al., 2020). Variation in predation risk can thus be associated with modification of prey phenotypically plastic traits (e.g., behaviour, physiology, morphology or life-history; Abbey-Lee et al., 2016; LaManna & Martin, 2016; Lima, 1998a, 1998b; Sheriff & Thaler, 2014; Ydenberg et al., 2023), known as risk-induced trait responses (Box 1; Peacor et al., 2020). In the lynx-hare example, predation risk alters hare foraging behaviour and physiology (Majchrzak et al., 2022; Sheriff et al., 2011). Risk-induced trait responses are often accompanied by a cost on prey fitness (e.g., through associated costs on growth, reproduction, recruitment or mortality) or abundance, corresponding to non-consumptive effects of predation risk (Box 1; Peacor et al., 2020). Lynx predation risk has thus been shown to have short- and long-term consequences on hare fitness through changes in fertility, offspring production or even vulnerability to diseases (Boonstra et al., 1998; Krebs et al., 2001; MacLeod et al., 2006; Peckarsky et al., 2008; Sinclair et al., 2003). Overall, predation risk effects are thought to accelerate predator-consumptive effects on prey (Peckarsky et al., 2008) and, although this idea is debated (LaManna & Martin, 2017), may even be more important in explaining prey population dynamics or trait evolution than predator-consumptive effects themselves (Creel & Christianson, 2008; Nelson et al., 2004; Pangle et al., 2007; Preisser et al., 2005).

## 1.2. Predation risk and the cost of reproduction

Predator-prey interactions are thus predicted to influence both predator and prey breeding decisions. From the predator's perspective, reproduction depends on the ability of the predator to consume a sufficient amount of suitable prey to both survive and produce offspring (Durant et al., 2007). From the prey's perspective, engaging in reproduction requires acquiring sufficient resources but also increases the risk of being preyed upon (Magnhagen, 1991). Indeed, reproductive activities are often associated with higher exposure or vulnerability to predators, be it through conspicuous displays to find and seduce a mate, reduced mobility during gestation or egg carrying, or depletion of energetic reserves during incubation or when rearing offspring (Magnhagen, 1991). These costs are often referred to as accessory costs of reproduction (Shaw & Levin, 2013). Consequently, the risk of predation on parents or their offspring overall exacerbates reproductive costs of prey (Candolin, 1998; Magnhagen, 1991).

As within an organism energy is inevitably limited, allocating resources into the current reproductive event reduces resources available for self-maintenance, with potential consequences on future reproduction and survival (Reznick, 1985; Stearns, 1992; Williams, 1966). In that context, life-history theory provides evidence for a trade-off between survival and reproduction, but also between investment in current versus future reproduction (Williams, 1966). Accordingly, an individual can be defined by its reproductive value, corresponding to the mean expected reproductive output of an individual of its age and sex in a given population (Fisher, 1930). This reproductive value can be further separated into two components: current reproductive effort and residual reproductive value, measuring future opportunities for reproduction (Williams, 1966).

Because investment in the current reproductive event can compromise investment in future reproduction, parents are predicted to adjust current reproductive effort to their internal state and to environmental conditions to maximise lifetime reproductive output (McNamara & Houston, 1996; Stearns, 1992). As it is now accepted that prey may possess the ability to assess their risk of being preyed upon, and are able to incorporate this information into decision-making (Lima & Dill, 1990; Malone et al., 2017; Sabal et al., 2021), prey individuals are expected to reduce investment in current reproduction when predation risk – on themselves or on their offspring – and the associated cost of reproduction increase (Candolin, 1998; DeWitt et al., 2019; Magnhagen, 1991; Malone et al., 2017; Mutzel et al., 2019). Adjustment of reproductive effort to the current breeding event is especially relevant for long-lived species, characterised by low annual mortality rates (Sæther & Bakke, 2000) and, consequently, high residual reproductive value (Roff, 1993; Stearns, 1992). For these individuals, even a small reduction of adult survival due to increased investment in current reproduction may largely reduce the number of future breeding opportunities and associated lifetime reproductive success (Erikstad et al., 1998; Gaillard & Yoccoz, 2003; Sæther & Bakke, 2000). These long-lived parents may, accordingly, also reduce reproductive effort when the changes of successfully raising offspring are low, leading to a low benefit of investing into current reproduction.

## 1.3. Maximising fitness under predation risk

In light of the trade-off between current and future reproduction, individuals are predicted to optimise life-history decisions, considering their state as well as environmental conditions (McNamara & Houston, 1996), including predation risk. A first crucial life-history decision encountered by iteroparous species is to decide whether to engage in reproduction or postpone reproduction to invest in the next reproductive opportunity in order to maximise their lifetime fitness (Erikstad et al., 1998; Williams, 1966). If engaging in reproduction, the following challenge is determining how much energy to invest in current offspring. For example, several species have been shown to reduce clutch size or offspring number under high predation risk (Eggers et al., 2006; Travers et al., 2010; Zanette et al., 2011). The amount and quality of parental care provided to offspring (referred to as parental effort; Angelier & Chastel, 2009) is also thought to be under the influence of the risk of predation (Candolin, 1998; Conway & Martin, 2000; Malone et al., 2017). Adjustment of reproductive investment is expected to be facilitated by modification of both phenotypically plastic and non-plastic selected traits such as life-history, morphology, behaviour or physiology.

### 1.3.1. Life-history decision-making: to breed or not?

In long-lived species, individuals are expected to have many opportunities to produce and raise offspring during their lifetime. As a small reduction of adult survival is likely to have great impacts on population growth rate, especially in long-lived species (Gaillard & Yoccoz, 2003; Sæther & Bakke, 2000), they are predicted to put a greater emphasis on their own survivorship, as opposed to that of their offspring (Roff, 1993; Stearns, 1992). Such maximisation of adult survival and associated lifetime reproductive output may be reached by reducing parental effort or terminating a current reproductive event, but also by skipping breeding entirely, leading to the evolution of intermittent breeding strategies in iteroparous species (Desprez et al., 2018; Shaw & Levin, 2013). Deciding to skip reproduction is thought to provide a fitness benefit by increasing adult survivorship and opportunities for future reproduction when accessory costs of reproduction are elevated (Shaw & Levin, 2013), for instance when facing extreme climatic events (Cubaynes et al., 2011; Soldatini et al., 2016), under high predation risk (Dulude-de Broin et al., 2020; Öst et al., 2018), or when energetic reserves are low (Desprez et al., 2018; Smout et al., 2020).

### 1.3.2. Optimising reproductive investment under predation risk through behavioural and physiological adjustments

During reproduction, a suite of morphological, behavioural and physiological traits and responses is thought to facilitate individual adjustment of reproductive investment as well as to reduce vulnerability to predators.

#### Behavioural traits

Parental care, the diversity of behaviour exhibited by parents that aim to increase offspring fitness (Royle et al., 2012), plays a major role in enhancing an individual's fitness through the production of high-quality offspring. It encompasses a wide variety of behaviour displayed before and after offspring birth, such as nest building, production and incubation of eggs, and guarding and provisioning of offspring (Clutton-Brock, 1991). As exhibiting parental care is often associated with a higher risk of predation, parental behaviour intertwines with diversity of behaviours reducing the risk of predation (i.e., antipredator behaviour) (Sih, 1994). Antipredator behaviours include for example behaviours reducing the risks of encountering a predator, those enhancing detection of predators by prey, but also warning signals and escape or defence behaviour (Caro, 2005). Prey may indeed adjust their use of habitat and time budget activities to avoid predators. It is the case of Leach's storm-petrels *Oceanodroma leucorhoa*, a nocturnal species synchronising its activity patterns with light levels to maximise predator-avoidance (Miles et al., 2013; Watanuki, 1986). Additionally and although subject to debate, colonial breeding strategies have evolved as a way to increase predator detection through group vigilance, deter predators with social mobbing or overall dilute the individual risk of predation (Coulson, 2002; Götmark & Andersson, 1984; Rodgers, 1987). Lastly, when confronted with an approaching predator, nest defence behaviours are also varied, comprising: crypsis, aggression, distraction displays or defensive defecation (Humphreys & Ruxton, 2020). These behaviours are not mutually exclusive and, when unfruitful, often result in the escape of the parent from the nest.

The behavioural escape response of a brooding prey to an approaching predator is particularly interesting, as it often directly reflects the trade-off between maximising either parent or offspring survival. Indeed, following the optimal escape theory, escape distance is thought to mirror the balance between the costs and benefits of fleeing (Cooper & Frederick, 2007; Ydenberg & Dill, 1986). Parents are often expected to delay escape to protect offspring, as fleeing from the nest is likely to indicate the offspring's location and render them vulnerable to predators, resulting in the termination of the current breeding event (Broom & Ruxton, 2005). Nevertheless, delaying escape may also lead to the death of the parent and to the loss of all future breeding opportunities (Albrecht & Klvaňa, 2004). Accordingly, measuring flight initiation distance, the distance at which a focal individual initiates escape from an approaching potential predator (Ydenberg & Dill, 1986), provides a standardised measurement of the degree of risk an individual is willing to tolerate before fleeing (Samia et al., 2016; Stankowich & Blumstein, 2005). It indeed measures the extent to which an individual prioritises survival over reproduction. Interestingly, although context- or state-dependent (Albrecht & Klvaňa, 2004; de Jong et al., 2021; Osiejuk & Kuczyński, 2007), risk-taking propensity is often repeatable within individuals (Cabrera et al., 2017; Carrete & Tella, 2010; Strong et al., 2017). This response is closely linked to a shy-bold continuum, with bolder individuals (i.e., risk-taking individuals) tolerating a closer approach than shier individuals (i.e., risk-avoiding individuals) that flee from a greater distance to the threat (Cooper Jr, 2009; Petelle et al., 2013; Réale et al., 2007).

## Physiological traits

Predation risk exerts chronic and acute physiological stress on prey organisms which can be reflected, for example, in variation in glucocorticoids, reproductive hormones, oxidative stress, plasma metabolites, telomeres or immune functions (reviewed in Hawlena & Schmitz, 2010; Zanette et al., 2014). Among these physiological traits, hormonal mechanisms orchestrate many life-history decisions in vertebrates, notably because the activation of specific endocrine pathways can redirect the allocation of resources from one activity (e.g., reproduction) to another (e.g., self-maintenance or survival) (Angelier et al., 2016; Sapolsky et al., 2000). While individuals may compensate and recover from exposure to acute stressors with little physiological consequences, prolonged exposure to predator presence or repeated exposure to acute stressors (e.g., through frequent predator attacks) may deeply alter physiology and interfere with essential body functions or activities (e.g., foraging or reproduction) (Romero, 2004; Zanette et al., 2014). To cope with chronic stress and resume essential activities, individuals are thus predicted to adjust the magnitude of their stress response to maximise fitness, either lessening or heightening stress sensitivity (Angelier & Wingfield, 2013; Brown et al., 2005; Zanette et al., 2014). Glucocorticoids are of particular interest within the study of reproductive investment under predation risk, due to their central role in the response to stressors but also in maintaining homeostasis – i.e., maintaining a physiological balance despite changes in internal and external conditions (McEwen & Wingfield, 2003) – and in the regulation of energetic balance, as well as reproductive hormones such as prolactin, with its central role in the expression of parental behaviour (Angelier et al., 2016; Angelier & Chastel, 2009; Sapolsky et al., 2000).

First, glucocorticoids – cortisol in most mammals and fish and corticosterone in birds, rodents, reptiles and amphibians – are involved in allostasis, i.e., in the process of maintaining stability through change (McEwen & Wingfield, 2003; Romero et al., 2009). Allostasis – and the associated secretion of glucocorticoids – is thought to enable organisms to actively adjust their phenotype to both predictable and unpredictable events (Grindstaff et al., 2022; McEwen & Wingfield, 2003; Wingfield, 2003). Because an elevation of glucocorticoid levels under chronic or acute stress can trigger an emergency life history stage (Wingfield et al., 1998), glucocorticoids are often thought of as “stress hormones” (Romero, 2004; Sapolsky et al., 2000). Through pleiotropic effects (i.e., by simultaneously affecting multiple phenotypic traits), glucocorticoids can therefore alter individual behaviour and life-history decisions (Crespi et al., 2013; Crossin et al., 2016; Sapolsky et al., 2000). Accordingly, several studies have shown that individuals can respond to environmental challenges (e.g., severe climatic events or high predation risk; Clinchy et al., 2004; Henderson et al., 2017; Kitaysky et al., 1999; Pravosudov et al., 2001; Scheuerlein et al., 2001) or energetic challenges (e.g., poor body reserves;

Williams et al., 2008, or hunger; Riechert, Chastel, et al., 2014) by displaying elevated baseline corticosterone levels that can sometimes completely suppress the expression of reproductive behaviour, leading to the termination of a breeding attempt (Groscolas et al., 2008; Love et al., 2004; Spée et al., 2011). In such a context, one can expect a negative association between corticosterone and fitness (referred to as the 'corticosterone-fitness hypothesis', Bonier et al., 2009; Figure 1A), with detrimental effects of elevated glucocorticoid levels on growth, survival and reproduction. Previous studies have thus highlighted reduced growth rate (Hayward & Wingfield, 2004; Hull et al., 2007; Müller et al., 2009), reduced survival (Ethan Pride, 2005; Goutte et al., 2010; Jimeno et al., 2018; Lancaster et al., 2008) and lower breeding success (Henderson et al., 2017; Ouyang et al., 2011; Sheriff et al., 2009) in individuals displaying elevated baseline glucocorticoid levels.

However, because glucocorticoids are also involved in maintaining energetic balance and as reproduction is energetically demanding (e.g., when fasting during incubation), upregulating glucocorticoid levels has been shown to increase fitness (the 'corticosterone-adaptation hypothesis', Bonier et al., 2009; Figure 1B). Accordingly, a moderate elevation of circulating glucocorticoid levels can be associated with increased metabolic activity (Jimeno et al., 2018), incubation commitment (Ouyang, Muturi, et al., 2013), higher offspring feeding rate (Ouyang, Sharp, et al., 2013), higher reproductive success or output (Béziers et al., 2020; Crossin et al., 2013; Fischer et al., 2020; Ouyang, Sharp, et al., 2013; Riechert, Becker, et al., 2014) and even higher survivorship (Comendant et al., 2003; Cote et al., 2006; Rivers et al., 2012). Such contrasting relationships highlight the context-dependency of glucocorticoids, but also the still poorly understood association between glucocorticoids and fitness under variable environmental conditions (Figure 1A and 1B) – according to which both positive and negative relationships could even be validated within individuals and across contexts (Escribano-Avila et al., 2013).

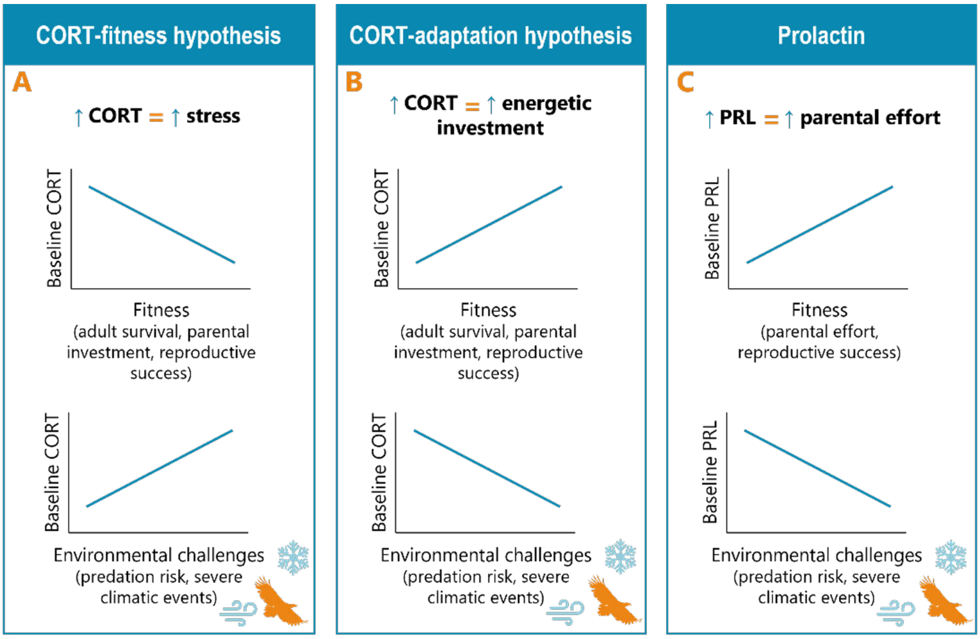

*Figure 1: Schematic representation of the theoretical expectations regarding the link between baseline corticosterone (CORT) and prolactin (PRL) levels, fitness, and environmental challenges.*

Second, prolactin is the main hormone governing the expression of parental and alloparental behaviour (Angelier et al., 2016; Angelier & Chastel, 2009; Buntin, 1996; Riddle, 1963). Consequently, baseline prolactin levels are thought to mirror parental effort – i.e., the amount and quality of care provided by a parent (Angelier & Chastel, 2009). Prolactin secretion is facilitated by egg or offspring visual or tactile stimuli (M. Hall, 1987; Massaro et al., 2007; Sharp et al., 1988; Smiley & Adkins-Regan, 2018a) (Figure 1C). Circulating prolactin levels have been shown to rise during egg laying, and high prolactin levels can promote incubation behaviour as well as brooding, feeding or defending offspring (Angelier et al., 2016; Clutton-Brock, 1991; Hope et al., 2020; Smiley & Adkins-Regan, 2018b; Wang & Buntin, 1999). Experimental studies have indeed demonstrated that a moderate increase in prolactin levels can enhance incubation behaviour and offspring care or protection (Farrar et al., 2022; Pedersen, 1989; Sockman et al., 2000), while a moderate decrease in prolactin levels can reduce incubation commitment (Angelier, Clément-Chastel, et al., 2009; Thierry et al., 2013), post-hatch parental care (Smiley & Adkins-Regan, 2018b), alloparental behaviour (Angelier, Barbraud, et al., 2006) and even lead to egg or offspring abandonment (Spée et al., 2011). Similarly, parents abandoning eggs or chicks often display low prolactin levels (Chastel & Lormée, 2002; Groscolas et al., 2008; Spée et al., 2010). Overall, breeding individuals and successful breeders have been shown to display higher baseline prolactin levels than non-breeders (Hall, 1986; Ouyang, Sharp, et al., 2013; Riou et al., 2010; Schoech et al., 1996) and failed breeders (Angelier, Clément-Chastel, et al., 2009; Angelier et al., 2013; Chastel et al., 2005; Crossin et al., 2012; Riou et al., 2010), respectively.

Interestingly, baseline prolactin levels can differ between breeding seasons (Angelier & Chastel, 2009; Delehanty et al., 1997; Riechert, Becker, et al., 2014), and although poorly understood, such variation has previously been linked to yearly changes in precipitation (Delehanty et al., 1997; Rubenstein et al., 2008) or food availability (Riechert, Becker, et al., 2014), suggesting a link to environmental conditions. Thus, despite the central role of prolactin in reproduction, possible adjustments of prolactin levels – and associated parental effort – to variation in environmental conditions have been overlooked (but see Delehanty et al., 1997; Riechert, Becker, et al., 2014; Rubenstein et al., 2008; Smith et al., 2023; reviewed in Angelier et al., 2016). Given that prolactin levels can be modulated by stressors (Angelier et al., 2016; Angelier & Chastel, 2009; Chastel et al., 2005), understanding how prolactin levels fluctuate in a context of fluctuating biotic environmental conditions such as predation pressure is crucial. Specifically, the link between prolactin and predation risk has been overlooked.

## 1.4. Coping with a fluctuating environment

The modification of behavioural or physiological traits, as well as life-history decisions, is thought to help organisms cope with environmental challenges (Jacobs & Wingfield, 2000; Sheriff & Thaler, 2014; Wingfield et al., 2011), such as fluctuating predation pressure. Overall, populations are maintained under changing environmental conditions through two main processes: within-individual adaptive plastic responses to environmental variations and among-individual selective changes of the optimum phenotype with environmental fluctuations (also referred to as environmental sensitivity of phenotypic selection; Ghalambor et al., 2007; Chevin et al., 2010).

Phenotypic plasticity or flexibility – the capacity to display different phenotypes in response to changing conditions – is thought to play a central role in the ability of an organism to cope with fluctuating extrinsic (e.g., climate, predation risk) or intrinsic conditions (e.g., body reserves) (Ghalambor et al., 2007; Taff & Vitousek, 2016). Individuals that are able to match their phenotype to environmental conditions often gain a fitness advantage over those mismatching their phenotype (Moran, 1992; Petrullo et al., 2023; Wada & Sewall, 2014), and are more likely to persist in the ecosystem, while others might disappear (Chevin et al., 2010; Fierst, 2011; Taff & Vitousek, 2016; Wingfield, 2003). Accordingly, previous research suggests that plasticity enhances environmental tolerance and thus buffers against and reduces the risk of extinction (Cerini et al., 2023; Nunney, 2016). This is because flexible responses offer individuals and populations more time to adjust their phenotype to a new optimum through directional selection (Ducatez et al., 2020; Ghalambor et al., 2007).

The matching of phenotype to environmental condition requires sufficient phenotypic plasticity, but this does not guarantee adaptation. A flawed assessment of environmental cues will not elicit the correct adaptive response despite the presence of sufficient plasticity. Such flawed assessments are costly as they lead to mismatches between phenotype and environment (Ghalambor et al., 2007; Petrullo et al., 2023). Interestingly, individuals belonging to the same population and facing the same environmental challenge often vary greatly in their behavioural or physiological response (Dammhahn et al., 2018; Montiglio et al., 2018; Réale et al., 2010). These differences between individuals are often consistently maintained across contexts and over time (Dingemanse et al., 2010). Several non-mutually exclusive hypotheses could explain the maintenance of inter-individual variation in phenotypes. Indeed, variation in behavioural or physiological traits among individuals can reflect adaptive responses to differences in state (i.e., variation in individual physical or physiological condition, age or experience; Dingemanse & Wolf, 2010; Wolf & Weissing, 2010). In addition, positive feedback between individual state and behavioural or physiological traits can reinforce and stabilise inter-individual phenotypic differences (Dingemanse & Wolf, 2010; Wolf & Weissing, 2010). Among-individual phenotypic variation may also be associated with different ways of solving life-history trade-offs (e.g., survival-reproduction trade-off, or trade-off between investment in current or future reproduction), and context-dependent fitness may favour the maintenance of interindividual variation (Moran, 1992; Wolf & Weissing, 2010).

While it is widely admitted that predation plays a central role in animal evolutionary processes (Abrams, 2000), the extent to which predator-consumptive and predation risk effects drive phenotypes within a population deserves further investigation (Figure 2). In particular, the relative roles played by adaptive plastic responses (i.e., within-individual phenotypic variation) and selective processes (i.e., among-individual phenotypic variation) in allowing populations and individuals to persist under fluctuating predation pressure have been overlooked.

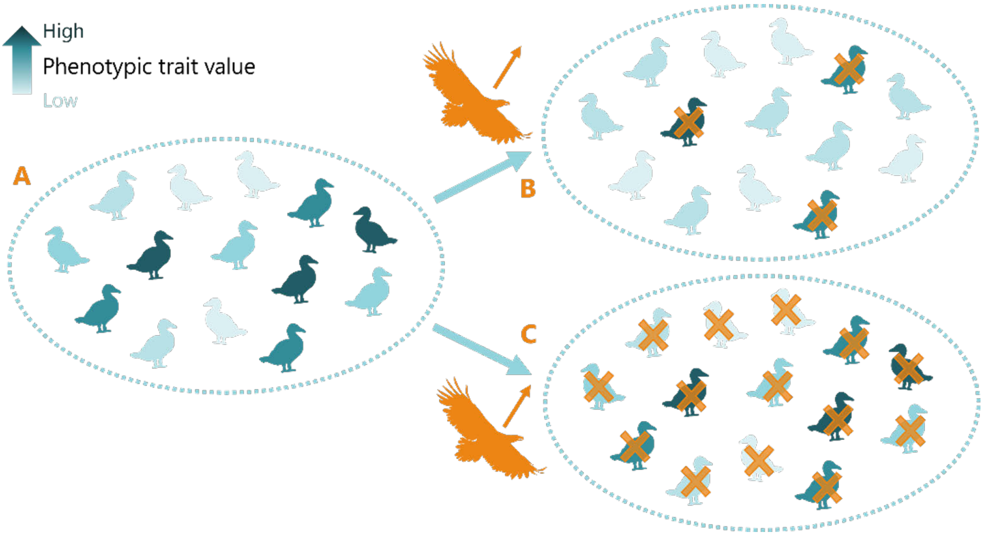

*Figure 2: Schematic representation of the evolution of (A) a prey population characterised by different phenotypes facing a change in predation regime. In (B) the population is maintained, with some prey individuals successfully adjusting their phenotype to cope with increasing predation while predators select against specific phenotypes (orange cross, predator-consumptive effects). (C) illustrates an extreme case in which prey individuals are not able to adjust their phenotype to changing environment and predation pressure drives prey population to extinction.*

## 1.5. The eagle-eider system

Predation by invasive and native predators play a major role in structuring ecosystems, notably through trophic cascades (Letnic et al., 2012; Natsukawa & Sergio, 2022). While the impact of the former is widely acknowledged as a key driver of extinctions (Doherty et al., 2016; Jones et al., 2008), the impact of the latter is still poorly understood (Anker-Nilssen et al., 2023; Barrett et al., 2006). Nevertheless, native predators can be a major threat to many taxa including seabirds, as they have been assessed to affect nearly 15% of all seabird species (Dias et al., 2019). A case in point is the rapid re-establishment of sea eagle *Haliaeetus spp*. populations in the temperate northern hemisphere, which may have severe repercussions on seabird populations in the region (Barrett et al., 2006; Hipfner et al., 2012).

Sea eagle populations have collapsed during the 19th and 20th centuries, primarily because of severe human persecution and low reproductive success linked with chemical pollutants such as dichlorodiphenyltrichloroethane (DDT) and polychlorinated biphenyls (PCBs) (Helander et al., 2002; Hipfner et al., 2012). These dramatic declines in sea eagle populations – the white-tailed eagle *Haliaeetus albicilla* in northern Europe and the bald eagle *Haliaeetus leucocephalus* in North America – even led to local extinctions in several countries, such as the United Kingdom, Lithuania and Denmark. In Finland, white-tailed eagles were on the brink of extinction during the mid-20th century. In the 1970s, Norway counted 700-800 breeding pairs, that were evaluated as accounting for more than 70% of the remaining northern and central European white-tailed eagle populations (Folkestad, 2000; Hailer et al., 2006; Helander, 2000). During this period, several seabird and waterfowl species, such as common eiders, thrived, benefiting from relaxed predation pressure.

Protection efforts, coupled with natural recolonisation and reintroduction programs – as well as the ban of DDT, PCBs and associated chemicals in the 1970s –, proved effective in conserving this apex predator and increasing population densities (Hipfner et al., 2012). However, rising white-tailed eagle abundance has been shown to directly and indirectly affect seabird populations (Anker-Nilssen et al., 2023; Barrett et al., 2006; Barrett, 2008; Hentati-Sundberg et al., 2023; Hipfner et al., 2012). Direct effects include killing of adults, nestlings as well as egg depredation by white-tailed eagles (Anker-Nilssen et al., 2023; Barrett, 2008; Bregnballe et al., 2022). White-tailed eagle predation attempts, by flushing birds away from their nest, have also been shown to widely facilitate seabird egg or nestling depredation by other avian predators such as gulls *Larus spp.* crows or ravens *corvus spp.* (Anker-Nilssen et al., 2023; Bregnballe et al., 2022). In addition, the mere presence of white-tailed eagles in the vicinity of seabird colonies has been linked to a modification of prey behaviour, including increased vigilance, changes in foraging or chick provisioning, reduction of breeding propensity, abandonment of breeding sites and even relocations nearby human settlement (Anker-Nilssen et al., 2023; Barrett et al., 2006; Hipfner et al., 2012; Öst et al., 2018).

In such a context of increasing white-tailed eagle abundance – perhaps above historical levels – the potential impact of eagles on seabird populations has yet to be assessed, and so is the ability of prey individuals to adapt to such rapid change in predation regime. Hence, concern has been raised on whether and how seabirds may adapt to rapidly increasing eagle populations, and this topic deserves further investigation. In the Finnish archipelago, white-tailed eagle diet is largely composed of birds (~70%, Ekblad et al., 2016), with the main prey species being the common eider *Somateria mollissima* (Ekblad et al., 2016) – also one of the most abundant waterfowl species in this area. The recent increase in white-tailed eagle abundance in Finland and the importance of eiders in its diet, combined with overlooked effects of eagles on seabird populations, turn predator-prey interactions between white-tailed eagles and common eiders into an ideal framework to assess how prey respond to rapid changes in predation regime, especially during reproduction – a key life-history stage driving population dynamics.

# 2. Aims and Scope of the Thesis

This thesis aims to shed light on the still poorly understood behavioural and physiological responses and adaptations of individuals and populations of long-lived prey species to a changing predation regime. To date, few studies have attempted to separate adaptive plastic responses (i.e., within-individual phenotypic variation) from selective processes (i.e., among-individual phenotypic variation) in wild populations – especially in a context of fluctuating predation risk –, since such analyses necessitate large longitudinal datasets covering a substantial part of the lifespan of study organisms, and are often difficult to obtain in the wild (Blumstein, 2019). Thus, I relied on a long-term individual-based monitoring scheme, a vital tool for the comprehension of processes shaping population and individual responses to environmental changes, such as variation in predation regime (Clutton-Brock & Sheldon, 2010; Sheldon et al., 2022). Accordingly, longitudinal individual-based approaches provide a unique opportunity to simultaneously control for other intrinsic and extrinsic factors affecting individual responses.

In light of the overlooked responses of seabirds to recovering sea eagle populations, I investigated whether and how the ongoing change in predation regime linked to the recovery of Finnish white-tailed eagle populations – and to the occurrence of invasive alien predators (Öst et al., 2018, 2022) – shaped breeding common eider behavioural and physiological traits. As a long-lived species that can rely on intermittent breeding strategies (Nicol-Harper et al., 2021), eiders are ideal for studying the life-history trade-off between reproduction and survival. I first explored behavioural adaptations to predation pressure (**I, II, III**), before focusing on the effects of predation threat on physiological markers of allostasis and parental effort (**IV, V, VI**) (Table 1).

In Chapter **I**, I investigated intrinsic and extrinsic drivers of risk-taking behaviour in breeding females exposed to fluctuating predation threat. Since few studies have attempted to separate plasticity and selection of risk-taking phenotypes, I specifically tested the mechanisms shaping the prey's behavioural response to a predation attempt over breeding events. Importantly, prey individuals are thought to possess the ability to assess the risk of being preyed upon and incorporate prior knowledge of predators into their decision-making. Thus, I further assessed in Chapter **II** whether incubating females adjusted flight initiation distance when repeatedly exposed to a non-lethal yet threatening stimulus – a human approach – over a short period of time (corresponding to the last days of incubation). Last, I used capture-mark-recapture data in Chapter **III** to evaluate the temporal trends in three key fitness components – survival, breeding propensity and reproductive success – and to shed light on the fitness consequences of inter-individual variation in risk-taking propensity.

In Chapter **IV**, I investigated the relationship between parental investment and physiology in incubating female eiders. In this short-term study, I aimed to validate the predicted links between circulating blood corticosterone and prolactin levels and reproductive investment in the study population. In addition, I evaluated the potential effects of fine-scale variation in predation risk on these relationships. In light of the results drawn from Chapter **IV**, I further explored the endocrine response to fluctuating predation pressure, using over a decade of physiological measurements of baseline corticosterone (**V**) or prolactin (**VI**) levels. These Chapters integrate state-dependency in hormonal responses and assess the link between hormone levels and reproductive success. In the last two Chapters of my thesis (**V, VI**), I thus explored variation in baseline corticosterone and prolactin levels as potential mechanisms shaping the adjustment of parental investment to fluctuating predation pressure, in order to assess the ability of prey individuals and populations to cope with a drastic change in predation regime.

*Table 1: Summary of the Chapters.*

| | **Study variable** | **Temporal scale of the response** | **Specific study questions** |
|---|---|---|---|
| **I** | FID(1) | Long-term | How do prey behaviourally respond to increasing predation risk and what other factors drive individual variation in risk-taking?<br>What are the parts played by plasticity and selection in such response? |
| **II** | FID | Short-term | Do individuals adjust FID to prior experience when repeatedly confronted to a threatening stimulus? |
| **III** | FID | Long-term | What are the lifetime fitness consequences of among-individual variation in risk-taking? |
| **IV** | CORT(2) and PRL(3) | Short-term | How are hormone levels related to parental investment and predation risk during reproduction? |
| **V** | CORT | Long-term | What drives individual variation in physiology, and what are the effects of predation?<br>What are the parts played by plasticity and selection?<br>What are the lifetime fitness consequences of individual differences in physiology |
| **VI** | PRL | Long-term | |

(1) FID: flight initiation distance; (2) CORT: baseline corticosterone levels; (3) PRL: baseline prolactin levels.

# 3. Material and Methods

I tested my research hypotheses on a natural population of female common eiders *Somateria mollissima* breeding in Tvärminne archipelago, southwestern Finland, as this species displays female-only parental care.

## 3.1. Ecology of the common eider

*Figure 3: Circumpolar distribution of common eiders Somateria mollissima including breeding (in pink) and wintering (in blue) range. Areas were breeding and wintering overlap are presented in violet. Adapted from e-bird wintering and breeding areas.*

The common eider is a circumpolar sea duck (Figure 3), primarily feeding on mussels *Mytilus spp.* – blue mussels *Mytilus trossulus* in the Baltic Sea (Jaatinen et al., 2021) – as well as other benthic invertebrates including bivalves, crustaceans, or echinoderms (Guillemette et al., 1992). As eiders often breed at high latitudes, where coastal seas are covered in ice during winter, they have evolved short- and long-distance migratory strategies, flying to a more favourable ice-free habitat during winter. The common eider is a long-lived species, with a mean life expectancy of 11.8 years, and living up to ~25 years (Wood et al., 2020). In addition, this species can rely on intermittent breeding strategies (Coulson, 1984; Öst et al., 2018; Nicol-Harper et al., 2021).

Eiders are colonial breeders and show high philopatry to their natal area (Coulson, 1984; Swennen, 1990), but also to their nest site (Öst et al., 2011). Indeed, the average annual breeding dispersal distance is estimated at 21 m and they rarely settle on a different island to breed (Öst et al., 2011). As other species with precocial nidifugous young, eiders exhibit female-only care. During the breeding season, females build a nest on the ground, filled with down, and incubate alone. Incubation lasts on average 26 days (Korschgen, 1977), during which females fast and only leave the nest for short recesses (Criscuolo et al., 2000; Tertitski et al., 2021) – in most cases to drink or as a response to a disturbance. Incubation is thus an energy-demanding period in the life-cycle of an individual, during which females may lose up to 46% of their body mass (Parker, 1990).

Reproduction is a critical period not only because of high energetic needs due to fasting and displaying exclusive female care, but also because of the increased vulnerability to predators associated with nesting on the ground (Ramula et al., 2018; Schüttler et al., 2009). The cryptic plumage of female eiders (Figure 4) is thought to provide a survival advantage by reducing visual detection by predators (Langerhans, 2007). Its brown colouration, associated with darker patterns, matches the rocky background on which they usually nest, as well as the ground or vegetation in forested habitats. Crypsis is also maximised through behavioural adaptations contributing to diminish the risk of predation, as females often prefer to breed in concealed nest sites, where survivorship is enhanced (Ekroos, Öst, et al., 2012).

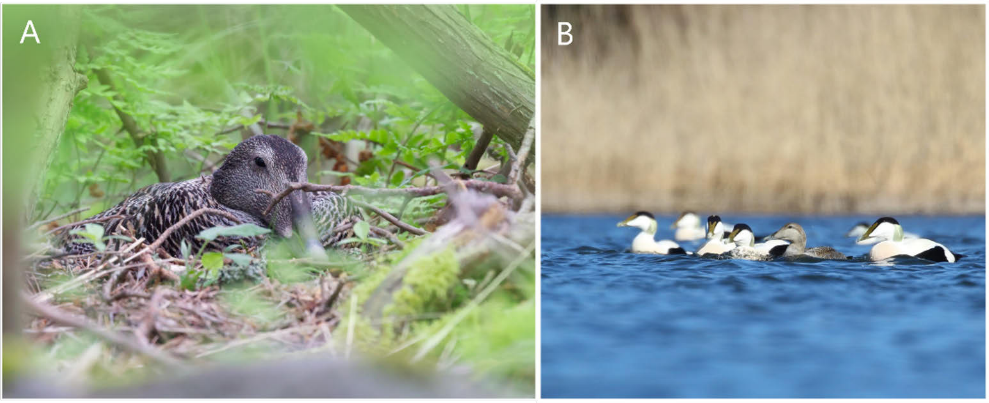

*Figure 4: Pictures of (A) a cryptic female common eider on a concealed nest in the forest and (B) a group of conspicuous males courting a female common eider. © B. Mohring.*

## 3.2. Study area

The studies of this thesis were conducted in an eider colony of the western Gulf of Finland, Baltic Sea, located in the archipelago surrounding Tvärminne Zoological Station (59°50′N, 23°15′E). The study area is composed of a set of up to 30 monitored islands (Figure 5) characterised by two contrasting habitat types: small open granitic islands – mainly covered by bare rocks and sparse patches of grasses or juniper *Juniperus communis* – and larger islands covered in pine *Pinus sylvestris* dominated forest and juniper shrubs. These islands are part of a nature reserve where island visits are only allowed for research purposes, limiting human disturbance.

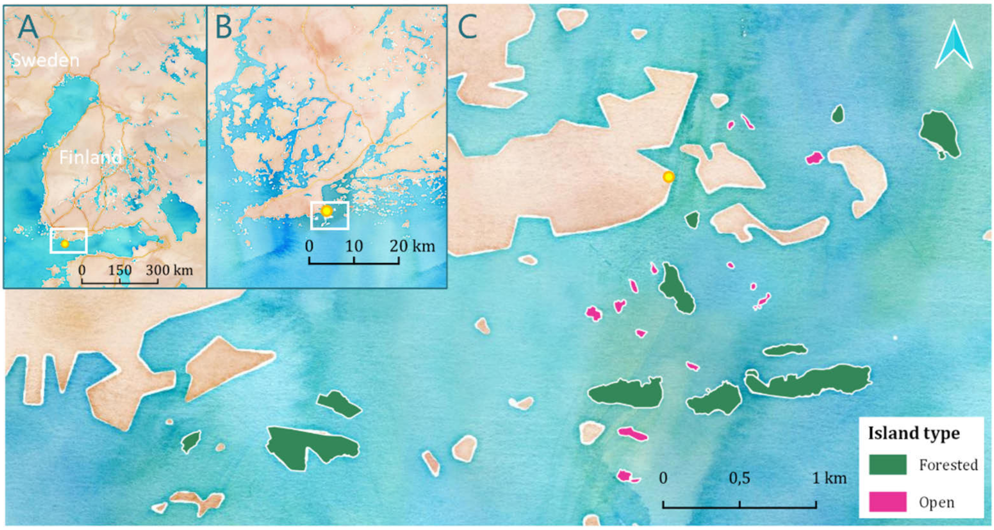

*Figure 5: Maps showing the location of Tvärminne archipelago (A) in Finland and (B) in southwestern Finland. (C) shows the study area and the islands where females were trapped and monitored (forested islands in green and open islands in pink). Tvärminne Zoological Station is indicated in yellow on all maps. Note that some of the surrounding islands are extensively monitored to catch and ring females (allowing the detection of potential change in breeding islands). Map tiles by Stamen Design, under CC BY 4.0. Data by OpenStreetMap, under CC BY SA.*

## 3.3. Field methods

### 3.3.1. Female eider monitoring

#### Trapping female eiders on their nest

The study eider colony has been extensively monitored since 1990. Between mid-May and early June – a period corresponding to the latter phase of the incubation in this eider colony and thus minimizing the risk of nest abandonment following disturbance (Bolduc & Guillemette, 2003) – three researchers carrying hand nets covered the monitored islands, walking 2-5m away from each other, to detect and catch incubating female eiders. All trapped females were ringed with a unique metal ring upon capture (since 1990) as well as a colour-ring combination allowing identification from a distance (since 2003).

The researchers attempted to trap all females breeding on the study islands. In the monitored area, female eiders are not ringed as ducklings, but when caught incubating for the first time. Hence, because the chronological age of females could not be determined, I instead used two – quantitative or qualitative – proxies: female minimum years of maternal experience (i.e., the number of years since ringing, **I, II, V, VI**) and female previous breeding experience (opposing inexperienced breeders caught breeding for the first time to experienced breeders, **IV**). These proxies are thought to be reliable since female eiders are philopatric to their breeding site (Öst et al., 2011) and trapping success probability is high (mean yearly trapping success of active nests in 2008-2022 ± SD = 0.68 ± 0.06; range: 0.60-0.77). In addition, trapped individuals were weighed and radius-ulna length was measured as a proxy of structural size.

During bird handling, nest coordinates were recorded with a handheld Global Positioning System (GPS) device and nest location was marked in the field with coloured tape. The number of eggs in the nest was counted and the entire clutch was weighed. Clutch size or mass were later used as proxies of initial energetic investment in reproduction (**I, II, IV-VI**). Using egg floatation to evaluate incubation stage (Kilpi & Lindström, 1997), I derived laying date and predicted hatching date for each clutch, on a basis of 26 days of incubation. Because population breeding phenology is likely to vary between years, I also calculated a relative laying date, by centring laying date around the yearly median laying date of the population, to assess whether a given female initiated laying earlier or later than yearly median breeding phenology (**V**).

Using bird weight, size and incubation stage, I derived two indices of body condition: one at trapping (**IV-VI**) and one at hatching (**I, II, IV**). The first body condition index was obtained by standardising the residuals of a linear regression of log-transformed body weight on log-transformed radius-ulna length. It corresponded to the instantaneous condition of the female – and associated body reserves – at the time of handling. However, because eider fast during incubation, they steadily lose weight (Criscuolo et al., 2000) and body condition at trapping is highly dependent on the number of days spent incubating (i.e., the number of days spent fasting) and does not allow comparison of females varying in incubation stage. Consequently, I calculated a second body condition index, based on estimated female weight at hatching, to allow a comparison of condition and body reserves of individuals sampled at different incubation stages. This body condition index has been built and used in previous studies carried out on Tvärminne eider population (Öst et al., 2008; Öst & Steele, 2010). Based on female weight at trapping, the number of days of incubation remaining before hatching, and a daily weight loss rate (derived separately for each year, and corresponding to the slope of the linear regression of log-transformed body mass on log-transformed incubation time and projected hatching date), I estimated female weight at hatching. As for the body condition index at trapping, the body condition index at hatching was obtained by standardising the residuals of a linear regression of log-transformed estimated body weight at hatching on log-transformed radius-ulna length.

## Monitoring reproductive success

Nests were revisited at predicted hatching date to assess hatching success (0: failure, 1: success; **III-VI**), based on the contents of the nest. Eiders are precocial breeders, and females leave the nest with ducklings within 24 hours of hatching (Öst & Bäck, 2003). If ducklings were found in the nest, the breeding attempt was considered successful. If no duckling was found in the nest, eggshells were examined to assess if ducklings had hatched or if the eggs had been depredated. Intact leathery membranes were characteristic of successfully hatched eggs, while bloody membranes, small egg pieces or missing eggshells indicated depredated eggs. Hatching was considered as successful if at least one duckling or one hatched egg was found.

If ducklings were present in the nest during nest revisit, they were weighed, and their tarsus length was measured. Duckling body condition was obtained by standardising the residuals of a linear regression of log-transformed body weight against log-transformed tarsus length and used as a proxy of offspring quality (**IV**). Precociality impeded us from monitoring additional parameters such as duckling growth, survival, or fledgling success. The analyses were therefore restricted to hatching success or hatched duckling quality.

## Monitoring untrapped females and assessing their breeding status

While individuals foregoing reproduction are elusive or absent from the breeding areas in many species (Gauthier et al., 2012; Souchay et al., 2014), it is not the case for eiders, allowing the monitoring of both breeding and non-breeding individuals. Following eider trapping, female eiders were thus monitored at sea with spotting scopes on a daily basis (two-six observers between late May and late June) to assess survival, breeding propensity and reproductive success of untrapped females (**III**). Colour-ring combinations were read to identify individuals. In addition, the number of ducklings and adult females accompanying the focal female were counted. Female eiders exhibit different parental care strategies: rearing their brood alone ('lone tenders'), pooling their ducklings to share brood-rearing duties with other females (forming 'brood-rearing coalitions' or 'crèches'), or abandoning their young to others after a short period of care (Öst, 1999; Öst et al., 2003). Solitary females without ducklings can also momentarily join brood-rearing coalitions (Kilpi et al., 2001). Therefore, females sighted in brood coalitions were followed until their status could be determined with certainty (Öst et al., 2003). At the end of the monitoring period, all observations of colour-ringed females were pooled to assess breeding status (breeder vs non-breeder). An individual was considered as skipping breeding if it was always seen as solitary – i.e., never seen associated with ducklings – or seldomly seen as non-tending, i.e., visiting a crèche.

## Survival, breeding propensity and hatching success

In order to build multi-event models incorporating uncertainty in reproductive success (**III**), I defined four possible biological states of female eiders in the population: successful breeder (SB), failed breeder (FB), non-breeder (NB), and dead female (†) (Figure 6). Using the data collected through the on-land and at-sea monitoring of trapped and untrapped females, observations of individually-marked females (i.e., capture-mark-recapture data) were categorised into five different events (i.e., types of observations): 0: female not observed; 1: female identified as a successful breeder (trapped female with nest fate known as successful or female seen at sea tending a brood); 2: female identified as a failed breeder (trapped female with nest fate known as failed, i.e., depredated or abandoned), 3: untrapped female observed at sea and identified as a non-breeder, 4: trapped female with unknown nest fate (Figure 6).

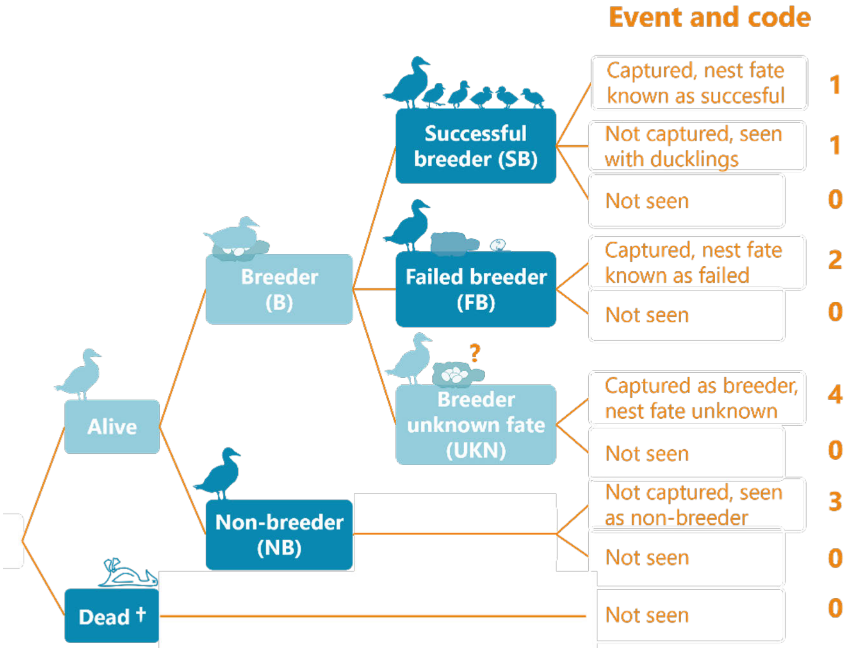

*Figure 6: Diagram of fate of adult female common eiders. The four possible states are presented in dark blue, and the five possible events described in orange, with their corresponding code.*

## 3.3.2. Behavioural and physiological traits reducing the risk of predation

### Risk-taking propensity

I used a standardised protocol based on a human approach to measure female eider flight initiation distance (FID), a widely used proxy of risk-taking propensity (Frid & Dill, 2002; Samia et al., 2016; Stankowich & Blumstein, 2005). The field team aimed to revisit nests the day preceding hatching to prevent any bias due to FID decreasing over the course of incubation (Albrecht & Klvaňa, 2004), as well as to limit the risk of nest abandonment or depredation due to nest disturbance and prolonged absence of the female from the nest (Bolduc & Guillemette, 2003; Stien & Ims, 2016). A researcher approached the nest, walking at a constant speed straight towards the focal incubating female and measured the distance at which the focal bird initiated escape (Seltmann et al., 2012) (**I,** Figure 7). If flight initiation distance was measured over several breeding seasons during a female's lifetime, the median value was calculated as a measurement of individual risk-taking (**III,** Figure 7). To further assess how individuals respond to repeated disturbance and use prior experience to adjust their behavioural response during a given breeding season, nests were revisited daily to measure FID until the female had left the nest with the ducklings (**II,** Figure 7).

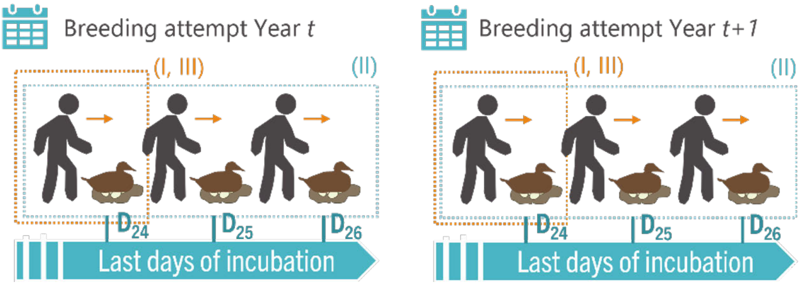

*Figure 7: Schematic representation of the standardised measurements of flight initiation distance used in the different Chapters, based on a human approach. Chapters I and III rely on the first measurement of flight initiation distance during a breeding event, while Chapter II uses multiple measurements within a breeding event.*

### Baseline corticosterone and prolactin levels

During handling, trapped females were sampled for blood from the ulnar vein (~1.5 mL) within 3 min following targeted capture on the nest. This ensured the obtention of baseline corticosterone (**IV, V**) and prolactin (**IV, VI**) levels (Angelier et al., 2010; Romero & Reed, 2005). Blood samples were brought back to the laboratory and centrifuged to separate blood serum from red cells. Centrifuged blood components were stored at −20°C until laboratory analyses.

Baseline corticosterone and prolactin levels were later assayed from blood serum by radioimmunoassay at the Centre d'Etudes Biologiques de Chizé (CEBC), as previously described (corticosterone: Lormée et al., 2003; Öst et al., 2020; prolactin: Criscuolo et al., 2002).

### 3.3.3. Perceived predation risk

The main predators of breeding female eiders that can be found in the study area are the white-tailed eagle and two invasive alien mammals: the American mink *Neogale vison* (formerly *Neovison vison;* Patterson et al., 2021) and the raccoon dog *Nyctereutes procyonoides* (Öst et al., 2018). Finnish American mink populations derive from individuals that escaped from fur farms (Kauhala, 1996), while raccoon dogs were intentionally introduced in Russia for fur hunting and naturally dispersed to Finland (Helle & Kauhala, 1991). Whereas white-tailed eagle abundance has been increasing over the past decades (Öst et al., 2022), American minks and raccoon dogs have been controlled since 2011 in the study area – thanks to an invasive alien predator removal scheme carried out on the study islands as well as some of the surrounding islands (Jaatinen et al., 2022). This removal scheme has permitted the maintenance of a low abundance of invasive alien predators, although American mink or raccoon dog individuals may still occur on some islands and years (Jaatinen et al., 2022). The ongoing effort to control mammalian predators makes of Tvärminne archipelago a distinct area, as these predators are, overall, on the rise in other parts of Finland (Nummi et al., 2019; Öst et al., 2018), and pose an important threat on duck species in the Nordic countries (Fox et al., 2015). Additionally, occasional predation by Eurasian eagle owls *Bubo bubo* and red foxes *Vulpes vulpes* has been observed in the study area (Ekroos, Öst, et al., 2012). While these avian and mammalian predators pose a threat to adults, they can also consume eider eggs (e.g., after a successful or unsuccessful predation attempt on the incubating female). However, egg predators such as hooded crows *Corvus cornix* or gulls *Larus spp.* are present in the study area and are the main predators responsible for nest depredation.

From an ecological perspective, predation risk on nests (hence, on offspring) has an indirect cost on breeding individuals, as opposed to predation risk on breeding individuals themselves, and may therefore trigger a different response (Ghalambor & Martin, 2000; Hua et al., 2014; Malone et al., 2017). This raises the need to consider them as separate mechanisms. Additionally, since prey respond to various cues of predator presence (Allen et al., 2022; Amo et al., 2011; Cockrem & Silverin, 2002) – including visual, auditory or olfactory contacts with predators – it is important to consider different metrics of predation risk. Therefore, I tested prey behavioural and physiological response to indices characterising both predation pressure and perceived risk, measured at different spatial scales. First, I evaluated individual nest concealment based on nest microhabitat (**I, VI**). Second, I measured indices of predation pressure on adults versus offspring at the scale of islands, based on depredation of females and nests (**I, II, IV, V**). Last, because indices based on effective predation events may be biased by prey behavioural or physiological compensation (e.g., nest site selection), I measured a yearly index of predator abundance and activity at the scale of the entire study area (**II, V, VI**).

### Nest microhabitat

Nest concealment (or nest cover), mirroring the amount of vegetation or rocks surrounding or covering the nest, was assessed for each nest by taking hemispherical photographs, aiming vertically from the centre of each nest cup. A 42-mm semi-fisheye lens mounted on an Olympus C-740 digital camera was used to take nest cover pictures, covering lateral and vertical nest surroundings (Öst & Steele, 2010). The proportion of vegetation or rocks covering the nest was extracted and used as a measure of nest concealment.

### Island-specific predation risk indices

First, I calculated a yearly index of island-specific predation risk on nests. For each island and year, this index was calculated by dividing the number of unsuccessful breeding attempts at the end of the monitoring by the number of nests whose hatching success (success or failure) was known. In addition, some females abandoned their nest, or incubated unviable eggs, leading to the failure of the breeding attempt.

Second, I calculated a yearly index of island-specific predation risk on adults, by dividing the number of predated females on a given island and year by the number of breeding attempts on this island and year . Dead females were counted when monitoring islands, and all carcasses were examined to assess whether the bird died from a predator attack or another causality (e.g., disease). Breeding attempts consisted of nests that had been depredated before eider monitoring started, active nests, and nests in which ducklings had already hatched when female monitoring was carried out.

### Large-scale index of white-tailed eagle abundance

In order to measure white-tailed eagle activity in the landscape, I relied on a yearly index of eagle abundance (hereafter, eagle index, Figure 8). This index was calculated as the average daily number of white-tailed eagles sighted at Hanko Bird Observatory (HALIAS, 59°49′N, 22°54′E, ca 20km away from the study area) between April 1 and June 15 every year, a period corresponding to eider breeding season (from the arrival of female eiders at the breeding area to the end of reproduction) (Öst et al., 2022). Following the observation protocol at HALIAS, the number of resident eagles (including both adults and subadults) was counted by one-six observers during a four-hour standardised period beginning at sunrise each day (Lehikoinen et al., 2008). Since white-tailed eagles, and especially non-breeding individuals, can travel long distances to forage (e.g., mean home range of non-territorial subadults: 180 km$^2$; May et al., 2013), this index is expected to reflect the temporal variation in white-tailed eagle abundance or activity in the study area, and none of the study islands – regardless of its isolation and forest cover – is devoid of eagle predation pressure.

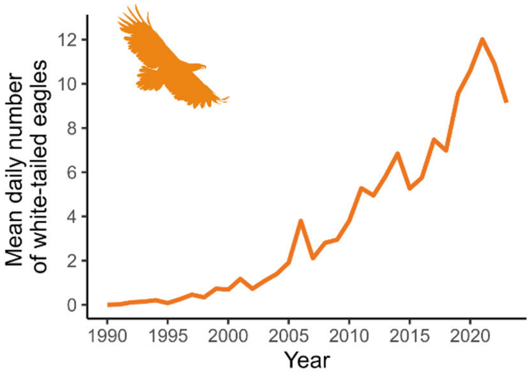

*Figure 8: Temporal variation in eagle index (average daily number of white-tailed eagle observations at HALIAS between April 1 and June 15 each year) in 1990-2023.*

## 3.3.4. Climatic conditions and food supply

Climatic conditions experienced during the winter, as well as during the pre-breeding period, are likely to have carry-over effects on reproductive decisions and performance (Descamps et al., 2010; Steenweg et al., 2022). Eiders rely on capital-income breeding strategies (Sénéchal, Bêty, & Gilchrist, 2011), meaning that females can use both endogenous reserves stored in the wintering grounds (Parker, 1990) and locally-ingested nutrients (Jaatinen et al., 2016; Sénéchal, Bêty, Gilchrist, et al., 2011) to produce eggs (Parker, 1990). I thus combined indices of winter severity, local meteorological data and an index of population-level body condition at the start of incubation in a principal component analysis (PCA) to summarise annual fluctuations in climatic conditions and body reserves (**VI**).

### Wintering and pre-breeding environmental conditions

In order to characterise winter severity, I used the winter North Atlantic Oscillation (NAO), a global climatic index. Winter NAO values are positively correlated with winter temperature, precipitation and storminess in northern Europe (Hurrell, 1995; Matulla et al., 2008), and NAO has previously been linked to female eider body condition in the subsequent breeding season (Descamps et al., 2010; Lehikoinen et al., 2006).

In addition, I relied on meteorological data collected at Tvärminne Zoological Station and provided by the Finnish Meteorological Institute (FMI) to evaluate weather conditions during eider breeding season. To this aim, I extracted daily average temperature and sum of precipitation between April 1 and June 15, a period corresponding to eider breeding season.

### Population-level body condition at the start of incubation

I also calculated an annual index of population-level body condition at the onset of incubation to characterise interannual variability in food supply. This index was obtained by averaging a body condition index estimated at the start of incubation, calculated for all monitored females on a given year. The calculation of individual body condition at the onset of incubation resembles that of body condition at hatching, except that I added the estimated mass lost during the days spent incubating to female weight at capture, instead of subtracting the estimated mass lost during the remaining days of incubation.

## 3.4. Data analysis

The statistical analyses were conducted using the software R (**I, II, IV-VI**), except for the capture-mark-recapture analysis in which the software E-SURGE and the program U-CARE were used (**III**).

### Repeatability

In Chapters **I, V** and **VI**, I measured within-individual repeatability in female eider behavioural (flight initiation distance) and physiological (baseline corticosterone and prolactin levels) traits. Repeatability measures the proportion of phenotypic variation that is due to differences between individuals (Bell et al., 2009; Nakagawa & Schielzeth, 2010), allowing an assessment of individual ability to cope with challenges. A high repeatability value suggests that individuals are consistent in the expression of their behavioural or endocrine phenotype, independently from current individual or environmental context. On the contrary, a low repeatability value may reflect high within-individual variation in the trait of interest, low among-individual variation in this trait, and/or high measurement error (Schoenemann & Bonier, 2018).

### (Generalised) linear mixed models

To study variation in risk-taking propensity (flight initiation distance; **I, II**), baseline corticosterone (**IV, V**) or baseline prolactin (**IV, VI**) levels in relation to a set of predefined intrinsic and extrinsic variables, I implemented generalised linear mixed models (GLMMs) with a Poisson error distribution (**I**), and linear mixed models (LMMs) (**II, IV-VI**). In the models investigating variation in reproductive success (**IV-VI**), I used GLMMs with a binomial error distribution to fit the nature of the data (binomial distribution, 0: failure, 1: success). Individual identity was included as a random effect to account for the pseudoreplication of the same individual over the study period (**I, II, V and VI**). Island identity (**I, IV**) and year (**V, VI**) were also included as random effects to account for the potential non-independence of individuals sampled on the same island or during the same breeding season. Model selection was performed according to Akaike's Information Criterion corrected for small sample sizes (AICc; Burnham & Anderson, 2002).

### Separation of within- and among-individual effects

One of the main goal of the studies was to assess the relative contributions of phenotypically plastic responses or individual-specific evolutionary fixed responses, respectively, in shaping prey response to fluctuating predation risk (van de Pol & Wright, 2009). When analysing long-term datasets – in which the same individual is sampled several times over changing individual or environmental conditions – I thus relied on a within-subject centring approach (Figure 9, van de Pol & Wright, 2009) to separate the effects of within- and among-individual variation in explanatory variables on flight initiation distance (**I**) and corticosterone (**V**). This method was not employed for the analysis of prolactin data (**VI**) because of the low within-individual repeatability of prolactin levels. Following the within-subject centring method, each selected explanatory variable was partitioned into its within- and among-individual components. The within-individual component shows how each repeated observation of the individual deviates from the individual's mean – suggesting individual plasticity – and is calculated by mean-centring values around individual means. The among-individual component shows how each individual differs from the population mean – highlighting the non-random distribution of phenotypes – and corresponds to the mean value for each individual.

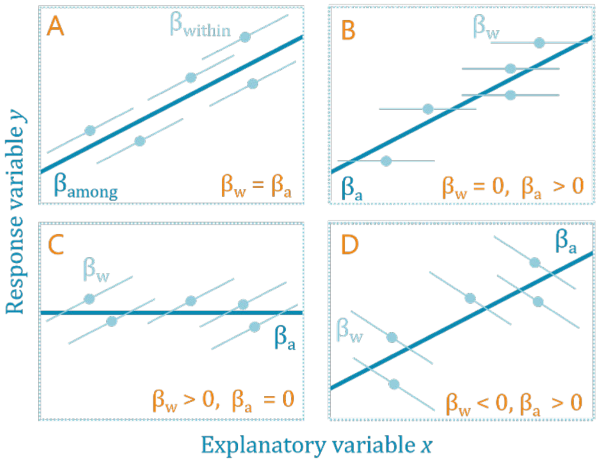

*Figure 9: Illustration of the different scenario of variation in within- and among-individual effects. The slopes of the within-individual effect ($\beta_{within}$) are depicted with thin light blue lines for five individuals, and the slope of the among-individual effect is depicted with a thick medium blue line. The different cases include (A) similar within- and among-individual effects, (B) among-individual effects only, (C) within-individual effects only, or (D) a combination of within- and among-individual effects. The figure is adapted from van de Pol and Wright, 2009.*

### Multi-event capture-mark-recapture model

I built a multi-event capture-mark-recapture model (MECMR; Pradel, 2005) to investigate variation in survival, breeding propensity and breeding success in relation to individual risk-taking (**III**), using observational data including individuals with uncertain breeding success on one or more occasions. The model considered the four states (SB, FB, NB and †) and five events associated with these states previously described (see 3.3.1 and Figure 6). Relying on the MECMR model, I modelled the transition of females in state *i* at time *t* to state *j* at time *t+1* by estimating the following demographic parameters: initial state probability (probability that an individual is in state *s* when first encountered at time *t*), apparent survival probability (probability that an individual alive at time *t* survives until time *t+1*), transition probability of remaining or becoming a breeder at time *t+1* (i.e., breeding probability), breeding success probability, recapture probability (probability that an individual in state *s* at time *t* is encountered at time *t*) and assignment probability (probability that the state of an individual is observed given that it is in state *s* at time *t* and encountered at time *t*). Females were initially caught breeding on the islands. Therefore, the probability of being encountered for the first time as a breeder (B) was fixed to 1, and initial state could be SB or FB.

I first verified that the data met model assumptions by performing goodness-of-fit tests. Then, I followed a step-down approach (Lebreton et al., 1992) to select the model with the lowest Akaike's information criterion adjusted for overdispersion and small sample size (QAICc; Burnham & Anderson, 2002) as the 'best' initial model. More specifically, I tested for state-dependency (breeder or non-breeder) in survival, breeding propensity and reproductive success (**III**). After model selection, I tested for (1) temporal variation in survival, breeding propensity and reproductive success, (2) a link between these demographic parameters and flight initiation distance during (2a) the entire study period and (2b) three consecutive time periods differing in predation pressure.

# 4. Results and Discussion

In this dissertation, I used a long-term individual-based monitoring of breeding female common eiders facing a drastic change in predation pressure to shed light on the overlooked impact of recovering populations of native avian predators on seabirds. I improved our understanding of prey behavioural (**I-III**) and physiological (**IV, VI**) responses to fluctuating predation threat. Specifically, I showed that prey adjusted their behaviour to the risk of predation, both within (**II**) and among breeding events (**I**), with consequences of interindividual variation in risk-taking phenotypes on fitness (**III**). I also found that prey physiological traits were plastic (**V-VI**). Increasing predation risk was associated with a downregulation of baseline corticosterone levels (**IV-V**) – positively correlated with reproductive investment – while elevated baseline prolactin levels – associated with parental effort – promoted hatching success under constraining environmental (e.g., rising predation threat) or internal state (**V**). Overall, concomitantly accounting for variation in predation risk, but also in internal state and other environmental variation is key to assessing the ability of prey populations to cope with a changing environment and persist in disrupted ecosystems.

## 4.1. Population-level changes over the study period

### 4.1.1. A fluctuating predation regime

The rapid recovery of sea eagle populations can be regarded as one of the most remarkable conservation achievements of our time (Hipfner et al., 2012; Stier et al., 2016), and this large-scale predation regime shift was apparent for all predation risk indices in my thesis. Over the 15-year study period, I observed a temporal increase in eagle index (Figure 10A) – a proxy of white-tailed eagle abundance and activity –, that was accompanied by an increase in island-specific predation risk on adult female eiders (Figure 10B) and their nests (Figure 10C). Interestingly, despite the proximity of the study islands, predation risk on adults and nests was additionally subject to spatial variation during the study period (**I**).

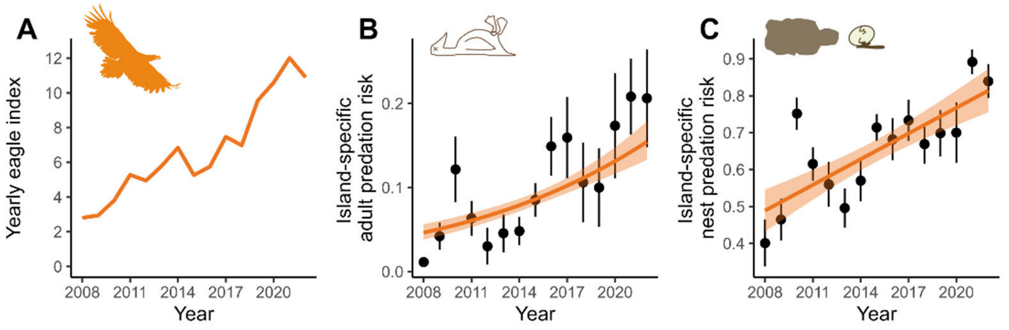

*Figure 10: Temporal increase in (A) yearly eagle index (mean daily number of white-tailed eagles during the breeding season of common eiders), (B) island-specific adult predation risk and (C) island-specific nest predation risk over the study period (2008-2022). Dots correspond to yearly estimates and bars account for standard errors. Regression lines and their 95% confidence interval are presented in orange.*

Increasing predation risk on adults reflects rising predation pressure from white-tailed eagles, as well as occasional occurrence of invasive alien predators such as American minks or raccoon dogs – despite the eradication scheme started in 2011 (Jaatinen et al., 2022) – whereas increasing nest predation risk reflects predation pressure from both primary predators of adults (i.e., eagles, minks or raccoon dogs) and opportunistic egg predators (i.e., crows or gulls). Since invasive alien predators are regulated (Jaatinen et al., 2022), gull populations are declining (Hario & Rintala, 2016; Hermansson et al., 2023; Langlois Lopez et al., 2023) and crow populations are likely to be stable, including in the study area (Hermansson et al., 2023), increasing nest predation risk is likely driven by recovering white-tailed eagles and their disturbance effect on seabird colonies (Hentati-Sundberg et al., 2023; Hipfner et al., 2012). Indeed, through successful or unsuccessful predation attempts on incubating adults, eagles offer egg specialist predators an opportunity to predate on nests in the absence of the parent (Hentati-Sundberg et al., 2021; Mehlum, 1991; Swennen et al., 1993).

Overall, the ongoing change in predation regime creates a major ecological change for the study eider population and, more generally, for seabirds. Such a rapid recovery of local white-tailed eagle populations is likely to exert top-down control on prey populations (e.g., altering breeding phenology and synchrony or fledgling production; Öst et al., 2022) that exceeds the influence of other environmental drivers, such as abiotic climatic variation (Öst et al., 2022). Since organisms are thought to cope with challenging conditions through the modification of morphological, behavioural, physiological or life-history traits (Jacobs & Wingfield, 2000; Sheriff & Thaler, 2014; Wingfield et al., 2011), this change in predation regime is predicted to lead to plastic responses and phenotypic selection, as I detail in the chapters below.

### 4.1.2. Temporal trends in female fitness

Demographic parameters such as survival rate, breeding propensity and reproductive success are key to understanding population dynamics (Lebreton & Clobert, 1991; Wilson et al., 2016), especially because a slight decrease in adult survivorship or reproductive success may have long-lasting effects on population growth rate (Lebreton & Clobert, 1991). In addition, breeding propensity is considered to be among the least-understood reproductive parameters shaping annual productivity in iteroparous species (Nicol-Harper et al., 2021; Reed et al., 2004). Interestingly, I found that female survival and reproductive success were stable during 2008-2022, despite the changing predation regime (**III,** Figure 11A and Figure 11C). In the meantime, breeding propensity decreased (**III,** Figure 11B), likely reflecting a life-history response to reduce the risk of predation on incubating females, since individuals are more vulnerable to predators during reproduction (Ekroos, Öst, et al., 2012; Lima, 2009; Magnhagen, 1991; Ramula et al., 2018).

In accordance with other eider populations, adult survival probability was high (estimate, E = 0.85, **III**; mean adult survival rate across several eider populations: 0.87; Nicol-Harper et al., 2021). As expected from a long-lived species with a high annual survival rate, adult survival seemed canalised against temporal fluctuations (Gaillard & Yoccoz, 2003; Sæther & Bakke, 2000), remaining constant over the study period despite increasing predation pressure. However, breeding propensity decreased over the study period. Average breeding propensity was estimated at 0.61. This value is below the one measured by a recent examination of breeding propensity across eider populations (0.72; Nicol-Harper et al., 2021), although still fitting estimates from various eider populations (ranging from 0.45 to 0.92; Nicol-Harper et al., 2021, 2023). Such a drop in breeding propensity likely reflects a response to the current extreme predation regime in the study area, especially given that engaging in reproduction is associated with higher vulnerability to predators (Magnhagen, 1991). This finding thus underlines the key role of intermittent breeding strategies as a response to increasing predation pressure. Indeed, by decreasing breeding propensity under high predation risk, females may balance the cost and benefits of engaging in reproduction during the current year, enhancing their own survivorship and postponing reproduction to engage in future breeding opportunities when conditions become favourable. This may overall translate into a maximisation of survival and offspring production. In agreement with this idea, hatching success was also buffered against temporal fluctuations. In addition, as reproduction is associated with higher vulnerability to predators (Candolin, 1998; Magnhagen, 1991), skipping breeding may enhance survivorship. However, a high incidence of non-breeding correlates with low offspring production, which may have significant and long-term effects on demography, as illustrated by the temporal decrease in fledgling production (Öst et al., 2018), recruitment (Öst et al., 2018), and the ageing of the pool of breeding females in the study area (**I**, Öst et al., 2022).

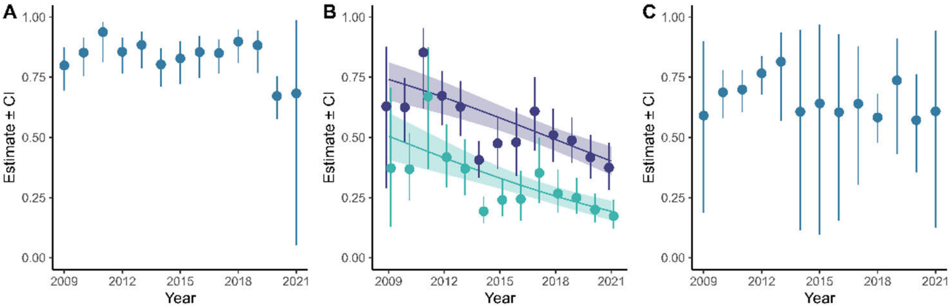

*Figure 11: Temporal variation in female common eider (A) survival, (B) breeding propensity and (C) hatching success over the study period (2009-2022). Dots correspond to yearly estimates and bars account for yearly confidence intervals (CI). Breeders and non-breeder combined are presented in medium blue in (A) and (C), while breeders are presented in dark blue and non-breeders light blue in (B). Regression lines are presented for the significant temporal trends with their 95% confidence intervals. The figure is adapted from Chapter III, and only includes females with known flight initiation distance.*

Noteworthy, these results may be confounded by methodological caveats. Indeed, it is important to note that breeding propensity in our population may be slightly underestimated as breeding failure prior to the onset of monitoring may lead to erroneous categorisation of failed breeders as non-breeders (cf., **III**). Consequently, the observed temporal decrease in breeding propensity may additionally mask a temporal increase in nest failure, supported by the known temporal decrease in fledgling production (Öst et al., 2018). Accordingly, a reduction of breeding propensity or reproduction success could equally lead to a reduction of overall fitness in the population.

Additionally, and non-exclusively, variation life-history decisions may reflect changes in individual quality. Indeed, I found that an individual skipping one reproductive event had a higher chance of also skipping the following one (mean breeding probability: breeder, E ± SE = 0.57 ± 0.02; non-breeder, E ± SE = 0.34 ± 0.03, **III**) and a lower survival probability (mean survival probability: breeder, E ± SE = 0.88 ± 0.01; non-breeder, E ± SE = 0.81 ± 0.02, **III**). Increasing predation risk could thus select against lower-quality individuals. Supporting the idea of among-individual differences in individual quality (Hanssen et al., 2003, 2022), female body condition is repeatable within individuals (**I**, Jaatinen & Öst, 2011), and so is hatching success (Öst & Steele, 2010) in the study area. The absence of a temporal decrease in adult survival or hatching success despite increasing predation pressure on adults and their nests suggests that eiders can, at least to a certain extent, compensate for such risk and adjust their behaviour, physiology or life-history decisions. These intriguing results hence raise the need for a better understanding of the mechanisms driving adjustment of breeding decisions and breeding investment under a changing predation regime.

### 4.1.3. Changes in female nest site, state and clutch size

Interestingly, eider nest site preferences have changed over the past decades, at both macro- and microhabitat scales. Indeed, while eiders used to predominantly nest on the open rocky islands of the outer archipelago, there are now more common close to mainland and on forested islands. This large-scale change in breeding habitat preferences is thought to reflect predator-induced selection processes, especially due to higher breeder mortality and low reproductive success on these open islands (Ekblad, 2022; Ekroos, Öst, et al., 2012; Kurvinen et al., 2016). In addition, at the microhabitat scale, nest concealment steadily increased over the study period (**I,** Figure 12A). In light of the high within-individual repeatability of nest cover (**I,** R ± SE = 0.71 ± 0.02), this also suggests selective processes by visually hunting white-tailed eagles, especially when considering that survival is higher on forested islands (Ekroos, Öst, et al., 2012). In addition to variation in nest microhabitat, clutch size decreased between 2009 and 2022 (**I,** Figure 12B). This finding is in agreement with the life-history prediction that an increase in predation risk should favour decreased investment in current reproduction (Eggers et al., 2006; Travers et al., 2010; Zanette et al., 2011). The response to increasing predation risk may thus have taken a subtle form, being reflected in a population-level decrease in fecundity (through clutch size reduction, **I**) rather than in lower hatching success (**III**). Additionally and non-exclusively, this finding could also be linked to an increase in partial nest depredation by egg-eating predators (Erikstad et al., 1993; Öst et al., 2008).

In accordance with a previous study carried out on this eider population (Öst et al., 2022), body condition of breeding females increased over the study period (**I,** Figure 12C). Two non-mutually exclusive hypotheses could explain this trend. First, as female body condition and survival are positively correlated (Ekroos, Öst, et al., 2012) and as female body condition is repeatable within individuals (**I,** R ± SE = 0.48 ± 0.04; Jaatinen & Öst, 2011), selective disappearance of individuals in overall poorer condition under elevated predation risk could explain this trend. This hypothesis follows the state-dependent safety model (Luttbeg & Sih, 2010), yielding the prediction that individuals in good condition are less likely to be killed by predators. Second, given the observed population-level decrease in breeding propensity (**III**) and considering the energetic cost of fasting during incubation (with females losing up to 46% of their body mass; Parker, 1990), females in poor condition may opt to skip breeding when risks outweigh benefits. The finding of a coincident ageing of the pool of breeding females (**I,** Figure 12D; Öst et al., 2022) is in agreement with this idea. Under elevated predation pressure, only females with low residual reproductive value (e.g., older ones) may choose to engage in reproduction under high predation risk, leading to an apparent population ageing. Younger ones may either refrain from engaging in reproduction or fail or abandon their breeding attempt at an early incubation stage. Additionally and non-exclusively, the ageing of the population could result from a decrease in recruitment, in particular through a decrease in offspring productivity (Öst et al., 2022) or a reduction of first-year survival (Tjørnløv et al., 2019). While data supporting the latter is currently lacking, evidence from the study area suggests that the survival rate of ducklings during the first weeks of their life is extremely low due to elevated predation pressure from groups of white-tailed eagles (Öst et al., 2018, 2022).

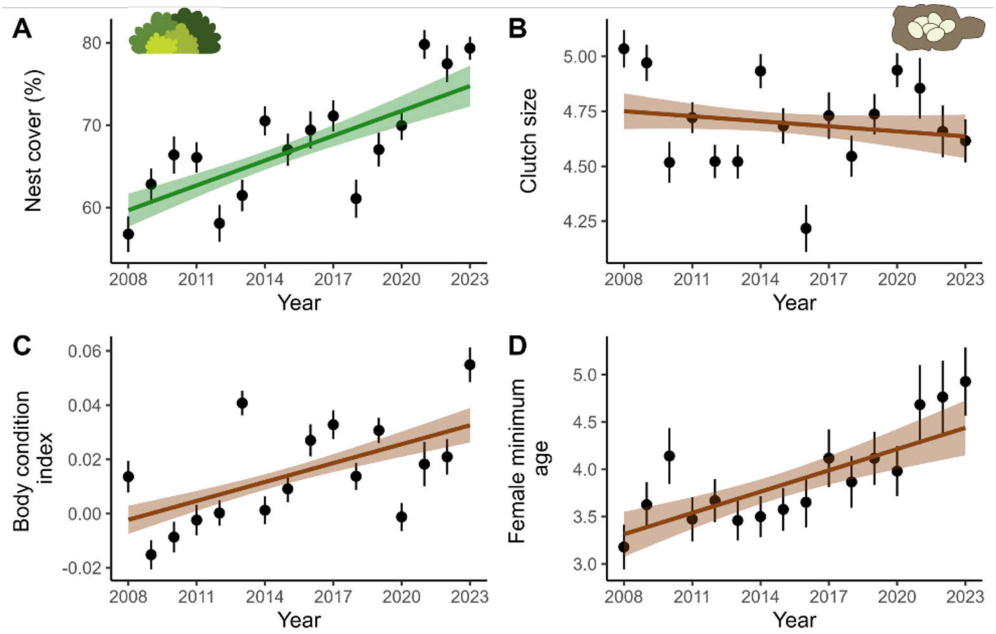

*Figure 12: Temporal variation in female common eider (A) nest cover, (B) clutch size, (C) body condition index (at hatching) and (D) minimum age over the study period (2008-2023). Dots correspond to yearly estimates and bars account for standard errors. Regression lines and their 95% confidence interval are presented in (A) green and (B-D) brown. Adapted from Chapter I.*

These observations, coincident with a changing predation regime, suggest that non-exclusive mechanisms such as plasticity (e.g., in nesting habitat or clutch size) and natural selection (e.g., on breeding habitat, female age or condition) are likely to occur in the study population. The temporal trends in population-level age, body condition or breeding habitat may explain some of the observed variation or consistency in demographic parameters over the study period. In particular, the increase in nest concealment, concurrent with the rise in predation pressure, may compensate the potential decrease in survival associated with higher predator abundance, as females breeding under vegetation cover also have higher chances of survival (Ekroos, Öst, et al., 2012). Additionally, older females or those in better condition are predicted to display higher reproductive investment (Curio, 1983), therefore increasing the probability of successful hatching of the clutch (Proaktor et al., 2007). The temporal increase in age and body condition may thus compensate potential negative effects of increasing predation pressure on hatching success. To improve our understanding of the proximate and ultimate mechanisms driving prey response to increasing predation risk, I further explored plastic phenotypic adjustments and selective processes in behaviour (flight initiation distance) and physiology (baseline corticosterone and prolactin levels).

## 4.2. Behavioural response reflected in variable risk-taking propensity

An increase in predation risk should decrease prey risk-taking propensity (Berger et al., 2007; Cooper Jr et al., 2009), especially in long-lived individuals that are predicted to favour survival over reproduction (Roff, 1993; Stearns, 1992). Intriguingly, however, I found that population-level flight initiation distance slightly but significantly decreased over the study period (2008-2019) (**I**, Figure 13), mirroring an increase in risk-taking. This trend was even stronger when extending the study period until 2023 (Figure 13). This intriguing result can be explained by the state-dependency of flight initiation distance and particularly by concurrent changes in age and body condition of breeding females (see 4.2.1).

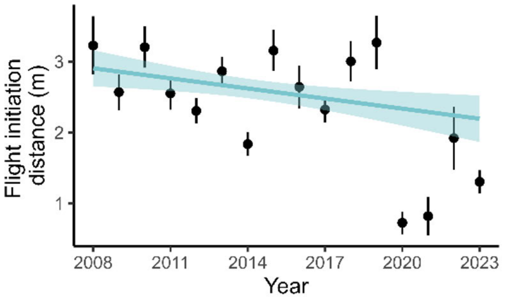

*Figure 13: Temporal variation in population-level female common eider flight initiation distance (FID) during incubation in 2008-2023. Estimates in 2020 and 2021 are unreliable as only a selection of older females were sampled. Consequently, these years were not included in the computation of the temporal trend and yearly population-level FID. Dots correspond to yearly estimates and bars account for standard errors. The regression line and its 95% confidence interval are presented in blue. Adapted from Chapter I.*

In addition, individual risk-taking propensity was significantly repeatable (repeatability, R ± SE = 0.40 ± 0.05). This moderate value is at the lower end of published repeatability estimates, classically comprised between 0.34 and 0.88 (Cabrera et al., 2017; Carrete & Tella, 2010; de Jong et al., 2021; Møller & Garamszegi, 2012; Seltmann et al., 2012; Strong et al., 2017). Importantly, it gives way to both potential within-individual plasticity in antipredator behaviour and individual natural selection on fixed average risk-taking behaviour.

### 4.2.1. Risk-taking propensity and individual characteristics

Older females were more prone to take risks (i.e., displayed shorter flight initiation distances) than younger ones (**I;** Figure 14). As the pool of breeding females has been ageing over the study period (**I;** Öst et al., 2022), population-level variation in age are likely to translate into a population-level reduction of flight initiation distances. The positive association between female age and risk-taking was found to be driven by plasticity, as females flexibly reduced flight initiation distance as they aged. The observed age-dependent adjustment of risk-taking is in agreement with the ‘restraint hypothesis” (Curio, 1983), stating that older breeders should be more prone to take risks to invest in current reproduction as they grow older and their residual reproductive value diminishes (due to scarcer opportunities for future reproduction). This theory is indeed supported by numerous studies (Candolin, 1998; Clark, 1994; de Jong et al., 2021; Moschilla et al., 2018).

Could this response be explained by a gradual dampening of antipredator response as incubating females gain experience and learn that approaching humans are harmless instead? Resolution of this question preferably requires repeated measurements of risk-taking behaviour collected in the short-term to circumvent potential age effects. To this end, I investigated the response of females subject to repeated daily human approaches during the last days of incubation (**II**). Females did not consistently habituate – i.e., reduce flight initiation distance – when confronted with repeated approaches, but rather tended to sensitise (**II**) – i.e., advance escape. Importantly, individuals exhibited different responses, ranging from habituation (i.e., progressive decrease in flight initiation distance) to sensitisation (i.e., progressive increase in flight initiation distance), and including an absence of modification of the antipredator response (i.e., constant flight initiation distances over approaches) (**II**). As it is unlikely that incubating females would habituate to humans over a long period of time (years) but not over a short period of time (days), these findings refute the hypothesis of consistent habituation of individuals to humans as they age and gain experience with the intimidating but harmless researchers. However, despite the absence of generalised habituation, older females and those in better condition were more prone to habituate to short-term disturbance (**II**), a result thought to reflect a higher investment in the current breeding event.

Moreover, females in better condition were more willing to take risks (i.e., displayed shorter flight initiation distances, **I**; Figure 14). Intriguingly, this response was not associated with flexible adjustments of flight initiation distances to individual body reserves, but with a predominance of risk-taking females with good body condition in the population. As female body condition

– estimated at hatching to allow comparison of individuals independently from incubation stage – was repeatable within individuals (**I**), this result suggests high interindividual variation in quality, which could be an important determinant of risk-taking behaviour. Individuals that are healthier or in better condition tolerate closer approaches from predators (Kenward, 1978; Martín et al., 2006), as also supported by this thesis (**I**). Good body condition may also be associated with enhanced flight ability and higher chances of successfully escaping from a predator attack (the 'state-dependent safety model'; Luttbeg & Sih, 2010; Tablado & Jenni, 2017). Indeed, females that are overall in poorer body condition may be more likely to reach phase III of fasting, during which the atrophy of flight muscles is increasingly observed (Cherel et al., 1988), which may conceivably impair flight performance during predator attacks. Risk-avoiding females in poorer condition may thus be more prone to skip breeding – notably due to lower survival probability (Ekroos, Öst, et al., 2012) – and prioritise self-maintenance over investment in reproduction.

The negative association between age, body condition and flight initiation distance, coincident with a temporal ageing and increase in body condition of the pool of breeding females, may therefore explain the observed slight downward trend in flight initiation distance – mirroring a temporal increase in population-level risk-taking.

### 4.2.2. Risk-taking propensity and predation risk

Even though I did not find evidence of a population-level predator-induced decrease in risk-taking (i.e., an overall increase in flight initiation distance), the investigation of individual-level responses revealed that females still reduced risk-taking under higher predation threat (**I**). Indeed, female eiders responded to rising predation risk by increasing flight initiation distance (**I**; Figure 14), a result in agreement with previous studies (Berger et al., 2007; Cooper Jr et al., 2009; Zamora-Camacho et al., 2018).

Importantly, this thesis provides among the first evidence that the mechanisms shaping behavioural responses to increasing predation risk can depend on the target of predators: incubating females or their eggs. Accordingly, individuals flexibly adjusted their flight initiation distance to the perceived risk of predation on themselves (island-specific adult predation risk) but not on their nest, by increasing flight initiation distance when nesting on an island with higher adult predation risk (**I**). Such a plastic response towards increasing threat on adults is in agreement with life-history trade-offs (Williams, 1966), as long-lived parents – whose high survival is thought to be canalised against environmental fluctuations – should preferentially display flexibility in responses enhancing their own survivorship, rather than that of their offspring (Gaillard & Yoccoz, 2003; Hamel et al., 2010). On a short-term basis, incubating females confronted with repeated human approaches during a breeding event also adjusted their behaviour over encounters. However, when nesting in a more dangerous environment, they were instead more prone to habituate to repeated exposure to a non-life-threatening stimulus (**II**). At first sight, this result seems contradictory to the long-term (i.e., over breeding seasons) adjustments of flight initiation distances in response to variation in prevailing predation risk. However, it is important to remember that a human approach, although stressful, is not life-threatening, as opposed to a real predation attempt. Thus, in risky environments, associated with high chronic stress, prey individuals are thought to benefit from dampening their stress sensitivity to benign cues, in order to maintain investment in the current breeding event (the 'risk allocation hypothesis'; Ferrari et al., 2009). This leads to a waning of antipredator responses to repeated harmless stimuli, mirrored through short-term habituation, and potentially reducing the risk of reproductive failure due to excessive flightiness (Sirot, 2010).

In addition, females displaying on average longer flight initiation distances were predominant on islands with high nest predation risk (**I**), suggesting the occurrence of selective processes on risk-taking phenotype. Breeding on open, conspicuous, nest sites – where the risk of predation is higher (Ekroos, Öst, et al., 2012; Öst et al., 2018) – was also associated with longer flight initiation distances (**I**), and sensitisation to repeated human approaches (**II**). On the contrary, females breeding in concealed nest sites tolerated a closer approach before fleeing (**I**) and were more prone to display short-term habituation (**II**), likely benefiting from the crypsis and protection offered by vegetation cover. Such habitat-dependent strategies suggest that eiders may be able to assess the effectiveness of their crypsis and adjust their flight decisions accordingly (Cooper & Sherbrooke, 2010). As higher stress sensitivity (associated with risk-avoidance or sensitisation) has previously been linked with a lower risk of nest depredation under high predation pressure on open habitats (Jaatinen et al., 2014), the progressive sensitisation of flight responses on open islands is likely adaptive. Further investigation showed that females did not adjust their behaviour to the degree of concealment of their nest, but rather settled in microhabitats matching their behavioural profile – consistent with the 'personality-matching hypothesis' (Holtmann et al., 2017). Accordingly, there was a predominance of individuals displaying short flight initiation distances in concealed nests and no evidence for within-individual plastic adjustment of behavioural response to varying nest microhabitat. The finding that females tended to settle in similar nest sites over breeding attempts – as there was low within-individual variance in nest cover over years (**I**) – also strengthens the idea that individuals may show preferences for specific features of their nesting sites.

Overall, these findings contribute to improving our understanding of adjustments of a behavioural antipredator response to a fluctuating predation regime, by highlighting a predation-induced reduction of risk-taking at the individual level. In addition, they shed light on the importance of considering the effects of both within- and among-individual variation in predation risk on adults and offspring in shaping individual risk-taking propensity.

### 4.2.3. Risk-taking propensity and fitness

Although flight initiation distance was not highly repeatable within individuals (**I**), it was still repeatable enough to be implemented in multi-event capture-mark-recapture models. I thus investigated the association between individual risk-taking (flight initiation distance) and fitness components (survival, breeding propensity and reproductive success) in Chapter **III**. There, I assigned lifetime median flight initiation distance as a fixed value of risk-taking to each female whose flight initiation distance had been measured during the study period.

It is predicted that phenotypic variation is maintained in a population because it represents different ways of solving life-history trade-offs (Wolf & Weissing, 2010). Therefore, I predicted that risk-avoiding females would prioritise survival over reproduction, while risk-taking females would put a greater emphasis on the current breeding event. Contrary to this expectation, risk-avoiding females (displaying longer flight initiation distances) were, overall, characterised by a tendency towards lower breeding success probability, but also a tendency towards lower survival rate and a reduced breeding propensity (**III**; Figure 14). This result suggests that individuals displaying longer flight initiation distances have a lower fitness than individuals displaying longer flight initiation distances, perhaps because they are of lower quality. Intriguingly, such difference in fitness value did not translate into a selective disappearance of risk-averse individuals from the population, as my results only indicate a mild population-level increase in risk-taking over the study period (**I**). However, by considering the context-dependency of these relationships, I was able to shed light on these seemingly counterintuitive findings, as variation in predation risk modified the association between life-history traits (in particular survival rates) and individual risk-taking.

Indeed, under relaxed predation pressure (i.e., during the first years of the study, 2009-2013), risk-avoiding females bred less often than risk-taking females and tended to have a higher hatching success but had a lower survival probability (**III**). Given that risk-avoiding phenotypes have been associated with lower body condition or breeding experience (**I**), this likely reflects the higher cost of reproduction on low-quality or inexperienced females, leading to lower survival and breeding propensity. Risk-averse individuals may thus only engage in reproduction under favourable environmental conditions to maximise reproductive output, resulting in a tendency towards higher reproductive success. Interestingly, this pattern was reversed under higher predation pressure (i.e., during the last years of the study, 2018-2022) as risk-avoiding phenotypes tended to have a lower hatching success than risk-taking ones (**III**). This last result is in line with predicted life-history trade-offs (Williams, 1966), as it suggests that risk-avoiding individuals favour their own survivorship over that of their offspring. Yet, while breeding propensity was still lower in individuals displaying longer flight initiation distances (likely postponing reproduction to breed if intrinsic or extrinsic conditions are more favourable), survival appeared independent from risk-taking under high predation threat (**III**). In spite of their lower-quality (associated with reduced survival), females displaying longer flight initiation distances may perform better at escaping predation than those displaying shorter flight initiation distances under elevated predation pressure. Overall, the fitness costs and benefits of the different phenotypes (in a gradient of risk-taking) may converge to an equilibrium, explaining the absence of strong phenotypic selection in the population (although a mild increase in risk-taking was observed through a population-level decrease in flight initiation distance, **I**).

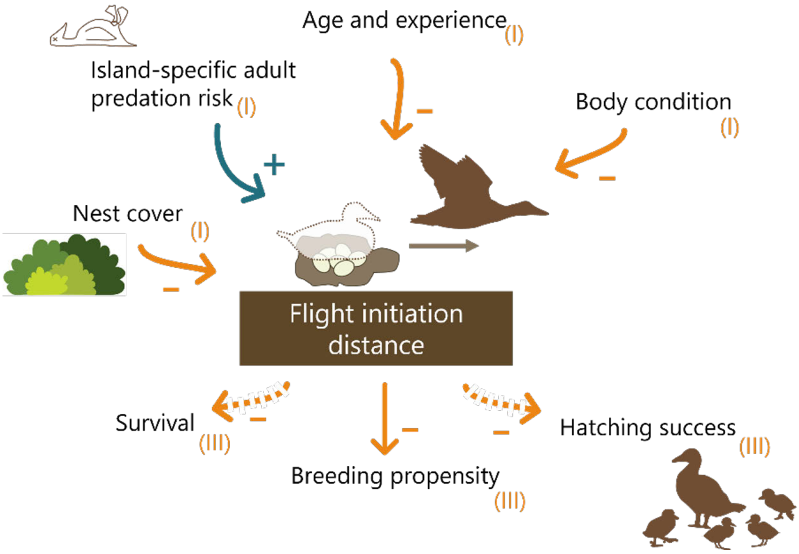

*Figure 14: Summary of the predictors of variation in female common eider flight initiation distance (over breeding attempts) and lifetime fitness consequences of among-individual variation in flight initiation distance (i.e., in risk-taking). Positive associations are depicted with medium blue arrows are negative associations are presented in orange. Significant effects are presented with plain arrows and nearly significant results with dashed arrows. Corresponding Chapters are indicated in orange. To simplify, only general fitness consequences (over the entire study period, independently from the changing predation regime) are presented.*

## 4.3. Physiological responses to predation risk mediated by baseline corticosterone

Over the study period (2009-2022), the increase in predation pressure was accompanied by a decrease in population-level baseline corticosterone levels (**V**, Figure 15). Baseline corticosterone levels were significantly but weakly repeatable within individuals (R ± SE = 0.16 ± 0.03), in accordance with other studies (reviewed in Schoenemann & Bonier, 2018; Taff et al., 2018). This result suggests a low degree of consistent among-individual differences and underlines that baseline corticosterone levels may be highly plastic and context-dependent (Jaatinen et al., 2013; Schoenemann & Bonier, 2018; Taff et al., 2018).

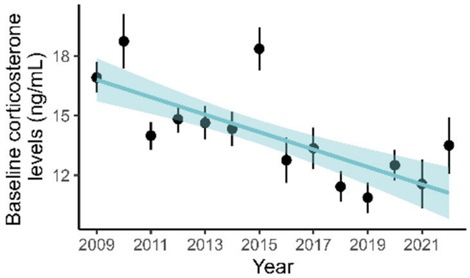

*Figure 15: Temporal variation in population-level female common eider baseline corticosterone levels (2009-2022). Dots correspond to yearly estimates and bars account for standard errors. The regression line and its 95% confidence interval are presented in blue. Adapted from Chapter V.*

### 4.3.1. Baseline corticosterone and reproductive investment: validation of the corticosterone-adaptation hypothesis

In agreement with the 'corticosterone-adaptation hypothesis' (Bonier et al., 2009), I highlighted positive correlations between baseline corticosterone levels of incubating female eider and reproductive investment (**IV, V;** Figure 16).

To begin with, although clutch weight and size explained a small percentage of the variance in baseline corticosterone levels, the relationship between clutch size and baseline corticosterone levels was significant (**IV, V**). Female baseline corticosterone levels were positively associated with clutch weight (**IV**) and size (**V**). Clutch weight or size is correlated with reproductive value (Hanssen et al., 2022) as well as initial energetic investment in reproduction (Hanssen et al., 2003; Jaatinen et al., 2013). Given that elevated baseline corticosterone levels can be positively related to incubation commitment (Ouyang, Muturi, et al., 2013) and nestling quality (Bonier et al., 2011; Rivers et al., 2017), this link between corticosterone and clutch size or weight suggests that females displaying higher baseline corticosterone levels make a higher investment in the current breeding event. Importantly, and in agreement with this idea, individual females showed a plastic increase in baseline corticosterone levels when incubating larger clutches (within-individual effect, **V**). Additionally but non-exclusively, this elevation of baseline corticosterone levels could mirror the higher allostatic load or metabolic cost of incubating a larger clutch (Jimeno et al., 2020; Tinbergen & Williams, 2002; Williams, 1996) and maintaining an optimal incubation temperature for embryo development (Erikstad & Tveraa, 1995). The remaining unexplained variance after accounting for the effect of clutch size (or weight) in predicting baseline corticosterone levels suggests that other intrinsic or extrinsic variables drive baseline corticosterone levels.

Indeed, female baseline corticosterone levels were also positively correlated with age and breeding experience (**IV, V**), paralleling results from previous studies (Angelier, Shaffer, et al., 2006; Carlitz et al., 2022). Importantly, this response was explained by a within-individual increase in baseline corticosterone levels with ageing, followed by a decrease in corticosterone levels in the oldest breeders. There is ample evidence that reproductive performance increases with age and experience before declining at very old ages (Angelier, Shaffer, et al., 2006; Angelier, Weimerskirch, et al., 2007; Bowen et al., 2006; Lemaître & Gaillard, 2017; Noreikienė et al., 2021). Likewise, this result suggests physiological senescence in corticosterone levels – a response only seldom demonstrated by studies carried out in the wild (but see Angelier, Shaffer, et al., 2006).

### 4.3.2. Baseline corticosterone and predation risk

Following the predictions of the 'corticosterone-adaptation hypothesis' (Bonier et al., 2009) regarding the link between corticosterone and environmental challenges, increasing predation pressure was associated with decreasing baseline corticosterone levels (Figure 16). My short-term study, based on one year of data, showed that females incubating on islands characterised by elevated nest predation risk displayed lower baseline corticosterone levels than females breeding on safer islands (**IV**). The long term-study, based on 14 years of data, supported and even refined these results. Females indeed displayed lower baseline corticosterone levels when breeding on open islands characterised by higher island-specific adult predation risk, and increasing abundance of white-tailed eagles (at the scale of the entire study area) was associated with a decrease in female baseline corticosterone levels (**V**).

Further investigation suggested that observed endocrine responses to increasing predation pressure were driven by flexible adjustments of baseline corticosterone levels to the risk of predation, rather than phenotypic selection. As for the assessment of behavioural responses to predation (**I**), females showed plasticity in responses promoting their own survival, rather than that of their offspring. This is in line with the life-history trade-off predicting that long-lived species with higher residual reproductive value should prioritise survival over reproduction (Gaillard & Yoccoz, 2003; Hamel et al., 2010; Williams, 1966).

### 4.3.3. Baseline corticosterone and fitness

The significant but low within-individual repeatability of baseline corticosterone levels (R ± SE = 0.16 ± 0.03) suggests flexibility in individual baseline corticosterone levels. Consequently, it does not appear relevant to characterise female eiders in our study populations by their average baseline corticosterone level. Therefore, the low within-individual repeatability of baseline corticosterone levels did not allow me to rely on multi-event capture-mark-recapture models – with fixed individual covariates – to investigate the association between individual corticosterone levels and fitness components (as in **III**). I thus restricted my analyses to exploring the link between hatching success and baseline corticosterone levels.

Baseline corticosterone levels were positively associated with fitness, as hatching success was higher for females characterised by elevated baseline corticosterone levels (**V**; Figure 16). This result is, once again, in line with the 'corticosterone-adaptation hypothesis' (Bonier et al., 2009). It also corroborates the notion that elevated baseline corticosterone levels can mediate an increase in reproductive investment to maximise reproductive success (Béziers et al., 2020; Crossin et al., 2013; Fischer et al., 2020; Ouyang, Sharp, et al., 2013; Riechert, Becker, et al., 2014). The absence of a link between reproductive success and corticosterone in the short-term analysis (**IV**) was likely due to the lower statistical power of a one-year analysis (n = 148 in 2013), as opposed to a long-term study (n = 1422 in 2009-2022).

Interestingly, however, a within-individual increase in baseline corticosterone levels over breeding seasons did not result in an increase in hatching success. The latter was instead driven by among-individual differences in baseline corticosterone levels (**V**). A similar among-individual effect was found when investigating laying date, as females breeding on average earlier also exhibited higher baseline corticosterone levels. This is in line with previous studies providing evidence for earlier initiation of reproduction in higher-quality females (Catry et al., 2017; Verhulst & Nilsson, 2008), or females laying larger clutches (Descamps et al., 2011; Perrins, 2008). Baseline corticosterone levels may therefore also, to a certain extent, reflect among-individual variation in individual quality or reproductive investment in incubating eiders, with some females consistently performing better than others (Öst & Steele, 2010).

Overall, baseline corticosterone were positively associated with energetic investment in reproduction or hatching success and negatively associated with predation pressure. The population-level decrease in baseline corticosterone levels over the study period might thus reflect a reduction of reproductive investment in this context of changing predation regime. However, one may ask why such potential temporal reduction of parental investment – mediated by decreasing baseline corticosterone levels – was not accompanied by a temporal decrease in population-level hatching success. Concomitant changes in other physiological (e.g., metabolism) or behavioural (e.g., personality) traits may also affect hatching success, independently from corticosterone levels. Although important, corticosterone may therefore not capture all the components of parental effort, potentially explaining why baseline corticosterone levels are not tightly linked to hatching success.

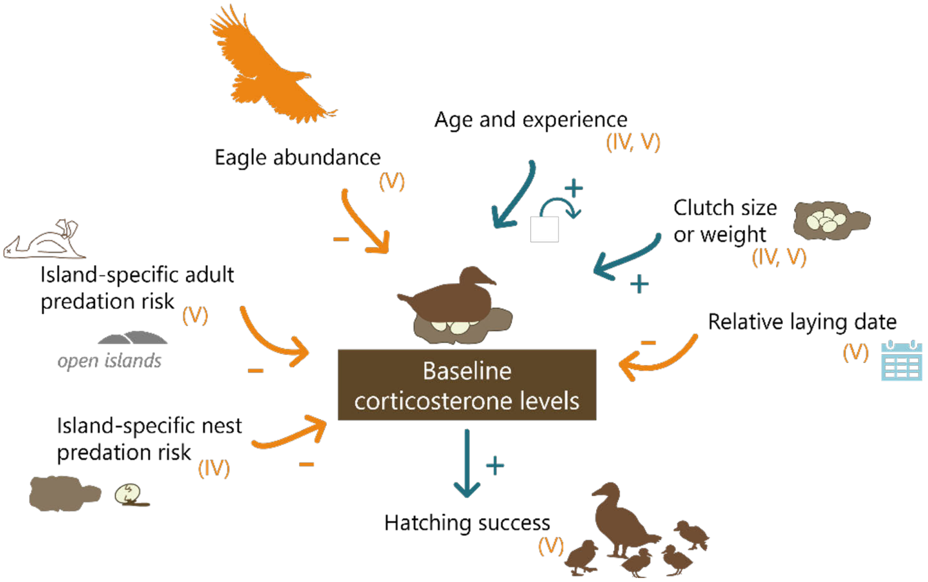

*Figure 16: Summary of the predictors of female common eider baseline corticosterone levels during incubation and their fitness consequences. Positive associations are depicted with medium blue arrows are negative associations are presented in orange. Corresponding Chapters are indicated in orange.*

## 4.4. Context-dependent variation in baseline prolactin in response to predation

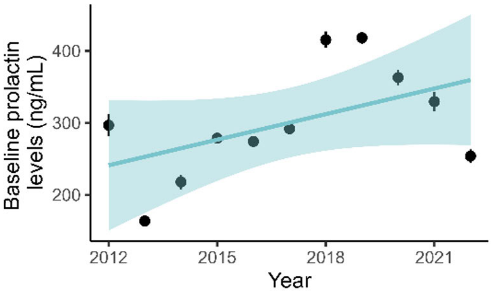

*Figure 17: Temporal variation in population-level female common eider baseline prolactin levels in 2012-2022. Dots correspond to yearly estimates and bars account for standard errors. The regression line and its 95% confidence interval are presented in blue. Adapted from Chapter VI.*

My thesis is among the first longitudinal studies to explore the association between baseline prolactin levels and predation risk, using longitudinal data of a wild population (**VI**). Prolactin is traditionally viewed as promoting parental effort (Angelier et al., 2016). Given that prey individuals should reduce parental effort under elevated predation risk (Candolin, 1998; Malone et al., 2017), a predicted response consistent with the temporal decrease in baseline corticosterone levels (**V**), the lack of a population-level decrease in baseline prolactin levels is, at first sight, surprising (**VI**). Indeed, and contrary to this prediction, baseline prolactin levels showed high interannual variability, and followed an upward trend over the study period (2012-2022) (**VI,** Figure 17). I believe that understanding the state- and context-dependency in the association between prolactin and fitness is key to resolving this complex variation (Figure 18). In addition, within-individual repeatability of baseline prolactin levels was significant but low (R ± SE = 0.07 ± 0.03). Such a value suggests that individuals are highly flexible in their baseline prolactin levels.

### 4.4.1. Baseline prolactin and parental effort

Iteroparous species often show an increase in breeding performance with age (Forslund & Pärt, 1995). Among non-exclusive factors explaining this trend are optimisation of reproductive effort, age-related improvements of competence and the progressive (dis)appearance of phenotypes (Forslund & Pärt, 1995). In agreement with this idea and with previous findings (Angelier, Shaffer, et al., 2006; Riechert et al., 2012; Smiley & Adkins-Regan, 2016; Ziegler et al., 1996), middle-aged females displayed higher baseline prolactin levels (**VI**). Importantly, the physiological senescence highlighted when exploring age-dependent variation in baseline corticosterone levels (**V**) extended to baseline prolactin levels, as baseline prolactin levels decreased in the oldest breeders (**VI**). Among the few studies assessing physiological senescence patterns in wild birds during reproduction, Angelier, Shaffer, et al. (2006) highlighted senescence in baseline corticosterone but not prolactin levels in wandering albatrosses *Diomedea exulans* and found the opposite pattern in black-browed albatrosses *Thallasarche melanophris* (i.e., senescence in baseline prolactin but not corticosterone levels; Angelier et al., 2007). In light of these results, these studies are among the first to provide evidence of simultaneous senescence in baseline corticosterone and prolactin levels in breeding individuals (**V-VI**).

Furthermore, poor female condition during incubation was associated with low baseline prolactin levels, and this relationship was exacerbated during years of unfavourable climatic conditions (poor winter and pre-breeding conditions, associated with low food quality or availability, **VI**). Although debated (Angelier, Moe, et al., 2009; Angelier et al., 2013), this negative correlation between body condition and prolactin levels is supported by several studies (Riechert et al., 2012; Schmid et al., 2011), notably in seabirds relying on prolonged fasting periods (Criscuolo et al., 2006; O'Dwyer et al., 2006; Groscolas et al., 2008; Angelier & Chastel, 2009). Indeed, poor-condition individuals are likely to reduce parental care to the benefit of their survivorship (Groscolas et al., 2008; Ledwoń et al., 2023; Wiggins et al., 1994). As baseline prolactin levels is thought to govern parental effort, this decrease in parental investment may be mediated by variation in prolactin levels.

### 4.4.2. Baseline prolactin and predation risk

In most species, individuals downregulate circulating prolactin levels when facing acute stress (Chastel et al., 2005; Gratto-Trevor et al., 1991; Ruiz-Raya et al., 2018). An identical downregulation of prolactin secretion could be expected in individuals confronted with chronic stress – such as increasing predation pressure or poor environmental conditions (reviewed in Angelier & Chastel, 2009; Angelier et al., 2016). This is because parents are predicted to reduce reproductive effort under high predation risk to enhance their own survival (Candolin, 1998; DeWitt et al., 2019; Malone et al., 2017).

Unexpectedly, and contrary to these *a priori* expectations, I found that baseline prolactin levels were higher – rather than lower – in females incubating on islands characterised by higher nest predation risk (**IV**). Since eiders are intermittent breeders and predation risk increases the probability of skipping breeding (Öst et al., 2018), it is possible that selective disappearance of poor-quality breeders may confound inference from the cross-sectional pattern. For instance, under high predation risk, only females exhibiting high parental effort (associated with high prolactin levels) could choose to engage in reproduction, while females less invested in reproduction would opt to skip breed. However, the low within-individual repeatability of baseline prolactin levels (**VI**) does not align with this idea, as it suggests that females are highly flexible in their baseline prolactin levels. Accordingly, selection on among-individual variation in prolactin levels is unexpected. Furthermore, the longitudinal study of baseline prolactin levels under fluctuating predation pressure did not support the hypothesis of a direct link between baseline prolactin levels and any of the studied predation risk indices (**VI**). Yet, by investigating the link between baseline prolactin levels and hatching success, I provided evidence for an indirect relationship between prolactin levels and environmental conditions – including predation pressure.

### 4.4.3. Context-dependent association between baseline prolactin levels and fitness

As for corticosterone, the assessment of the link between prolactin levels and fitness was restricted to the association between female baseline prolactin levels and hatching success. The low within-individual repeatability of baseline prolactin levels over years rendered irrelevant the characterisation of individual female eiders from the study population by their average baseline prolactin levels. I thus tested whether there was a positive association between baseline prolactin and hatching success – consistent with its putative role in mediating parental care (Angelier, Clément-Chastel, et al., 2009; Angelier et al., 2013; Chastel et al., 2005; Crossin et al., 2012; Riou et al., 2010; Wang et al., 2020). Contrary to expectations, successful breeders did not exhibit higher baseline prolactin levels (**IV and VI**). Elevated baseline prolactin levels instead seemed to promote hatching success under constraining intrinsic or environmental conditions (**VI;** Figure 18).

Accordingly, elevated baseline prolactin levels were associated with higher hatching success in young breeders (**VI**). High baseline prolactin levels may enhance incubation behaviour in young birds, that have little breeding experience, therefore increasing their chances of successfully breeding. Additionally, elevated baseline prolactin levels may be beneficial when incubating a large clutch (**VI**), associated with high energetic demands (Tinbergen & Williams, 2002; Williams, 1996). Baseline prolactin levels were also positively associated with higher hatching success under challenging environmental conditions, including years of high white-tailed eagle abundance and years of poorer climatic conditions and low eider body reserves at the start of incubation (**VI**). Such a context-dependent link between baseline prolactin levels and reproductive success could explain the negative association between prolactin and hatching success that was found in Chapter **IV**. Since individuals displaying low baseline prolactin levels are more likely to neglect their eggs (Angelier et al., 2015) or abandon their nest or offspring (Chastel & Lormée, 2002; Groscolas et al., 2008; Spée et al., 2010, 2011), maintaining high baseline prolactin levels when incubating under poor environmental conditions may be beneficial by enhancing the investment in current reproduction. For instance, parents displaying higher baseline prolactin levels may return to their nest and resume incubation more quickly than those with lower levels following a disturbance (e.g., Angelier, Clément-Chastel, et al., 2009). Population-level interannual fluctuation in baseline prolactin levels, and in particular the observed upward trend, might thus reflect degrading environmental conditions in the study area, but perhaps also in the wintering grounds, deserving further investigation.

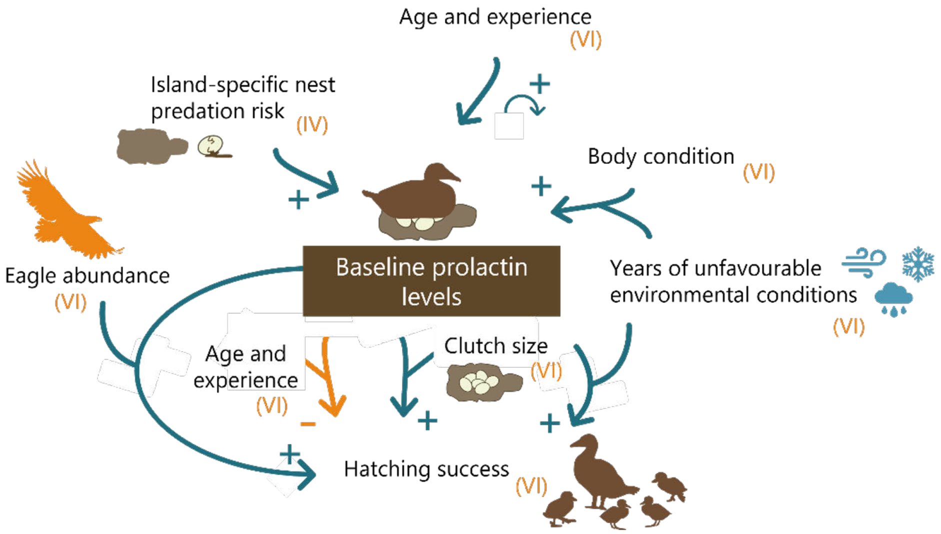

*Figure 18: Summary of the predictors of female common eider baseline prolactin levels during incubation and their fitness consequences. Positive associations are depicted with medium blue arrows. Corresponding Chapters are indicated in orange.*

# 5. Conclusions and perspectives

## 5.1. Significance of the results

### 5.1.1. Behavioural and physiological responses to increasing predation pressure

In my thesis, I investigated prey population- and individual-level responses to increasing predation pressure from both a short-term (**II, IV**) and a long-term perspective (**I, III, V, VI**). I specifically focused on the monitoring of behavioural (flight initiation distance, **I-III**) and physiological (baseline corticosterone and prolactin levels, **IV-VI**) traits, by repeatedly sampling individual traits and fitness outcomes in a context of changing predation regime. The comprehensive and long-term data collection was not restricted to the focal behavioural and physiological variables of this thesis. It also included a monitoring of intrinsic characteristics (e.g., female age, body condition or clutch size) and extrinsic parameters (e.g., nesting microhabitat and fine- and large-scale predation pressure), which allowed a good understanding also of the changes occurring in some of these other factors.

At the population scale, the temporal increase in predation pressure – reflected in rising predator abundance and predation on adult eiders and their nest – was correlated with a decrease in flight initiation distance (**I**) and baseline corticosterone levels (**V**), and a slight increase in baseline prolactin levels (**VI**). At first glance, these results may appear contradictory, as they mirror a temporal increase in risk-taking (flight initiation distance), decrease in reproductive investment (baseline corticosterone levels, according to the 'corticosterone-adaptation hypothesis'; Bonier et al., 2009) and increase in parental effort (baseline prolactin levels). Understanding other concomitant changes occurring in the population – notably temporal trends in female age, body condition or nest cover – as well as individual-level responses to variation in other intrinsic and extrinsic factors, was key to interpreting these findings.

Moving from population-level responses to exploring the plasticity of individual responses, I found that females adjusted behavioural (flight initiation distance, **I**) and physiological (baseline corticosterone levels, **V**) traits to prevailing predation risk, amplifying or dampening behavioural and physiological responses, respectively, under increasing risk of predation. At the individual level, females reduced risk-taking when breeding in dangerous nest sites (**I**). In such an environment, they were also more likely to rely on prior experience with a threat to dampen their behavioural stress response when repeatedly confronted with a harmless stimulus (here, a human approach, **II**) over a short period of time (i.e., the last days of incubation). While the long-term (i.e., over breeding seasons) increase in risk-avoidance associated with increasing predation pressure (**I**) is likely an adaptive response favouring individual survivorship, the short-term (i.e., within a breeding season) habituation to repeated human approaches under elevated predation risk (**II**) suggests that individuals are able to differentiate 'real' life-threatening stimuli (i.e., predation attempts) from stressful but non-life-threatening human disturbance. In line with the 'risk allocation hypothesis' (Ferrari et al., 2009), this short-term habitation is thought to limit excessive flightiness to benign stimuli that could jeopardise reproduction. In addition to behavioural responses, breeding under higher predation risk was associated with a plastic among-year downregulation of baseline corticosterone levels (**V**), interpreted as mediating a decrease in energetic investment in reproduction.

Over breeding attempts, the finding that eiders plastically reduce risk-taking (i.e., increase flight initiation distances, **I**) as well as energetic investment in reproduction (mediated by a downregulation of baseline corticosterone levels, **V**) when nesting under increasing predation risk is in line with the life-history trade-off between survival and reproduction (Williams, 1966). This theory predicts that parents would reduce their investment in reproduction under predation pressure, to the benefit of their own survivorship. In further support of this theory (Williams, 1966), during the recent years of high predation pressure (2018-2022), females displaying longer flight initiation distances (i.e., risk-avoiding individuals) were characterised by lower reproductive success and breeding propensity but higher survival (**III**). Risk-avoiding phenotypes thus seemed to prioritise survival – and prospects of investment in future reproduction – over current reproduction. In addition, females displaying higher baseline corticosterone levels had a higher hatching success (**V**). The temporal decrease in population-level baseline corticosterone levels may thus correlate with a decrease in energetic investment in reproduction. This decrease could be mediated by a downregulation of baseline corticosterone levels and coincide with increasing predation pressure. Surprisingly, despite this likely reduction of energetic investment in reproduction, I did not detect any decrease in population-level hatching success over the study period (**III**). Several concurrent changes occurring in the population could buffer the negative impact of increasing predation pressure on breeding females, such as increasing breeding experience associated with the ageing of the pool of breeding females (**I**), increasing body condition of breeders (**I**) or nest concealment (associated with a lower risk of predation, **I**). Additionally, and non-exclusively, I also provide evidence for a concomitant increase in highly plastic baseline prolactin levels – positively associated with parental care behaviour (**VI**). Accordingly, females displaying higher baseline prolactin levels had a higher hatching success probability during years of challenging environmental conditions, and especially during years of high predation pressure (**VI**).

The three traits of interest – flight initiation distance, baseline corticosterone and baseline prolactin levels – provided contrasting, yet complementary, insights on prey adjustment of behaviour, physiology and how individuals solve life-history trade-offs in a changing world. Most responses to increasing predation pressure were underpinned by plastic responses (**I, II, V, VI**), but selective disappearance effects were also found when investigating individual variation in risk-taking (**I, III**). This thesis underlines the need to couple population- and individual-level analyses to better understand processes shaping observed variation in traits of interest (Cam et al., 2002).

### 5.1.2. Age-dependent responses and senescence

My thesis supports the idea that chronic or acute stress is often associated with a reduction of reproductive effort (DeWitt et al., 2019; Malone et al., 2017; Mutzel et al., 2019), or even a complete suppression of reproduction (**III;** Dulude-de Broin et al., 2020; Mappes et al., 1998; Ruxton & Lima, 1997). This response is generally considered as an adaptive response to maximise investment in reproduction under low stress or mild predation risk (Ruxton & Lima, 1997). However, individuals may gain an advantage in maintaining reproduction under stressful conditions as they grow older and their residual reproductive value decreases (Wingfield & Sapolsky, 2003). In agreement with this idea, also known as the ‘restraint hypothesis’ (Curio, 1983), older female eiders engaging in reproduction were more prone to take risks (i.e., displayed shorter flight initiation distances, **I**), and were also more likely to habituate to short-term repeated exposure to a stressful but non-life-threatening stimulus (**II**). In addition, they displayed higher baseline corticosterone levels (**IV-V**) – a proxy of energetic investment in reproduction – and higher baseline prolactin levels (**VI**), a proxy of parental effort (Angelier et al., 2016). Altogether, these results support the theory of increased reproductive investment and associated breeding performance with ageing in this species (Forslund & Pärt, 1995; Lemaître & Gaillard, 2017; Moschilla et al., 2018).

Importantly, in iteroparous species, reproductive performance often increases during the first breeding attempts, before peaking or reaching a plateau at an intermediate age, and this pattern is followed by a decrease in breeding performance at old age, when reaching the onset of senescence (Angelier, Weimerskirch, et al., 2007; Forslund & Pärt, 1995; Sharp & Clutton-Brock, 2010). The findings of my thesis suggest that the age-dependent increase in reproductive performance may be limited by physiological senescence at old age, perhaps associated with an effect of accumulated costs of previous breeding attempts on secretion of corticosterone (**V**; Angelier, Shaffer, et al., 2006) or prolactin (**VI**; Angelier et al., 2007).

## 5.2. Towards stress-coping strategies?

Do studied behavioural and physiological traits covary and form a gradient of individual stress-coping strategies in incubating female eiders? Despite the existence of phenotypic plasticity, it is now admitted that animal behaviour and physiology are less flexible than previously thought (Sih, Bell, & Johnson, 2004; Wolf et al., 2007). As a result, individuals may consistently differ in a suite of correlated traits such as boldness, aggressiveness, exploration or stress sensitivity (Koolhaas et al., 1999; MacKay & Haskell, 2015; Montiglio et al., 2018; Wolf & Weissing, 2010). These consistent differences among individuals are predicted to be maintained across contexts (Bell, 2007; Sih, Bell, & Johnson, 2004), and the measurement of individual-level behavioural and physiological traits enables the determination of coping styles (Koolhaas et al., 1999) – also sometimes referred to as personalities (Réale et al., 2010) or temperaments (Réale et al., 2007; Réale & Festa-Bianchet, 2003). The pace-of-life syndrome theory – initially confined to an interspecific scale and later expanded to intraspecific and intrapopulation scales (Ricklefs & Wikelski, 2002; Van De Walle et al., 2023) – has been proposed as a framework integrating covariation in behaviour, physiology and life-history traits (Dammhahn et al., 2018; Montiglio et al., 2018; Réale et al., 2010).

Following this theory, individuals are predicted to be scattered along a fast-slow life-history continuum. On the one end of this continuum, 'fast' individuals are predicted to prioritise reproduction over survival. They are often characterised by risk-taking, explorative or aggressive behaviour, as well as a low stress sensitivity. On the other end, 'slow' individuals prioritise survival over reproduction, and are predicted to be shier, less risk-taking, explorative or aggressive, and more sensitive to stress. This led me to consider whether such a fast-slow continuum is also present in female eiders. Based on the pace-of-life syndrome theory, I predicted that 'fast' life histories would be characterised by greater risk-taking propensity (i.e., shorter flight initiation distances), and higher baseline corticosterone and prolactin levels (mirroring higher emphasis on reproduction).

To this end, I did an extended analysis exploring among-individual correlations in the three traits of interest (flight initiation distance, baseline corticosterone and prolactin levels), based on the data included in my thesis. This analysis relied on a multivariate mixed model – controlling for covariates of importance identified in Chapters **I, V** and **VI** (e.g., female age, body condition, nest cover and predation risk indices). This preliminary analysis revealed a weak but positive among-individual correlation between female flight initiation distance and baseline corticosterone levels (E ± SE = 0.34 ± 0.11, 95% credible interval, CI = (0.14, 0.55); Figure 19A) and negative among-individual correlation between flight initiation distance and baseline prolactin levels (E ± SE = - 0.28 ± 0.14, 95% CI = (-0.57, -0.01); Figure 19B). There was no among-individual correlation between baseline corticosterone and prolactin levels (E ± SE = 0.03 ± 0.16, 95% CI = (-0.28, 0.35); Figure 19C).

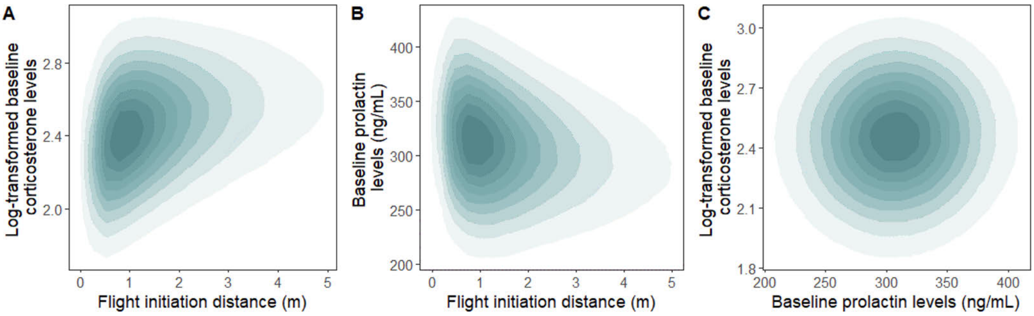

*Figure 19: Among-individual correlation between incubating female eider (A) log-transformed baseline corticosterone levels and flight initiation distance, (B) baseline prolactin levels and flight initiation distance and (C) log-transformed baseline corticosterone levels and baseline prolactin levels. The contours delimit regions of probabilities from 0.1 (darkest colour; 10% of estimated values around the mean estimate contained within it) to 0.9 (lightest colour; 90% of estimated values contained within it), corresponding to joint posterior distributions obtained from a multivariate model.*

Among-individual elevation of baseline corticosterone levels was associated with risk-aversion, while high baseline prolactin levels correlated with risk-taking. The positive association between prolactin and risk-taking is consistent with the pace-of-life syndrome, as risk-taking individuals are expected to prioritise reproduction (**I**) and because prolactin acts as a mediator of increased parental effort (**VI**; Angelier et al., 2016). In agreement with this idea, a previous study highlighted shorter flight initiation distances and higher offspring protection in willow ptarmigans *Lagopus lagopus* displaying elevated baseline prolactin levels (Pedersen, 1989). In contrast, the negative correlation between corticosterone and risk-taking is challenging to reconcile with the pace-of-life syndrome, given that elevated baseline corticosterone levels are associated with increased reproductive investment and success (**IV, V**). However, the observed positive correlation between baseline corticosterone levels and flight initiation distance is in agreement with the results previously drawn from a meta-analysis carried out at the interspecific scale (Tablado et al., 2021). Circulating corticosterone levels are thought to prepare an individual for coping with future stressful situations (Sapolsky et al., 2000), and this can include a preparative effect on antipredator behavioural responses (Herr et al., 2017; Tablado et al., 2021; Thaker et al., 2009). Possibly, the enhanced preparative effect could be a physiological candidate mechanism underlying state-dependent safety (Luttbeg & Sih, 2010), i.e., that individuals in superior condition, typically highly committed to reproduction, possess superior escape abilities. In line with this idea, female eiders in good body condition have better survival prospects than their poor-condition counterparts (Ekroos, Öst, et al., 2012). Additionally, and non-exclusively, stress-induced corticosterone levels, rather than baseline corticosterone levels, may be more closely related to risk-taking (Baugh et al., 2017). Thus, as the next step, I recommend further exploring the relationship between stress-induced corticosterone and flight initiation distance.

Given the correlation between physiological and behavioural traits, the lack of correlation between female eider baseline corticosterone and prolactin levels is, at first glance, surprising. Indeed, several studies support the idea of significant positive or negative relationships between corticosterone and prolactin levels (reviewed in Angelier et al., 2013). However, these associations do not seem consistent across species, as some studies provide evidence for a significant association while others do not (Paterlini et al., 2017; reviewed in Angelier et al., 2013). The results obtained here indeed parallel previous findings on eiders (Criscuolo et al., 2006). Such a lack of association between these two physiological variables may arise from the fact that baseline corticosterone and prolactin levels reflect different components of reproduction. Indeed, baseline corticosterone may reflect energetic investment (**IV, V**), while prolactin levels is associated with parental effort and the expression of parental behaviours (**IV, VI**).

Overall, these results provide low support for the pace-of-life syndrome theory at the individual level, by joining mixed findings on the relationship between behavioural and physiological traits (Garamszegi et al., 2012; Montiglio et al., 2018), and supporting the conclusions of the meta-analysis conducted by Royauté et al. (2018). Pace-of-life syndromes may indeed be better supported across species, rather than with species or populations (Van De Walle et al., 2023). Importantly, the traits of interest may be highly plastic, and individuals may differ in plasticity. Indeed, while risk-taking was moderately repeatable within individuals (**I**), it was not the case for baseline corticosterone and prolactin levels – that were significantly but lowly repeatable (**V, VI**). The choice of the study variables could thus have a role to play in the observed correlations between behavioural and physiological traits, and integrating additional traits could enable a better understanding of observed correlations. For instance, stress-induced glucocorticoid or prolactin levels, rather than baseline levels, may be related to behaviours associated with risk-taking (Baugh et al., 2012, 2017; Seltmann et al., 2012) or parental care (Hope et al., 2020).

## 5.3. Implications for conservation

### 5.3.1. Implications for the conservation of eider populations

Throughout the past decades, the declining Baltic/Wadden Sea flyway population of eiders has invoked attention and raised concern. Currently, common eiders are listed as endangered in Europe (Birdlife International, 2021). Several non-exclusive drivers of this decline have been proposed, with variable support in different segments of the population distribution (Ekroos, Fox, et al., 2012; Lehikoinen et al., 2022; Tjørnløv et al., 2020). Nevertheless, few long-term studies prior to my thesis work have evaluated the extent of behavioural and physiological responses to predation risk, a prime putative driver of the population decline (Öst et al., 2022). Such knowledge is a vitally important prerequisite for successful management and for assessing the population's resilience to a changing predation regime.

My thesis provides evidence that the underlying mechanisms shaping eider behavioural and physiological responses to increasing predation threat may differ. Overall, plasticity seems to shape most of the responses, such as the adjustment of behavioural stress response to predation threat within and among breeding seasons (**I, II**), or the flexible reduction of baseline corticosterone levels under increasing predation risk (**V**). In addition, selective processes were found to underpin the behavioural response to predation threat (**III**). These findings support the general idea that predation risk effects are likely more important than predator-consumptive effects in explaining trait evolution (Creel & Christianson, 2008; Nelson et al., 2004; Pangle et al., 2007; Preisser et al., 2005). While flexible behavioural and physiological adjustments may prove adaptive against rising predation risk, it is still uncertain whether they will enable eiders to adjust their phenotype to the new optimum induced by the change in predation pressure. Further work is thus still needed to assess the resilience of eider populations to a rapidly changing predation regime.

The efficient ongoing alien predator removal scheme – maintaining low abundance of invasive mammalian predators (Jaatinen et al., 2022) – provided the opportunity to primarily evaluate the responses of eiders to the recovery of white-tailed eagles. Depredation of adults or nests by invasive mammalian predators was nonetheless included in the calculation of island-specific indices of predation risk to monitor the overall risk of predation. However, the presence of mammalian predators on islands is often accompanied with a reduction of breeding propensity or density of waterfowl (Jaatinen et al., 2022; Nordström et al., 2002), hence inducing a methodological bias by limiting the probability of sampling these individuals. Nevertheless, it is primordial to acknowledge that the low invasive predator abundance around Tvärminne does not reflect the situation in other areas of the Baltic Sea, as predation pressure induced by American minks and raccoon dogs is likely to be increasing in Finland (Nummi et al., 2019; Öst et al., 2018) and still spreading elsewhere in Europe (Bonesi & Palazon, 2007; Vada et al., 2023), posing a threat to many waterfowl species (Fox et al., 2015; Holopainen et al., 2021). In my thesis, I showed that eiders were more prone to habituate to repeated human approaches on islands characterised by high predation risk (**II**). If this response generalises not only to humans, but also to other terrestrial mammalian predators, this could increase the vulnerability of ground-nesting species to alien mammal predators. Further work is thus needed to assess adjustments of antipredator behaviour to taxonomically diverse predators.

Importantly, adaptations to some predators may not prove effective against others. For instance, nesting under thick vegetation cover may be adaptive against visually-hunting predators like eagles, but not against mammalian predators, that rely on olfactory cues. Given that nesting under thick vegetation cover will likely hinder escape upon predator detection (Öst & Steele, 2010), a change in breeding habitat may lead to an ecological trap if invasive mammals become abundant. Similar maladaptive responses to taxonomically diverse predators may be found in the northern parts of eider distribution range, where ground-nesting birds face a climate-induced increase in egg depredation by polar bears (Prop et al., 2015). Whereas in these areas, incubating female eiders protect their clutch from gull depredation by staying on the nest or exhibiting defensive behaviour, these responses are not effective against bears, that could easily devour an adult that would not leave its nest. Due to the novelty of this predator on an ontogenetic time scale, eiders may not have yet evolved appropriate responses to cope with bear-induced predation risk, which translates into high or extremely high nest failure at the scale of entire colonies (Jagielski, Dey, Gilchrist, Richardson, Love, et al., 2021; Jagielski, Dey, Gilchrist, Richardson, & Semeniuk, 2021). This further strengthens the need for multi-colony studies evaluating the cumulative effect of predation risk by diverse native and non-native predators and the ability of eiders to cope with different types of predation pressure (Hanifin et al., 2008).

In order to be able to propose and implement relevant and accurate conservation measures to protect eider populations during the breeding season, it is thus essential to acknowledge that, although drastic, shifts in predation regimes are not the only factors affecting eider – and more generally seabird – populations. To predation, one can add numerous stressors such as climate or habitat change, reduced food availability or quality, oil spills and other pollutants, hunting pressure, disease outbreaks or bycatch in fishing gear, and some of these pressures are still to be evaluated (Fox et al., 2015; Lehikoinen et al., 2022; Tjørnløv et al., 2019). These multiple stressors can act in concert, with additive or synergetic effects on individuals and populations (Bårdsen et al., 2018; Sih, Bell, & Kerby, 2004). In addition, it is vital to consider that common eiders are migratory, and that migrating decisions (e.g., phenology of migration and location of wintering areas) may have carry-over effects on survival and reproduction. Virtually nothing is known about whether and to what extent individual eider migrating strategies may differ, especially in response to variation in risk-taking or physiological state. The first step of this work is to correctly evaluate movements between breeding and wintering areas as well as population exchanges in the Baltic/Wadden Sea flyway (Lehikoinen et al., 2022), for example through the tagging of individuals with geolocating devices.

### 5.3.2. Implications for seabird conservation

On a global scale, seabirds are considered one of the most threatened bird groups, and about half of seabird species are suspected to be declining (Croxall et al., 2012; Dias et al., 2019). In the meantime, sea eagle populations are rapidly recovering in the northern hemisphere (Hipfner et al., 2012). A few studies document direct and indirect effects of this increase in native avian predator abundance (this thesis; Anker-Nilssen et al., 2023; Barrett, 2008; Barrett et al., 2006; Hentati-Sundberg et al., 2023; Hipfner et al., 2012), but the extent to which they affect seabird populations and communities is still undocumented – especially for white-tailed eagles.

As top predators, eagles have the potential to shape marine food-web structure (Harvey et al., 2012), especially by acting on trophic cascades (Heithaus et al., 2008; Terraube & Bretagnolle, 2018). The importance of sea eagles in shaping ecosystem processes and community structures stresses out the need to monitor white-tailed and bald eagle population dynamics – and especially assess whether they are reaching carrying capacity. Whereas seabirds may buffer – to some extent – the negative impact of rising eagle populations through behavioural, physiological or life-history adaptations (as supported by this thesis), these responses are sometimes insufficient and local populations may simply go extinct (Anker-Nilssen et al., 2023). Changing predation regime may thus lead to a change in the habitat in which prey fitness is maximised (e.g., from natural cliffs to harbours for black-legged kittiwakes *Rissa tridactyla*, Anker-Nilssen et al., 2023; or from isolated rocky islands to forested islands closer to mainland for common eiders, Ekblad, 2022), constituting a major challenge for national species monitoring schemes based on fixed monitoring sites, as well as for targeting conservation actions (e.g., for the establishment of protected areas).

Given the lack of a general understanding of seabird responses and resilience to variation in predation regime, further research is still needed to document seabird adaptations and assess the risk induced by native avian predators. This knowledge will prove crucial to implementing relevant conservation measures.

## 5.4. Future directions

### 5.4.1. Baseline corticosterone and prolactin levels as conservation biomarkers?

At the individual level, physiological mechanisms mediate a wide range of behavioural, morphological or life-history traits, playing an essential role in triggering phenotypic responses to predictable and unpredictable environmental stressors (Ames et al., 2020; Lawton, 1991; Wikelski & Cooke, 2006). Physiological responses may thus be thought of as monitoring tools to asses individual and population status (Bergman et al., 2019; Wikelski & Cooke, 2006). This raises the need to define relevant biomarkers.

Classically, glucocorticoid levels are used as tools measuring stress responses to environmental perturbations. However, there is ongoing debate whether glucocorticoid levels can be used as biomarkers to monitor fitness, condition or health in wild populations, and more generally provide information on environmental conditions (Busch & Hayward, 2009; Madliger & Love, 2014; Walker, 2005; Wikelski & Cooke, 2006). This is because the context-dependency of variation in glucocorticoid levels renders their interpretation complex (Bonier et al., 2009) and raises a need for primarily understanding how a particular species or population respond to intrinsic and extrinsic challenges before concluding on the health status of the population. Supporting this idea, the observed decrease in baseline corticosterone levels in the study eider population (**V**) reflected an increase, rather than a decrease, in environmental stress, but this interpretation was only feasible after having assessed that corticosterone was positively associated with reproductive investment. Combining multiple metrics of physiology and behaviour may thus be more relevant to monitor the state of wild species and populations (Sorenson et al., 2017). Coupling these metrics with measurements of survival, breeding propensity or success may also allow a better assessment of population status. In my thesis, I highlighted the importance of looking at temporal variation in breeding propensity – a poorly-understood yet important demographic parameter (Nicol-Harper et al., 2021; Reed et al., 2004) – to understand population-level responses to a changing predation regime (**III**).

Additional results suggest that baseline prolactin levels could also be useful to integrate in conservation biology (**VI**), for instance paired with glucocorticoid measurements. Indeed, baseline prolactin levels showed high interannual variation (**VI**) and likely played a role in buffering the effects of environmental fluctuations on reproductive success (**VI**), as previously suggested (reviewed in Angelier & Chastel, 2009; Angelier et al., 2016). However, the observed high interannual variation in population-level baseline prolactin levels suggests that we still understand very little about the mechanisms that regulate prolactin secretion in the wild.

### 5.4.2. Integrating stress-induced responses to measure stress sensitivity

As previously suggested (see 5.2.), integrating other possibly relevant parameters could provide a broader understanding of the ability of individuals to cope with a changing environment. By investigating baseline levels of corticosterone and prolactin, this thesis focuses on physiological response to chronic stressors, rather than acute ones – although the behavioural response to an acute stress is measured through flight initiation distance. Physiological responses to acute stressors are at least equally important, as failure to correctly respond to a sudden – unpredicted – stressor will likely jeopardise survival.

Confrontation to an acute stressor – e.g., a predation attempt – therefore triggers two main pathways, driving behavioural and physiological stress responses at different temporal scales (Hawlena & Schmitz, 2010). First, the sympathetic-adrenal-medullary axis (SAM) is activated, triggering an emergency behavioural fight-or-flight response within tenths of a second (that can for example be measured through flight initiation distance or defence behaviour). Second, the hypothalamic-pituitary-adrenal axis (HPA) is activated within minutes and up to hours, triggering an 'emergency life-history stage' (Wingfield et al., 1998), that redirects individuals – and allocation of energetic resources – from non-essential activities (e.g., reproduction) to essential activities (e.g., immediate survival) to maximise lifetime fitness (Ricklefs & Wikelski, 2002; Wingfield, 2003; Wingfield & Sapolsky, 2003). An important mediator of such energy reallocation occurs through the secretion of glucocorticoids (often referred to as the glucocorticoid stress response) (Angelier et al., 2013).

Thus, the glucocorticoid stress response is thought to play a major role in enabling individuals to cope with sudden environmental perturbations (Angelier et al., 2013; Angelier & Chastel, 2009; Angelier & Wingfield, 2013). While the rise of glucocorticoid levels in response to an acute stress benefits immediate survival (Patterson et al., 2014; Ricklefs & Wikelski, 2002), it may also lead to elevated fitness cost, for example through breeding failure or territory loss. As a consequence, the downregulation of the glucocorticoid stress response can also provide fitness benefits, and stress-induced glucocorticoid levels can reflect among-individual variation in the ways of solving life-history trade-offs (Angelier & Wingfield, 2013). Previous studies carried out in the study system also underline the relevance of looking at the hormonal stress response of incubating female eiders. Indeed, stress responsiveness was linked to risk-taking behaviour (Seltmann et al., 2012), but also found to reflect habitat-specific responses, as females nesting in concealed nests also displayed lower stress-induced corticosterone levels (Seltmann et al., 2014). Given the short-term nature of these studies, further work is now needed to investigate individual resilience to a changing predation regime based on long-term longitudinal data. Indeed, stress-induced glucocorticoid levels may be more relevant to characterise evolutionary patterns of selection of physiological responses or stress sensitivity.

Similarly, exposure to acute stressors is known to trigger a decrease in circulating prolactin levels (Angelier & Chastel, 2009; Chastel et al., 2005; Gratto-Trevor et al., 1991; Ruiz-Raya et al., 2018). Under challenging conditions, a decrease in prolactin levels is likely adaptive, by mediating a reduction of parental effort and promoting immediate survival to the detriment of current reproduction (Angelier & Chastel, 2009; Chastel et al., 2005). Importantly, such stress-induced decrease in prolactin levels has been shown to vary among individuals and species (Angelier et al., 2016; Kosztolányi et al., 2012). The magnitude of the reduction of prolactin levels in response to a standardised stress protocol may thus provide complementary information on prey adjustment of parental effort and sensitivity to both chronic and acute stress in a changing environment (Angelier & Chastel, 2009). This is especially relevant as the neuro-endocrine pathways governing secretion of glucocorticoids and prolactin under acute stress differ (Angelier & Chastel, 2009; Sharp et al., 1998; Wingfield & Sapolsky, 2003). When examined simultaneously, the investigation of stress-induced corticosterone and prolactin levels is likely to provide complementary information on parental investment (Angelier et al., 2013, 2016; Angelier, Moe, et al., 2007). Additionally, other components of the fight-or-flight response than escape behaviour could be monitored, such as heart rate (Viblanc et al., 2015; Williams et al., 2017).

### 5.4.3. Exploring transgenerational effects of maternal stress and exposure to predators

In this thesis, I have centred my attention on predator-consumptive and predation risk effects on parents. However, there is growing evidence that parental exposure to predation risk can also shape offspring phenotype, notably through transgenerational effects on morphology, physiology, or behaviour (McGhee et al., 2012; Sheriff et al., 2010; Sheriff & Thaler, 2014; Sirot, 2010; Storm & Lima, 2010; Yin et al., 2019). These prenatal effects of predation risk on offspring are thought to arise from variation in parental – and, in particular, maternal – resource allocation or investment in current reproduction. An important pathway is the change in egg composition under predation pressure (Coslovsky et al., 2012; Giesing et al., 2011; Morosinotto et al., 2013; Mouton et al., 2022) and especially maternal transfer of hormones to the eggs (Almasi et al., 2012; Hayward & Wingfield, 2004; Saino et al., 2005). These prenatal effects are likely to have cascading effects on offspring development and survival (Agrawal et al., 1999; Bell et al., 2016; Saino et al., 2005). Although debated (Hayward & Wingfield, 2004; Öst et al., 2020; Saino et al., 2005; Sopinka et al., 2017), elevated embryonic glucocorticoid levels have been suggested to be associated with preparative responses enhancing offspring survivorship in a low-quality environment (Meylan et al., 2012) – including under high predation risk (Giesing et al., 2011) –, for example through better flight ability (Chin et al., 2009), accelerated growth (Coslovsky & Richner, 2011; Palacios et al., 2022) or enhanced antipredator defence (Giesing et al., 2011) or response (Kulkarni & Gramapurohit, 2017).

In light of the observed temporal trends in maternal corticosterone (**V**) and prolactin (**VI**) levels, and given the suggested sex-dependent effects of maternal corticosterone levels on eider ducklings (Öst et al., 2020), I encourage further exploration of the transgenerational effects of maternal exposure to predation on offspring. These studies are fundamental to better assess the adaptative value of the match or mismatch between maternal and offspring phenotype (Coslovsky & Richner, 2012; Love & Williams, 2008), especially under fluctuating predation pressure. In addition, there is growing evidence that early-life environment affects lifetime fitness (Langenhof & Komdeur, 2018; Pigeon & Pelletier, 2018). Accordingly, predation risk during the early stages of life may have long-term effects on behaviour (Liesenjohann & Krause, 2012), growth (Bell et al., 2011; Liesenjohann & Krause, 2012), morphology (Hossie et al., 2010), or even cognitive abilities (Vila Pouca et al., 2021). As eider ducklings are precocial and leave the nest within 24 hours of hatching (Öst & Bäck, 2003), they are rapidly exposed to predation risk when reaching the sea, and the environmental stress experienced during their early life may have long-term effects on their fitness.

### 5.4.4. Conclusion

In my thesis, I relied on a long-term individual-based monitoring of eiders facing the recovery of their native avian predator to assess whether and how long-lived prey individuals and populations respond to a changing predation regime. The temporal increase in predation pressure correlated with population-level variation in a suite of traits, including: behavioural antipredator trait (i.e., through a reduction of risk-taking, **I**), physiological traits (i.e., through a decrease in baseline corticosterone levels and an increase in baseline prolactin levels, **V, VI**), but also life-history traits (i.e., through a reduction of breeding propensity, **III**). The rise in predation risk was also accompanied by an ageing of the breeding population (**I**), an increase in female body condition (**I**) and nest concealment (**I**), and a decrease in clutch size (**I**).

In light of these population-level changes, I conducted individual-level analyses to improve our understanding of the processes shaping behavioural and physiological responses to fluctuating predation threat. First, I found that increasing predation pressure was associated with a decrease in risk-taking (i.e., a lengthening of flight initiation distance, **I**). Interestingly, this response was shaped by a plastic adjustment of flight initiation distance to the risk of predation on breeding females, and the selective disappearance of risk-taking phenotypes from islands characterised by high risk of offspring predation. Supporting this idea, risk-avoiding individuals were characterised by lower reproductive success and breeding propensity but higher survival during years of high predation risk (**III**). These results provide, to my knowledge, among the first evidence that the target of predation (adults or offspring) determines the mechanisms driving the adjustment of risk-taking propensity to the perceived level of threat. Further analyses highlighted that individuals are able to adjust their behavioural escape response to prior experience with a threat (**II**). Second, I provide evidence for a plastic decrease in baseline corticosterone levels of females incubating during years of high predation risk (**V**). This downregulation of baseline corticosterone levels is thought to mirror a decrease in energetic investment in reproduction. An interesting additional finding was that at the fine scale (i.e., at the island scale) the physiological response to predation risk on adults was habitat-dependent, being visible only on open islands (**V**) – where adult survival is also lower (Ekroos, Öst, et al., 2012). Last, my findings did not validate the prediction of direct relationship between baseline prolactin levels – promoting parental effort – and predation risk (**VI**). Instead, I showed that prolactin was indirectly related to predation pressure, likely promoting hatching success during years characterised by challenging environmental conditions, including elevated predation pressure (**VI**).

While the results drawn from my thesis provide valuable insight into the response of prey individuals and populations to a change in predation regime, much remains to be explored to assess seabirds' resilience to the recovery of sea eagle populations in the northern hemisphere. My results suggest that plasticity and selection shape prey behavioural and physiological responses to fluctuating predation risk. At the individual level, most responses were found to be – at least partially – driven by flexible adjustments of traits to the risk of predation. However, when using longitudinal data to test for within-individual plasticity in response to changing environmental and internal conditions (**I, V**), I assumed that individuals displayed consistent plastic responses, by relying on a within-subject centring approach (van de Pol & Wright, 2009). This assumption is likely reductive, as individuals may differ in behavioural and endocrine flexibility (Grindstaff et al., 2022; Guindre-Parker, 2020; Malkoc et al., 2022). Such individual-level variation in flexibility may *in fine* determine the resilience of individuals and populations in a changing environment. I thus advocate the continuation of the long-term monitoring of this eider population, and the use of a reaction norm approach (Malkoc et al., 2022) after the collection of a sufficient number of behavioural and physiological samples on known individuals along variation in environmental and internal conditions.

In addition, using a long-term field monitoring has the advantage of allowing the assessment of the complexity of natural processes occurring in wild populations, integrating additive and synergetic effects of concurrent stressors. However, these data are, by nature, correlational, and do not allow to fully address causality. Consequently, I encourage future studies combining long-term monitoring of wild populations with experimental settings to further assess the causality of the links between individual traits and predation regime.

# Acknowledgements

I am very grateful to all the people who have supported me during the past four years! First and foremost, I would like to thank my official and unofficial supervisors: Dr Markus Öst, Dr Frédéric Angelier and Dr Kim Jaatinen.

**Markus**, thank you for offering me the opportunity to work with this fantastic and unique dataset and for coping with my endless questions. I have learned a lot during these years. Thank you for sharing your knowledge on eiders, from how it used to be in the "good old days" until nowadays. Thank you for giving me the flexibility to develop my research projects and being open to new ideas, trials and collaborations. Last, but not least, thank you for your meticulousness while proofreading manuscripts (and this thesis).

**Fred**, I would have never guessed that joining the CEBC to study house sparrows in Paris during a gap year would lead me to start a PhD in Finland on eiders (with physiology, on top of that!). Thank you for trusting me during all these years and helping me develop research projects and meet amazing people! Your moral support, supervision and availability during all these years have been excellent and unrivalled!

**Kimi**, although we haven't seen each other much outside of the field season, you have always been of great help and been promptly available when needed! Thank you for the experience and mentoring in the field. I have learnt so much about eiders with you! The last field season without you has been challenging, but we did our best to keep the long-term monitoring going, and your advice was precious. Your feedback has always been positive and enthusiastic! Thank you for encouraging and trusting me!

**Børge** and **Sveinn Are**, enormous thanks for accepting this collaboration and offering me the opportunity to join you in the field! Thank you for such a unique and unforgettable experience! Entering the Seatrack network has also been a big step forward to learning new skills! Børge and Vegard, thank you for hosting me at NINA, making this collaboration possible and teaching me how to analyse GLS data! Thank you, Vegard, for last-minute help with the GLS reader! The results of the geolocator study are, in the end, not part of the thesis, but they will help improve our understanding of Baltic Sea eider migration and, hopefully, long-term conservation of the populations.

**Christophe**, thank you for your time, availability, advice and for teaching me E-SURGE!

I also want to thank the **Service Anabio** (CEBC) for running the hormone assays for these – too numerous and too jelly – samples, and for taking the time to train me! Thank you very much Charline, Marie, Cécile, Emmanuelle and Mathieu! As part of a cotutelle, I have had the chance to spend part of my PhD time at the CEBC, where I have met amazing people and made good friends!

I thank all the people who have been part in the **Eider Team** since the beginning of the monitoring. These long-term data would not have been the same without your help and implication. I acknowledge the ones I met – with special thanks to Heikki Erikkson, Niilo Aro, Ben Steele and Ida Hernansson – but also the ones I did not meet! Thank you, Martin and Kristina, for paving the road with your PhDs, with inspiring papers on behaviour and physiology! I am also grateful to observers at HALIAS for the hours spent counting eagles and eiders, with special acknowledgement to Aleksi Lehikoinen for compiling the data and providing information on eider phenology and eagle abundance.

Speaking of fieldwork teams, I cannot forget to mention the extraordinary people that I have had the chance to meet and spend time with at Ny-Ålesund! My greatest thanks go to the Svalbard Eider Team: Børge, Sveinn Are and Céline, with whom I have shared amazing memories! I'm also grateful for the friendly moments and unplanned fieldwork excursions with many other bird (or not) people. Joanna, Clément, Mo, Lea, Torjus, Jesper, Delphin, Geir (thanks for your help during the last days in the field!), Seb, Christophe, Marteen, Nomikos, Hilde, Sam and Tash (see you soon!), without forgetting the French Kittiwake Team: thank you and I'm sure we will cross paths again somewhere!

I want to thank everyone from the Department of Environmental and Marine Biology at ÅAU. Thanks, Jean-François, Lucinda (and Niklas!), Floriaan, Viktor (and Linnea!), Phoebe (and Jazzie), Heidi, Jolle, Johanna (thanks for the company at the ISBE!), Ida, Janni, Joao, Henna, Patrik, Maïté, Pierre, Louise, Lukas, Christina! It was nice meeting you and spending time with you. I also acknowledge the staff team at EMB: Christian (thank you for the interesting discussions and for giving me the opportunity to assist you in your stats course), Tiina (thank you for organising the PhD meetings), Marie, Christoffer, Anna, Conny, Henna, Henka, Mikael, Kai, Karine, Kati, Martin and Sonja. Miguel, Mara and Meme, I have been so happy meeting you, see you soon somewhere around the world! Big thanks to UTU people for all the good times with drinks, food and sometimes science and birds! Special thanks to Elie, Nina, Robin, Aida and Sajjad!

I also thank Tvärminne Zoological Station for providing excellent working facilities and equipment as well as granting access to the monitoring islands. Handling of animals was carried out under approval from the Finnish National Animal Experiment Board and complied with specific regulations at Tvärminne Zoological Station. I am grateful to Åbo Akademi University doctoral program and La Rochelle Universi for funding my PhD project and, more generally, to the Swedish Cultural Foundation in Finland, the Academy of Finland, the Ministry of Agriculture and Forestry of Finland, the Sophie von Julins Stiftelse, Walter and Andrée de Nottbeck Foundation and French CNRS for participating in funding the long-term monitoring of eiders at Tvärminne and data analyses.

I thank Prof Oliver Love and Dr Christophe Barbraud for participating in my PhD committee and providing me guidance as well as a really inspiring discussion. I also thank Prof Kai Lindström for acting as half-time seminar opponent and custos during my upcoming PhD defence. I acknowledge Prof Michaela Hau and associate Prof Kimberley Mathot for pre-examining my thesis, as well as assistant Prof Suvi Ruuskanen and Prof Jon Brommer for agreeing to act as opponents during the upcoming PhD defence.

Last, but not least, I cannot conclude without thanking my dearest friends and family. Thank you, Julie and Martin, for being the best housemates ever and I'm happy that we keep exchanging about life and projects despite the distance! Léa, thank you for being a great friend, and for always being supportive! Pauline, I'm glad to have met you and to share an office with you (you're the best officemate!), it's always a pleasure to come back to Chizé thanks to you! Adrien, thank you for listening to me, and taking me out to see birds and spend time in the wild. The biggest thank you of course goes to my family, who has always been there for me and supported me along the way, merci!

Villiers-en-Bois, September 15, 2023

*Bertille Mohring*

# References

Abbey-Lee, R. N., Mathot, K. J., & Dingemanse, N. J. (2016). Behavioral and morphological responses to perceived predation risk: A field experiment in passerines. *Behavioral Ecology*, *27*(3), 857–864. https://doi.org/10.1093/beheco/arv228

Abrams, P. A. (2000). The evolution of predator-prey interactions: Theory and evidence. *Annual Review of Ecology and Systematics*, *31*(1), 79–105. https://doi.org/10.1146/annurev.ecolsys.31.1.79

Agrawal, A. A., Laforsch, C., & Tollrian, R. (1999). Transgenerational induction of defences in animals and plants. *Nature*, *401*(6748), 60–63. https://doi.org/10.1038/43425

Albrecht, T., & Klvaňa, P. (2004). Nest crypsis, reproductive value of a clutch and escape decisions in incubating female mallards *Anas platyrhynchos*. *Ethology*, *110*(8), 603–613. https://doi.org/10.1111/j.1439-0310.2004.00992.x

Allen, M. C., Clinchy, M., & Zanette, L. Y. (2022). Fear of predators in free-living wildlife reduces population growth over generations. *Proceedings of the National Academy of Sciences*, *119*(7), e2112404119. https://doi.org/10.1073/pnas.2112404119

Almasi, B., Rettenbacher, S., Müller, C., Brill, S., Wagner, H., & Jenni, L. (2012). Maternal corticosterone is transferred into the egg yolk. *General and Comparative Endocrinology*, *178*(1), 139–144. https://doi.org/10.1016/j.ygcen.2012.04.032

Ames, E. M., Gade, M. R., Nieman, C. L., Wright, J. R., Tonra, C. M., Marroquin, C. M., Tutterow, A. M., & Gray, S. M. (2020). Striving for population-level conservation: Integrating physiology across the biological hierarchy. *Conservation Physiology*, *8*(1), coaa019. https://doi.org/10.1093/conphys/coaa019

Amo, L., Visser, M. E., & Oers, K. van. (2011). Smelling out predators is innate in birds. *Ardea*, *99*(2), 177–184. https://doi.org/10.5253/078.099.0207

Angelier, F., Barbraud, C., Lormée, H., Prud'homme, F., & Chastel, O. (2006). Kidnapping of chicks in emperor penguins: A hormonal by-product? *Journal of Experimental Biology*, *209*(8), 1413–1420. https://doi.org/10.1242/jeb.02138

Angelier, F., & Chastel, O. (2009). Stress, prolactin and parental investment in birds: A review. *General and Comparative Endocrinology*, *163*(1–2), 142–148. https://doi.org/10.1016/j.ygcen.2009.03.028

Angelier, F., Clément-Chastel, C., Welcker, J., Gabrielsen, G. W., & Chastel, O. (2009). How does corticosterone affect parental behaviour and reproductive success? A study of prolactin in black-legged kittiwakes: *Corticosterone, prolactin and parental behaviour*. *Functional Ecology*, *23*(4), 784–793. https://doi.org/10.1111/j.1365-2435.2009.01545.x

Angelier, F., Moe, B., Blanc, S., & Chastel, O. (2009). What factors drive prolactin and corticosterone responses to stress in a long-lived bird species (Snow Petrel *Pagodroma nivea* )? *Physiological and Biochemical Zoology*, *82*(5), 590–602. https://doi.org/10.1086/603634

Angelier, F., Moe, B., Weimerskirch, H., & Chastel, O. (2007). Age-specific reproductive success in a long-lived bird: Do older parents resist stress better? *Journal of Animal Ecology*, *76*(6), 1181–1191. https://doi.org/10.1111/j.1365-2656.2007.01295.x

Angelier, F., Shaffer, S. A., Weimerskirch, H., & Chastel, O. (2006). Effect of age, breeding experience and senescence on corticosterone and prolactin levels in a long-lived seabird: The wandering albatross. *General and Comparative Endocrinology*, *149*(1), 1–9.

https://doi.org/10.1016/j.ygcen.2006.04.006

Angelier, F., Tonra, C. M., Holberton, R. L., & Marra, P. P. (2010). How to capture wild passerine species to study baseline corticosterone levels. *Journal of Ornithology*, *151*(2), 415–422. https://doi.org/10.1007/s10336-009-0471-6

Angelier, F., Weimerskirch, H., Dano, S., & Chastel, O. (2007). Age, experience and reproductive performance in a long-lived bird: A hormonal perspective. *Behavioral Ecology and Sociobiology*, *61*(4), 611–621. https://doi.org/10.1007/s00265-006-0290-1

Angelier, F., & Wingfield, J. C. (2013). Importance of the glucocorticoid stress response in a changing world: Theory, hypotheses and perspectives. *General and Comparative Endocrinology*, *190*, 118–128. https://doi.org/10.1016/j.ygcen.2013.05.022

Angelier, F., Wingfield, J. C., Parenteau, C., Pellé, M., & Chastel, O. (2015). Does short-term fasting lead to stressed-out parents? A study of incubation commitment and the hormonal stress responses and recoveries in snow petrels. *Hormones and Behavior*, *67*, 28–37. https://doi.org/10.1016/j.yhbeh.2014.11.009

Angelier, F., Wingfield, J. C., Tartu, S., & Chastel, O. (2016). Does prolactin mediate parental and life-history decisions in response to environmental conditions in birds? A review. *Hormones and Behavior*, *77*, 18–29. https://doi.org/10.1016/j.yhbeh.2015.07.014

Angelier, F., Wingfield, J. C., Trouvé, C., de Grissac, S., & Chastel, O. (2013). Modulation of the prolactin and the corticosterone stress responses: Do they tell the same story in a long-lived bird, the Cape petrel? *General and Comparative Endocrinology*, *182*, 7–15. https://doi.org/10.1016/j.ygcen.2012.10.008

Anker-Nilssen, T., Fayet, A. L., & Aarvak, T. (2023). Top-down control of a marine mesopredator: Increase in native white-tailed eagles accelerates the extinction of an endangered seabird population. *Journal of Applied Ecology*, 1365-2664.14343. https://doi.org/10.1111/1365-2664.14343

Bårdsen, B.-J., Hanssen, S. A., & Bustnes, J. O. (2018). Multiple stressors: Modeling the effect of pollution, climate, and predation on viability of a sub-arctic marine bird. *Ecosphere*, *9*(7), e02342. https://doi.org/10.1002/ecs2.2342

Barrett, R. T. (2008). Recent establishments and extinctions of Northern Gannet *Morus bassanus* colonies in North Norway, 1995-2008. *Ornis Norvegica*, *31*(0), 172. https://doi.org/10.15845/on.v31i0.168

Barrett, R. T., Lorentsen, S.-H., & Anker-Nilssen, T. (2006). The status of breeding seabirds in mainland Norway. *Atlantic Seabirds*, *8*(3), 97–126.

Baugh, A. T., Schaper, S. V., Hau, M., Cockrem, J. F., De Goede, P., & Oers, K. V. (2012). Corticosterone responses differ between lines of great tits (*Parus major*) selected for divergent personalities. *General and Comparative Endocrinology*, *175*(3), 488–494. https://doi.org/10.1016/j.ygcen.2011.12.012

Baugh, A. T., Senft, R. A., Firke, M., Lauder, A., Schroeder, J., Meddle, S. L., Van Oers, K., & Hau, M. (2017). Risk-averse personalities have a systemically potentiated neuroendocrine stress axis: A multilevel experiment in Parus major. *Hormones and Behavior*, *93*, 99–108. https://doi.org/10.1016/j.yhbeh.2017.05.011

Bell, A. M. (2007). Future directions in behavioural syndromes research. *Proceedings of the Royal Society B: Biological Sciences*, *274*(1611), 755–761. https://doi.org/10.1098/rspb.2006.0199

Bell, A. M., Dingemanse, N. J., Hankison, S. J., Langenhof, M. B. W., & Rollins, K. (2011). Early exposure to nonlethal predation risk by size-selective predators increases somatic growth and decreases size at adulthood in threespined sticklebacks: Predation, growth and life history in sticklebacks. *Journal of Evolutionary Biology*, *24*(5), 943–953. https://doi.org/10.1111/j.1420-9101.2011.02247.x

Bell, A. M., Hankison, S. J., & Laskowski, K. L. (2009). The repeatability of behaviour: A meta-analysis. *Animal Behaviour*, *77*(4), 771–783. https://doi.org/10.1016/j.anbehav.2008.12.022

Bell, A. M., McGhee, K. E., & Stein, L. R. (2016). Effects of mothers' and fathers' experience with predation risk on the behavioral development of their offspring in threespined sticklebacks. *Current Opinion in Behavioral Sciences*, *7*, 28–32. https://doi.org/10.1016/j.cobeha.2015.10.011

Berger, S., Wikelski, M., Romero, L. M., Kalko, E. K. V., & Rödl, T. (2007). Behavioral and physiological adjustments to new predators in an endemic island species, the Galápagos marine iguana. *Hormones and Behavior*, *52*(5), 653–663. https://doi.org/10.1016/j.yhbeh.2007.08.004

Bergman, J. N., Bennett, J. R., Binley, A. D., Cooke, S. J., Fyson, V., Hlina, B. L., Reid, C. H., Vala, M. A., & Madliger, C. L. (2019). Scaling from individual physiological measures to population-level demographic change: Case studies and future directions for conservation management. *Biological Conservation*, *238*, 108242. https://doi.org/10.1016/j.biocon.2019.108242

Béziers, P., Korner-Nievergelt, F., Jenni, L., Roulin, A., & Almasi, B. (2020). Glucocorticoid levels are linked to lifetime reproductive success and survival of adult barn owls. *Journal of Evolutionary Biology*, *33*(12), 1689–1703. https://doi.org/10.1111/jeb.13707

Birdlife International. (2021). European red list of birds. *Publications Office of the European Union*.

Blumstein, D. T. (2019). What chasing birds can teach us about predation risk effects: Past insights and future directions. *Journal of Ornithology*, *160*(2), 587–592. https://doi.org/10.1007/s10336-019-01634-1

Bolduc, F., & Guillemette, M. (2003). Human disturbance and nesting success of common eiders: Interaction between visitors and gulls. *Biological Conservation*, *110*(1), 77–83. https://doi.org/10.1016/S0006-3207(02)00178-7

Bonesi, L., & Palazon, S. (2007). The American mink in Europe: Status, impacts, and control. *Biological Conservation*, *134*(4), 470–483. https://doi.org/10.1016/j.biocon.2006.09.006

Bonier, F., Martin, P. R., Moore, I. T., & Wingfield, J. C. (2009). Do baseline glucocorticoids predict fitness? *Trends in Ecology & Evolution*, *24*(11), 634–642. https://doi.org/10.1016/j.tree.2009.04.013

Bonier, F., Moore, I. T., & Robertson, R. J. (2011). The stress of parenthood? Increased glucocorticoids in birds with experimentally enlarged broods. *Biology Letters*, *7*(6), 944–946. https://doi.org/10.1098/rsbl.2011.0391

Boonstra, R., Hik, D., Singleton, G. R., & Tinnikov, A. (1998). The impact of predator-induced stress on the snowshoe hare cycle. *Ecological Monographs*, *68*(3), 371–394.

Bowen, W. D., Iverson, S. J., Mcmillan, J. I., & Boness, D. J. (2006). Reproductive performance in grey seals: Age-related improvement and senescence in a capital breeder. *Journal of Animal Ecology*, *75*(6), 1340–1351. https://doi.org/10.1111/j.1365-2656.2006.01157.x

Bregnballe, T., Tofft, J., Kotzerka, J., Lehikoinen, A., Rusanen, P., Herrmann, C., Krone, O., Engström, H., Rattiste, K., Reich, J., & Kouzov, S. A. (2022). Occurrence and behaviour of white-tailed eagles *Haliaeetus albicilla* in great cormorant *Phalacrocorax carbo sinensis* colonies in countries around the Baltic Sea. *Ardea*, *109*(3).

https://doi.org/10.5253/arde.v109i2.a24

Broom, M., & Ruxton, G. D. (2005). You can run—Or you can hide: Optimal strategies for cryptic prey against pursuit predators. *Behavioral Ecology*, *16*(3), 534–540. https://doi.org/10.1093/beheco/ari024

Brown, C., Gardner, C., & Braithwaite, V. A. (2005). Differential stress responses in fish from areas of high- and low-predation pressure. *Journal of Comparative Physiology B*, *175*(5), 305–312. https://doi.org/10.1007/s00360-005-0486-0

Buntin, J. D. (1996). Neural and hormonal control of parental behavior in birds. In *Advances in the Study of Behavior* (Vol. 25, pp. 161–213). Elsevier. https://doi.org/10.1016/S0065-3454(08)60333-2

Burnham, K. P., & Anderson, D. R. (2002). A practical information-theoretic approach. *Model Selection and Multimodel Inference, 2nd Ed. Springer, New York*, *2*.

Busch, D. S., & Hayward, L. S. (2009). Stress in a conservation context: A discussion of glucocorticoid actions and how levels change with conservation-relevant variables. *Biological Conservation*, *142*(12), 2844–2853. https://doi.org/10.1016/j.biocon.2009.08.013

Cabrera, D., Andres, D., McLoughlin, P. D., Debeffe, L., Medill, S. A., Wilson, A. J., & Poissant, J. (2017). Island tameness and the repeatability of flight initiation distance in a large herbivore. *Canadian Journal of Zoology*, *95*(10), 771–778. https://doi.org/10.1139/cjz-2016-0305

Cam, E., Link, W. A., Cooch, E. G., Monnat, J., & Danchin, E. (2002). Individual covariation in life-history traits: Seeing the trees despite the forest. *The American Naturalist*, *159*(1), 96–105. https://doi.org/10.1086/324126

Candolin, U. (1998). Reproduction under predation risk and the trade–off between current and future reproduction in the threespine stickleback. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *265*(1402), 1171–1175. https://doi.org/10.1098/rspb.1998.0415

Carlitz, E. H. D., Lindholm, A. K., Gao, W., Kirschbaum, C., & König, B. (2022). Steroid hormones in hair and fresh wounds reveal sex specific costs of reproductive engagement and reproductive success in wild house mice (*Mus musculus domesticus*). *Hormones and Behavior*, *138*, 105102. https://doi.org/10.1016/j.yhbeh.2021.105102

Caro, T. (2005). *Antipredator defenses in birds and mammals*. University of Chicago Press.

Carrete, M., & Tella, J. L. (2010). Individual consistency in flight initiation distances in burrowing owls: A new hypothesis on disturbance-induced habitat selection. *Biology Letters*, *6*(2), 167–170. https://doi.org/10.1098/rsbl.2009.0739

Catry, T., Moreira, F., Alcazar, R., Rocha, P. A., & Catry, I. (2017). Mechanisms and fitness consequences of laying decisions in a migratory raptor. *Behavioral Ecology*, *28*(1), 222–232. https://doi.org/10.1093/beheco/arw150

Ceballos, G., Ehrlich, P. R., Barnosky, A. D., García, A., Pringle, R. M., & Palmer, T. M. (2015). Accelerated modern human–induced species losses: Entering the sixth mass extinction. *Science Advances*, *1*(5), e1400253. https://doi.org/10.1126/sciadv.1400253

Ceballos, G., García, A., & Ehrlich, P. R. (2010). The sixth extinction crisis: Loss of animal populations and species. *Journal of Cosmology*, *8*(1821), 31.

Cerini, F., Childs, D. Z., & Clements, C. F. (2023). A predictive timeline of wildlife population collapse. *Nature Ecology & Evolution*, *7*(3), 320–331. https://doi.org/10.1038/s41559-023-01985-2

Chastel, O., Lacroix, A., Weimerskirch, H., & Gabrielsen, G. (2005). Modulation of prolactin but not corticosterone responses to stress in relation to parental effort in a long-lived bird. *Hormones and Behavior*, *47*(4), 459–466.

https://doi.org/10.1016/j.yhbeh.2004.10.009

Chastel, O., & Lormée, H. (2002). Patterns of prolactin secretion in relation to incubation failure in a tropical seabird, the Red-footed booby. *The Condor*, *104*(4), 873–876. https://doi.org/10.1093/condor/104.4.873

Cherel, Y., Robin, J.-P., & Maho, Y. L. (1988). Physiology and biochemistry of long-term fasting in birds. *Canadian Journal of Zoology*, *66*(1), 159–166. https://doi.org/10.1139/z88-022

Chevin, L.-M., Lande, R., & Mace, G. M. (2010). Adaptation, plasticity, and extinction in a changing environment: Towards a predictive theory. *PLoS Biology*, *8*(4), e1000357. https://doi.org/10.1371/journal.pbio.1000357

Chin, E. H., Love, O. P., Verspoor, J. J., Williams, T. D., Rowley, K., & Burness, G. (2009). Juveniles exposed to embryonic corticosterone have enhanced flight performance. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1656), 499–505. https://doi.org/10.1098/rspb.2008.1294

Clark, C. W. (1994). Antipredator behavior and the asset-protection principle. *Behavioral Ecology*, *5*(2), 159–170. https://doi.org/10.1093/beheco/5.2.159

Clinchy, M., Zanette, L., Boonstra, R., Wingfield, J. C., & Smith, J. N. M. (2004). Balancing food and predator pressure induces chronic stress in songbirds. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *271*(1556), 2473–2479. https://doi.org/10.1098/rspb.2004.2913

Clutton-Brock, T. H. (1991). *The evolution of parental care* (Vol. 64). Princeton University Press.

Clutton-Brock, T., & Sheldon, B. C. (2010). Individuals and populations: The role of long-term, individual-based studies of animals in ecology and evolutionary biology. *Trends in Ecology & Evolution*, *25*(10), 562–573. https://doi.org/10.1016/j.tree.2010.08.002

Cockrem, J. F., & Silverin, B. (2002). Sight of a predator can stimulate a corticosterone response in the Great tit (*Parus major*). *General and Comparative Endocrinology*, *125*(2), 248–255. https://doi.org/10.1006/gcen.2001.7749

Comendant, T., Sinervo, B., Svensson, E. I., & Wingfield, J. (2003). Social competition, corticosterone and survival in female lizard morphs. *Journal of Evolutionary Biology*, *16*(5), 948–955. https://doi.org/10.1046/j.1420-9101.2003.00598.x

Conway, C. J., & Martin, T. E. (2000). Evolution of passerine incubation behavior: Influence of food, temperature, and nest predation. *Evolution*, *54*(2), 670–685. https://doi.org/10.1111/j.0014-3820.2000.tb00068.x

Cooper Jr, W. E. (2009). Variation in escape behavior among individuals of the striped plateau lizard *Sceloporus virgatus* may reflect differences in boldness. *Journal of Herpetology*, 495–502. https://www.jstor.org/stable/25599244

Cooper Jr, W. E., Hawlena, D., & Pérez-Mellado, V. (2009). Effects of predation risk factors on escape behavior by Balearic lizards (*Podarcis lilfordi*) in relation to optimal escape theory. *Amphibia-Reptilia*, *30*(1), 99–110. https://doi.org/10.1163/156853809787392720

Cooper, W. E., & Frederick, W. G. (2007). Optimal flight initiation distance. *Journal of Theoretical Biology*, *244*(1), 59–67. https://doi.org/10.1016/j.jtbi.2006.07.011

Cooper, W. E., & Sherbrooke, W. C. (2010). Crypsis influences escape decisions in the Round-tailed Horned Lizard (*Phrynosoma modestum*). *Canadian Journal of Zoology*, *88*(10), 1003–1010. https://doi.org/10.1139/Z10-068

Coslovsky, M., Groothuis, T., De Vries, B., & Richner, H. (2012). Maternal steroids in egg yolk as a pathway to translate predation risk to offspring: Experiments with great tits. *General and Comparative Endocrinology*, *176*(2), 211–214. https://doi.org/10.1016/j.ygcen.2012.01.013

Coslovsky, M., & Richner, H. (2011). Predation risk affects offspring growth via maternal effects: Maternal effects due to predation risk. *Functional Ecology*, *25*(4), 878–888. https://doi.org/10.1111/j.1365-2435.2011.01834.x

Coslovsky, M., & Richner, H. (2012). Preparing Offspring for a Dangerous World: Potential Costs of Being Wrong. *PLoS ONE*, *7*(11), e48840. https://doi.org/10.1371/journal.pone.0048840

Cote, J., Clobert, J., Meylan, S., & Fitze, P. S. (2006). Experimental enhancement of corticosterone levels positively affects subsequent male survival. *Hormones and Behavior*, *49*(3), 320–327. https://doi.org/10.1016/j.yhbeh.2005.08.004

Coulson, J. (1984). The population dynamics of the Eider Duck *Somateria mollissima* and evidence of extensive non-breeding by adult ducks. *Ibis*, *126*(4), 525–543. https://doi.org/10.1111/j.1474-919X.1984.tb02078.x

Coulson, J. (2002). Colonial breeding in seabirds. *Biology of Marine Birds*, 87–113.

Creel, S., & Christianson, D. (2008). Relationships between direct predation and risk effects. *Trends in Ecology & Evolution*, *23*(4), 194–201. https://doi.org/10.1016/j.tree.2007.12.004

Crespi, E. J., Williams, T. D., Jessop, T. S., & Delehanty, B. (2013). Life history and the ecology of stress: How do glucocorticoid hormones influence life-history variation in animals? *Functional Ecology*, *27*(1), 93–106. https://doi.org/10.1111/1365-2435.12009

Criscuolo, F., Bertile, F., Durant, J. M., Raclot, T., Gabrielsen, G. W., Massemin, S., & Chastel, O. (2006). Body mass and clutch size may modulate prolactin and corticosterone levels in eiders. *Physiological and Biochemical Zoology*, *79*(3), 514–521. https://doi.org/10.1086/501065

Criscuolo, F., Chastel, O., Gabrielsen, Geir. W., Lacroix, A., & Le Maho, Y. (2002). Factors affecting plasma concentrations of prolactin in the Common eider *Somateria mollissima*. *General and Comparative Endocrinology*, *125*(3), 399–409. https://doi.org/10.1006/gcen.2001.7767

Criscuolo, F., Gauthier-Clerc, M., Gabrielsen, G. W., & Le Maho, Y. (2000). Recess behaviour of the incubating Common Eider *Somateria mollissima*. *Polar Biology*, *23*(8), 571–574. https://doi.org/10.1007/s003000000123

Crossin, G. T., Dawson, A., Phillips, R. A., Trathan, P. N., Gorman, K. B., Adlard, S., & Williams, T. D. (2012). Seasonal patterns of prolactin and corticosterone secretion in an Antarctic seabird that moults during reproduction. *General and Comparative Endocrinology*, *175*(1), 74–81. https://doi.org/10.1016/j.ygcen.2011.10.003

Crossin, G. T., Love, O. P., Cooke, S. J., & Williams, T. D. (2016). Glucocorticoid manipulations in free-living animals: Considerations of dose delivery, life-history context and reproductive state. *Functional Ecology*, *30*(1), 116–125. https://doi.org/10.1111/1365-2435.12482

Crossin, G. T., Phillips, R. A., Lattin, C. R., Romero, L. M., & Williams, T. D. (2013). Corticosterone mediated costs of reproduction link current to future breeding. *General and Comparative Endocrinology*, *193*, 112–120. https://doi.org/10.1016/j.ygcen.2013.07.011

Croxall, J. P., Butchart, S. H. M., Lascelles, B., Stattersfield, A. J., Sullivan, B., Symes, A., & Taylor, P. (2012). Seabird conservation status, threats and priority actions: A global assessment. *Bird Conservation International*, *22*(1), 1–34. https://doi.org/10.1017/S0959270912000020

Cubaynes, S., Doherty, P. F., Schreiber, E. A., & Gimenez, O. (2011). To breed or not to breed: A seabird's response to extreme climatic events. *Biology Letters*, *7*(2), 303–306. https://doi.org/10.1098/rsbl.2010.0778

Curio, E. (1983). Why do young birds reproduce less well? *Ibis*, *125*(3), 400–404. https://doi.org/10.1111/j.1474-919X.1983.tb03130.x

Dammhahn, M., Dingemanse, N. J., Niemelä, P. T., & Réale, D. (2018). Pace-of-life syndromes: A framework for the adaptive integration of behaviour, physiology and life history. *Behavioral Ecology and Sociobiology*, *72*(3), 62, s00265-018-2473-y. https://doi.org/10.1007/s00265-018-2473-y

de Jong, M. E., Nicolaus, M., Fokkema, R. W., & Loonen, M. J. J. E. (2021). State dependence explains individual variation in nest defence behaviour in a long-lived bird. *Journal of Animal Ecology*, *90*(4), 809–819. https://doi.org/10.1111/1365-2656.13411

Delehanty, D. J., Oring, L. W., Fivizzani, A. J., & El Halawani, M. E. (1997). Circulating prolactin of incubating male Wilson's phalaropes corresponds to clutch size and environmental stress. *The Condor*, *99*(2), 397–405. https://doi.org/10.2307/1369946

Descamps, S., Bêty, J., Love, O. P., & Gilchrist, H. G. (2011). Individual optimization of reproduction in a long-lived migratory bird: A test of the condition-dependent model of laying date and clutch size: Optimal reproduction in a long-lived bird. *Functional Ecology*, *25*(3), 671–681. https://doi.org/10.1111/j.1365-2435.2010.01824.x

Descamps, S., Yoccoz, N. G., Gaillard, J.-M., Gilchrist, H. G., Erikstad, K. E., Hanssen, S. A., Cazelles, B., Forbes, M. R., & Bêty, J. (2010). Detecting population heterogeneity in effects of North Atlantic Oscillations on seabird body condition: Get into the rhythm. *Oikos*, *119*(9), 1526–1536. https://doi.org/10.1111/j.1600-0706.2010.18508.x

Desprez, M., Gimenez, O., McMahon, C. R., Hindell, M. A., & Harcourt, R. G. (2018). Optimizing lifetime reproductive output: Intermittent breeding as a tactic for females in a long-lived, multiparous mammal. *Journal of Animal Ecology*, *87*(1), 199–211. https://doi.org/10.1111/1365-2656.12775

DeWitt, P. D., Visscher, D. R., Schuler, M. S., & Thiel, R. P. (2019). Predation risks suppress lifetime fitness in a wild mammal. *Oikos*, *128*(6), 790–797. https://doi.org/10.1111/oik.05935

Dias, M. P., Martin, R., Pearmain, E. J., Burfield, I. J., Small, C., Phillips, R. A., Yates, O., Lascelles, B., Borboroglu, P. G., & Croxall, J. P. (2019). Threats to seabirds: A global assessment. *Biological Conservation*, *237*, 525–537. https://doi.org/10.1016/j.biocon.2019.06.033

Dingemanse, N. J., Kazem, A. J. N., Réale, D., & Wright, J. (2010). Behavioural reaction norms: Animal personality meets individual plasticity. *Trends in Ecology & Evolution*, *25*(2), 81–89. https://doi.org/10.1016/j.tree.2009.07.013

Dingemanse, N. J., & Wolf, M. (2010). Recent models for adaptive personality differences: A review. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1560), 3947–3958. https://doi.org/10.1098/rstb.2010.0221

Doherty, T. S., Glen, A. S., Nimmo, D. G., Ritchie, E. G., & Dickman, C. R. (2016). Invasive predators and global biodiversity loss. *Proceedings of the National Academy of Sciences*, *113*(40), 11261–11265. https://doi.org/10.1073/pnas.1602480113

Ducatez, S., Sol, D., Sayol, F., & Lefebvre, L. (2020). Behavioural plasticity is associated with reduced extinction risk in birds. *Nature Ecology & Evolution*, *4*(6), 788–793. https://doi.org/10.1038/s41559-020-1168-8

Dulude-de Broin, F., Hamel, S., Mastromonaco, G. F., & Côté, S. D. (2020). Predation risk and mountain goat reproduction: Evidence for stress-induced breeding suppression in a wild ungulate. *Functional Ecology*, *34*(5), 1003–1014. https://doi.org/10.1111/1365-2435.13514

Durant, J., Hjermann, D., Ottersen, G., & Stenseth, N. (2007). Climate and the match or mismatch between predator requirements and resource availability. *Climate Research*, *33*, 271–283. https://doi.org/10.3354/cr033271

Eggers, S., Griesser, M., Nystrand, M., & Ekman, J. (2006). Predation risk induces changes in nest-site selection and clutch size in the Siberian jay. *Proceedings of the Royal Society B: Biological Sciences*, *273*(1587), 701–706. https://doi.org/10.1098/rspb.2005.3373

Ekblad, C. (2022). The return of the white-tailed eagle: Ecology of predator-prey relationships in the Baltic Sea and Arctic inland [Doctoral dissertation]. University of Turku.

Ekblad, C. M. S., Sulkava, S., Stjernberg, T. G., & Laaksonen, T. K. (2016). Landscape-scale gradients and temporal changes in the prey species of the White-tailed eagle (*Haliaeetus albicilla*). *Annales Zoologici Fennici*, *53*(3–4), 228–240. https://doi.org/10.5735/086.053.0401

Ekroos, J., Fox, A. D., Christensen, T. K., Petersen, I. K., Kilpi, M., Jónsson, J. E., Green, M., Laursen, K., Cervencl, A., & De Boer, P. (2012). Declines amongst breeding Eider *Somateria mollissima* numbers in the Baltic/Wadden Sea flyway. *Ornis Fennica*, *89*(2), 81.

Ekroos, J., Öst, M., Karell, P., Jaatinen, K., & Kilpi, M. (2012). Philopatric predisposition to predation-induced ecological traps: Habitat-dependent mortality of breeding eiders. *Oecologia*, *170*(4), 979–986. https://doi.org/10.1007/s00442-012-2378-9

Erikstad, K. E., Bustnes, J. O., & Moum, T. (1993). Clutch-size determination in precocial birds: A study of the common eider. *The Auk*, *110*(3), 623–628. https://doi.org/10.2307/4088426

Erikstad, K. E., Fauchald, P., Tveraa, T., & Steen, H. (1998). On the cost of reproduction in long-lived birds: The influence of environmental variability. *Ecology*, *79*(5), 1781–1788. https://doi.org/10.1890/0012-9658(1998)079[1781:OTCORI]2.0.CO;2

Erikstad, K. E., & Tveraa, T. (1995). Does the cost of incubation set limits to clutch size in common eiders *Somateria mollissima*? *Oecologia*, *103*(3), 270–274. https://doi.org/10.1007/BF00328614

Escribano-Avila, G., Pettorelli, N., Virgós, E., Lara-Romero, C., Lozano, J., Barja, I., Cuadra, F. S., & Puerta, M. (2013). Testing Cort-Fitness and Cort-Adaptation hypotheses in a habitat suitability gradient for roe deer. *Acta Oecologica*, *53*, 38–48. https://doi.org/10.1016/j.actao.2013.08.003

Ethan Pride, R. (2005). High faecal glucocorticoid levels predict mortality in ring-tailed lemurs (*Lemur catta*). *Biology Letters*, *1*(1), 60–63. https://doi.org/10.1098/rsbl.2004.0245

Farrar, V. S., Flores, L., Viernes, R. C., Ornelas Pereira, L., Mushtari, S., & Calisi, R. M. (2022). Prolactin promotes parental responses and alters reproductive axis gene expression, but not courtship behaviors, in both sexes of a biparental bird. *Hormones and Behavior*, *144*, 105217. https://doi.org/10.1016/j.yhbeh.2022.105217

Ferrari, M. C. O., Sih, A., & Chivers, D. P. (2009). The paradox of risk allocation: A review and prospectus. *Animal Behaviour*, *78*(3), 579–585. https://doi.org/10.1016/j.anbehav.2009.05.034

Fierst, J. L. (2011). A history of phenotypic plasticity accelerates adaptation to a new environment: Phenotypic plasticity accelerates adaptation. *Journal of Evolutionary Biology*, *24*(9), 1992–2001. https://doi.org/10.1111/j.1420-9101.2011.02333.x

Fischer, D., Marrotte, R. R., Chin, E. H., Coulson, S., & Burness, G. (2020). Maternal glucocorticoid levels during incubation predict breeding success, but not reproductive investment, in a free-ranging bird. *Biology Open*, *9*(10), bio045898. https://doi.org/10.1242/bio.045898

Fisher, R. A. (1930). The genetical theory of natural selection. Clarendon.

Folkestad, A. (2000). Status of the white-tailed sea eagle in Norway. I: Helander, B., Marquiss, M. & Bowerman, W.(eds). Sea eagle 2000. 13–17.

Forslund, P., & Pärt, T. (1995). Age and reproduction in birds—Hypotheses and tests. *Trends in Ecology & Evolution*, *10*(9), 374–378. https://doi.org/10.1016/S0169-5347(00)89141-7

Fox, A. D., Jónsson, J. E., Aarvak, T., Bregnballe, T., Christensen, T. K., Clausen, K. K., Clausen, P., Dalby, L., Holm, T. E., Pavón-Jordan, D., Laursen, K., Lehikoinen, A., Lorentsen, S.-H., Møller, A. P., Nordström, M., Öst, M., Söderquist, P., & Roland Therkildsen, O. (2015). Current and potential threats to Nordic duck populations—A horizon scanning exercise. *Annales Zoologici Fennici*, *52*(4), 193–220. https://doi.org/10.5735/086.052.0404

Frid, A., & Dill, L. (2002). Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology*, *6*(1). https://doi.org/10.5751/ES-00404-060111

Gaillard, J.-M., & Yoccoz, N. G. (2003). Temporal variation in survival of mammals: A case of environmental canalization? *Ecology*, *84*(12), 3294–3306. https://doi.org/10.1890/02-0409

Garamszegi, L. Z., Rosivall, B., Rettenbacher, S., Markó, G., Zsebők, S., Szöllősi, E., Eens, M., Potti, J., & Török, J. (2012). Corticosterone, avoidance of novelty, risk-taking and aggression in a wild bird: No evidence for pleiotropic effects. *Ethology*, *118*(7), 621–635. https://doi.org/10.1111/j.1439-0310.2012.02049.x

Gauthier, G., Milot, E., & Weimerskirch, H. (2012). Estimating dispersal, recruitment and survival in a biennially breeding species, the Wandering Albatross. *Journal of Ornithology*, *152*(S2), 457–467. https://doi.org/10.1007/s10336-010-0541-9

Genovart, M., Negre, N., Tavecchia, G., Bistuer, A., Parpal, L., & Oro, D. (2010). The young, the weak and the sick: Evidence of natural selection by predation. *PLoS ONE*, *5*(3), e9774. https://doi.org/10.1371/journal.pone.0009774

Ghalambor, C. K., & Martin, T. E. (2000). Parental investment strategies in two species of nuthatch vary with stage-specific predation risk and reproductive effort. *Animal Behaviour*, *60*(2), 263–267. https://doi.org/10.1006/anbe.2000.1472

Ghalambor, C. K., McKAY, J. K., Carroll, S. P., & Reznick, D. N. (2007). Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. *Functional Ecology*, *21*(3), 394–407. https://doi.org/10.1111/j.1365-2435.2007.01283.x

Giesing, E. R., Suski, C. D., Warner, R. E., & Bell, A. M. (2011). Female sticklebacks transfer information via eggs: Effects of maternal experience with predators on offspring. *Proceedings of the Royal Society B: Biological Sciences*, *278*(1712), 1753–1759. https://doi.org/10.1098/rspb.2010.1819

Götmark, F., & Andersson, M. (1984). Colonial breeding reduces nest predation in the common gull (*Larus canus*). *Animal Behaviour*, *32*(2), 485–492. https://doi.org/10.1016/S0003-3472(84)80285-7

Goutte, A., Angelier, F., Welcker, J., Moe, B., Clément-Chastel, C., Gabrielsen, G. W., Bech, C., & Chastel, O. (2010). Long-term survival effect of corticosterone manipulation in Black-legged kittiwakes. *General and Comparative Endocrinology*, *167*(2), 246–251. https://doi.org/10.1016/j.ygcen.2010.03.018

Gratto-Trevor, C. L., Oring, L. W., & Fivizzani, A. J. (1991). Effects of blood sampling stress on hormone levels in the semipalmated sandpiper. *Journal of Field Ornithology*, 19–27. https://www.jstor.org/stable/4513598

Grindstaff, J. L., Beaty, L. E., Ambardar, M., & Luttbeg, B. (2022). Integrating theoretical and empirical approaches for a robust understanding of endocrine flexibility. *Journal of Experimental Biology*, *225*(Suppl_1), jeb243408. https://doi.org/10.1242/jeb.243408

Groscolas, R., Lacroix, A., & Robin, J.-P. (2008). Spontaneous egg or chick abandonment in energy-depleted king penguins: A role for corticosterone and prolactin? *Hormones and Behavior*, *53*(1), 51–60. https://doi.org/10.1016/j.yhbeh.2007.08.010

Guillemette, M., Ydenberg, R. C., & Himmelman, J. H. (1992). The role of energy intake rate in prey and habitat selection of common eiders *Somateria mollissima* in winter: A risk-sensitive interpretation. *The Journal of Animal Ecology*, *61*(3), 599. https://doi.org/10.2307/5615

Guindre-Parker, S. (2020). Individual variation in glucocorticoid plasticity: Considerations and future directions. *Integrative and Comparative Biology*, *60*(1), 79–88. https://doi.org/10.1093/icb/icaa003

Hailer, F., Helander, B., Folkestad, A. O., Ganusevich, S. A., Garstad, S., Hauff, P., Koren, C., Nygård, T., Volke, V., Vilà, C., & Ellegren, H. (2006). Bottlenecked but long-lived: High genetic diversity retained in white-tailed eagles upon recovery from population decline. *Biology Letters*, *2*(2), 316–319. https://doi.org/10.1098/rsbl.2006.0453

Hall, M. (1987). External stimuli affecting incubation behavior and prolactin secretion in the duck (Anas platyrhynchos). *Hormones and Behavior*, *21*(3), 269–287. https://doi.org/10.1016/0018-506X(87)90015-8

Hall, M. R. (1986). Plasma concentrations of prolactin during the breeding cycle in the Cape gannet (*Sula capensis*): A foot incubator. *General and Comparative Endocrinology*, *64*(1), 112–121. https://doi.org/10.1016/0016-6480(86)90036-5

Hamel, S., Gaillard, J.-M., Yoccoz, N. G., Loison, A., Bonenfant, C., & Descamps, S. (2010). Fitness costs of reproduction depend on life speed: Empirical evidence from mammalian populations: Fitness costs of reproduction in mammals. *Ecology Letters*, *13*(7), 915–935. https://doi.org/10.1111/j.1461-0248.2010.01478.x

Hanifin, C. T., Brodie, E. D., & Brodie, E. D. (2008). Phenotypic mismatches reveal escape from arms-race coevolution. *PLoS Biology*, *6*(3), e60. https://doi.org/10.1371/journal.pbio.0060060

Hanssen, S. A., Erikstad, K. E., Johnsen, V., & Jan, O. B. (2003). Differential investment and costs during avian incubation determined by individual quality: An experimental study of the common eider (*Somateria mollissima*). *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *270*(1514), 531–537. https://doi.org/10.1098/rspb.2002.2262

Hanssen, S. A., Erikstad, K. E., Sandvik, H., Tveraa, T., & Bustnes, J. O. (2022). Eyes on the future: Buffering increased costs of incubation by abandoning offspring. *Behavioral Ecology*, arac116. https://doi.org/10.1093/beheco/arac116

Hario, M., & Rintala, J. (2016). Population trends in herring gulls (*Larus argentatus*), great black-backed gulls (*Larus marinus*) and lesser black-backed gulls (*Larus fuscus fuscus*) in Finland. *Waterbirds*, *39*(sp1), 10–14. https://doi.org/10.1675/063.039.sp107

Harvey, C. J., Good, T. P., & Pearson, S. F. (2012). Top–down influence of resident and overwintering Bald Eagles (*Haliaeetus leucocephalus*) in a model marine ecosystem. *Canadian Journal of Zoology*, *90*(7), 903–914. https://doi.org/10.1139/z2012-059

Hawlena, D., & Schmitz, O. J. (2010). Physiological stress as a fundamental mechanism linking predation to ecosystem functioning. *The American Naturalist*, *176*(5), 537–556. https://doi.org/10.1086/656495

Hayward, L. S., & Wingfield, J. C. (2004). Maternal corticosterone is transferred to avian yolk and may alter offspring growth and adult phenotype. *General and Comparative Endocrinology*, *135*(3), 365–371. https://doi.org/10.1016/j.ygcen.2003.11.002

Heithaus, M. R., Frid, A., Wirsing, A. J., & Worm, B. (2008). Predicting ecological consequences of marine top predator declines. *Trends in Ecology & Evolution*, *23*(4), 202–210. https://doi.org/10.1016/j.tree.2008.01.003

Helander, B. (2000). The White-tailed Sea Eagle in Sweden–reproduction numbers and trends. Str. 57–67 V: Helander, B., Marquiss, M. & Bowerman, W.(eds). Sea Eagle 2000. 13–17.

Helander, B., Olsson, A., Bignert, A., Asplund, L., & Litzén, K. (2002). The role of DDE, PCB, coplanar PCB and eggshell parameters for reproduction in the white-tailed sea eagle (*Haliaeetus albicilla*) in Sweden. *Ambio*, 386–403.

Helle, E., & Kauhala, K. (1991). Distribution history and present status of the raccoon dog in Finland. *Ecography*, *14*(4), 278–286. https://doi.org/10.1111/j.1600-0587.1991.tb00662.x

Henderson, L. J., Evans, N. P., Heidinger, B. J., Herborn, K. A., & Arnold, K. E. (2017). Do glucocorticoids predict fitness? Linking environmental conditions, corticosterone and reproductive success in the blue tit, *Cyanistes caeruleus*. *Royal Society Open Science*, *4*(10), 170875. https://doi.org/10.1098/rsos.170875

Hentati-Sundberg, J., Berglund, P.-A., Hejdström, A., & Olsson, O. (2021). COVID-19 lockdown reveals tourists as seabird guardians. *Biological Conservation*, *254*, 108950. https://doi.org/10.1016/j.biocon.2021.108950

Hentati-Sundberg, J., Melchiori, S., Berglund, P.-A., & Olsson, O. (2023). Eagle effects on seabird productivity: Effects of a natural experiment. *Biological Conservation*, *284*, 110145. https://doi.org/10.1016/j.biocon.2023.110145

Hermansson, I., Von Numers, M., Jaatinen, K., & Öst, M. (2023). Predation risk and landscape properties shape reproductive output of an endangered sea duck from two subpopulations with contrasting predation risk. *Journal of Ornithology*, *164*(2), 311–326. https://doi.org/10.1007/s10336-022-02036-6

Herr, M. W., Graham, S. P., & Langkilde, T. (2017). Stressed snakes strike first: Hormone levels and defensive behavior in free ranging cottonmouths (*Agkistrodon piscivorus*). *General and Comparative Endocrinology*, *243*, 89–95. https://doi.org/10.1016/j.ygcen.2016.11.003

Hipfner, M. J., Blight, L. K., Lowe, R. W., Wilhelm, S. I., Robertson, G. J., Barrett, R. T., Anker-Nilssen, T., & Good, T. P. (2012). *Unintended consequences: How the recovery of sea eagle* Haliaeetus spp. *populations in the northern hemisphere is affecting seabirds*.

Holopainen, S., Väänänen, V.-M., Vehkaoja, M., & Fox, A. D. (2021). Do alien predators pose a particular risk to duck nests in Northern Europe? Results from an artificial nest experiment. *Biological Invasions*, *23*(12), 3795–3807. https://doi.org/10.1007/s10530-021-02608-2

Holtmann, B., Santos, E. S. A., Lara, C. E., & Nakagawa, S. (2017). Personality-matching habitat choice, rather than behavioural plasticity, is a likely driver of a phenotype-environment covariance. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1864), 20170943. https://doi.org/10.1098/rspb.2017.0943

Hope, S. F., DuRant, S. E., Angelier, F., Hallagan, J. J., Moore, I. T., Parenteau, C., Kennamer, R. A., & Hopkins, W. A. (2020). Prolactin is related to incubation constancy and egg temperature following a disturbance in a precocial bird. *General* *and Comparative Endocrinology*, *295*, 113489. https://doi.org/10.1016/j.ygcen.2020.113489

Hossie, T. J., Ferland-Raymond, B., Burness, G., & Murray, D. L. (2010). Morphological and behavioural responses of frog tadpoles to perceived predation risk: A possible role for corticosterone mediation? *Écoscience*, *17*(1), 100–108. https://doi.org/10.2980/17-1-3312

Hua, F., Sieving, K. E., Fletcher, R. J., & Wright, C. A. (2014). Increased perception of predation risk to adults and offspring alters avian reproductive strategy and performance. *Behavioral Ecology*, *25*(3), 509–519. https://doi.org/10.1093/beheco/aru017

Hull, K. L., Cockrem, J. F., Bridges, J. P., Candy, E. J., & Davidson, C. M. (2007). Effects of corticosterone treatment on growth, development, and the corticosterone response to handling in young Japanese quail (*Coturnix coturnix japonica*). *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, *148*(3), 531–543. https://doi.org/10.1016/j.cbpa.2007.06.423

Humphreys, R. K., & Ruxton, G. D. (2020). Avian distraction displays: A review. *Ibis*, *162*(4), 1125–1145. https://doi.org/10.1111/ibi.12814

Hurrell, J. W. (1995). Decadal trends in the North Atlantic Oscillation: Regional temperatures and precipitation. *Science*, *269*(5224), 676–679. https://doi.org/10.1126/science.269.5224.676

Husak, J. F., Macedonia, J. M., Fox, S. F., & Sauceda, R. C. (2006). Predation cost of conspicuous male coloration in collared lizards (*Crotaphytus collaris*): An experimental test using clay-covered model lizards. *Ethology*, *112*(6), 572–580. https://doi.org/10.1111/j.1439-0310.2005.01189.x

Jaatinen, K., Hermansson, I., Mohring, B., Steele, B. B., & Öst, M. (2022). Mitigating impacts of invasive alien predators on an endangered sea duck amidst high native predation pressure. *Oecologia*, *198*(2), 543–552. https://doi.org/10.1007/s00442-021-05101-8

Jaatinen, K., & Öst, M. (2011). Experience attracts: The role of age in the formation of cooperative brood-rearing coalitions in eiders. *Animal Behaviour*, *81*(6), 1289–1294. https://doi.org/10.1016/j.anbehav.2011.03.020

Jaatinen, K., Öst, M., & Hobson, K. A. (2016). State-dependent capital and income breeding: A novel approach to evaluating individual strategies with stable isotopes. *Frontiers in Zoology*, *13*(1), 24. https://doi.org/10.1186/s12983-016-0157-x

Jaatinen, K., Öst, M., & Lehikoinen, A. (2011). Adult predation risk drives shifts in parental care strategies: A long-term study: Predation and parental care strategies. *Journal of Animal Ecology*, *80*(1), 49–56. https://doi.org/10.1111/j.1365-2656.2010.01757.x

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. https://doi.org/10.1016/j.ygcen.2013.06.022

Jaatinen, K., Seltmann, M. W., & Öst, M. (2014). Context-dependent stress responses and their connections to fitness in a landscape of fear: Stress responses and their connections to fitness. *Journal of Zoology*, *294*(3), 147–153. https://doi.org/10.1111/jzo.12169

Jaatinen, K., Westerbom, M., Norkko, A., Mustonen, O., & Koons, D. N. (2021). Detrimental impacts of climate change may be exacerbated by density-dependent population regulation in blue mussels. *Journal of Animal Ecology*, *90*(3), 562–573. https://doi.org/10.1111/1365-2656.13377

Jacobs, J. D., & Wingfield, J. C. (2000). Endocrine control of life-cycle stages: A constraint on response to the environment?

*The Condor*, *102*(1), 35–51. https://doi.org/10.1093/condor/102.1.35

Jagielski, P. M., Dey, C. J., Gilchrist, H. G., Richardson, E. S., Love, O. P., & Semeniuk, C. A. D. (2021). Polar bears are inefficient predators of seabird eggs. *Royal Society Open Science*, *8*(4), rsos.210391, 210391. https://doi.org/10.1098/rsos.210391

Jagielski, P. M., Dey, C. J., Gilchrist, H. G., Richardson, E. S., & Semeniuk, C. A. D. (2021). Polar bear foraging on common eider eggs: Estimating the energetic consequences of a climate-mediated behavioural shift. *Animal Behaviour*, *171*, 63–75. https://doi.org/10.1016/j.anbehav.2020.11.009

Jimeno, B., Briga, M., Hau, M., & Verhulst, S. (2018). Male but not female zebra finches with high plasma corticosterone have lower survival. *Functional Ecology*, *32*(3), 713–721. https://doi.org/10.1111/1365-2435.13021

Jimeno, B., Prichard, M. R., Landry, D., Wolf, C., Larkin, B., Cheviron, Z., & Breuner, C. (2020). Metabolic rates predict baseline corticosterone and reproductive output in a free-living passerine. *Integrative Organismal Biology*, *2*(1), obaa030. https://doi.org/10.1093/iob/obaa030

Jones, H. P., Tershy, B. R., Zavaleta, E. S., Croll, D. A., Keitt, B. S., Finkelstein, M. E., & Howald, G. R. (2008). Severity of the effects of invasive rats on seabirds: A global review: *Effects of rats on seabirds*. *Conservation Biology*, *22*(1), 16–26. https://doi.org/10.1111/j.1523-1739.2007.00859.x

Karanth, K. U., & Sunquist, M. E. (1995). Prey selection by tiger, leopard and dhole in tropical forests. *The Journal of Animal Ecology*, *64*(4), 439. https://doi.org/10.2307/5647

Kauhala, K. (1996). Introduced carnivores in Europe with special reference to central and northern Europe. *Wildlife Biology*, *2*(3), 197–204. https://doi.org/10.2981/wlb.1996.019

Kenward, R. (1978). Hawks and doves: Factors affecting success and selection in goshawk attacks on woodpigeons. *The Journal of Animal Ecology*, *47*(2), 449–460. https://doi.org/10.2307/3793

Kilpi, M., & Lindström, K. (1997). Habitat-specific clutch size and cost of incubation in common eiders, *Somateria mollissima*. *Oecologia*, *111*(3), 297–301. https://doi.org/10.1007/s004420050238

Kilpi, M., Öst, M., Lindström, K., & Rita, H. (2001). Female characteristics and parental care mode in the crèching system of eiders, *Somateria mollissima*. *Animal Behaviour*, *62*(3), 527–534. https://doi.org/10.1006/anbe.2001.1784

Kitaysky, A. S., Wingfield, J. C., & Piatt, J. F. (1999). Dynamics of food availability, body condition and physiological stress response in breeding Black-legged Kittiwakes: Food availability and stress response in Kittiwakes. *Functional Ecology*, *13*(5), 577–584. https://doi.org/10.1046/j.1365-2435.1999.00352.x

Koolhaas, J. M., Korte, S. M., De Boer, S. F., Van Der Vegt, B. J., Van Reenen, C. G., Hopster, H., De Jong, I. C., Ruis, M. A. W., & Blokhuis, H. J. (1999). Coping styles in animals: Current status in behavior and stress-physiology. *Neuroscience & Biobehavioral Reviews*, *23*(7), 925–935. https://doi.org/10.1016/S0149-7634(99)00026-3

Korschgen, C. E. (1977). Breeding stress of female eiders in Maine. *The Journal of Wildlife Management*, *41*(3), 360–373. https://doi.org/10.2307/3800505

Kosztolányi, A., Küpper, C., Chastel, O., Parenteau, C., Yılmaz, K. T., Miklósi, Á., Székely, T., & Lendvai, Á. Z. (2012). Prolactin stress response does not predict brood desertion in a polyandrous shorebird. *Hormones and Behavior*, *61*(5), 734–740. https://doi.org/10.1016/j.yhbeh.2012.03.011

Krebs, C. J., Boonstra, R., Boutin, S., & Sinclair, A. R. E. (2001). What drives the 10-year cycle of snowshoe hares? *BioScience*, *51*(1), 25.

https://doi.org/10.1641/0006-3568(2001)051[0025:WDTYCO]2.0.CO;2

Krebs, C. J., Boutin, S., Boonstra, R., Sinclair, A. R. E., Smith, J. N. M., Dale, M. R. T., Martin, K., & Turkington, R. (1995). Impact of food and predation on the snowshoe hare cycle. *Science*, *269*(5227), 1112–1115. https://doi.org/10.1126/science.269.5227.1112

Kulkarni, P. S., & Gramapurohit, N. P. (2017). Effect of corticosterone on larval growth, antipredator behaviour and metamorphosis of *Hylarana indica*. *General and Comparative Endocrinology*, *251*, 21–29. https://doi.org/10.1016/j.ygcen.2016.09.001

Kurvinen, L., Kilpi, M., Nordström, M., & Öst, M. (2016). Drivers of decline and changed nest-site preference of the Baltic eider: An island-level analysis from south-western Finland. *Ornis Fennica*, *93*(1).

LaManna, J. A., & Martin, T. E. (2016). Costs of fear: Behavioural and life-history responses to risk and their demographic consequences vary across species. *Ecology Letters*, *19*(4), 403–413. https://doi.org/10.1111/ele.12573

LaManna, J. A., & Martin, T. E. (2017). Seasonal fecundity and costs to λ are more strongly affected by direct than indirect predation effects across species. *Ecology*, *98*(7), 1829–1838. https://doi.org/10.1002/ecy.1860

Lancaster, L. T., Hazard, L. C., Clobert, J., & Sinervo, B. R. (2008). Corticosterone manipulation reveals differences in hierarchical organization of multidimensional reproductive trade-offs in r-strategist and K-strategist females. *Journal of Evolutionary Biology*, *21*(2), 556–565. https://doi.org/10.1111/j.1420-9101.2007.01478.x

Langenhof, M. R., & Komdeur, J. (2018). Why and how the early-life environment affects development of coping behaviours. *Behavioral Ecology and Sociobiology*, *72*(3), 34. https://doi.org/10.1007/s00265-018-2452-3

Langerhans, R. B. (2007). Evolutionary consequences of predation: Avoidance, escape, reproduction, and diversification. In A. M. T. Elewa (Ed.), *Predation in Organisms* (pp. 177–220). Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-540-46046-6_10

Langlois Lopez, S., Bond, A. L., O'Hanlon, N. J., Wilson, J. M., Vitz, A., Mostello, C. S., Hamilton, F., Rail, J.-F., Welch, L., Boettcher, R., Wilhelm, S. I., Anker-Nilssen, T., Daunt, F., & Masden, E. (2023). Global population and conservation status of the Great Black-backed Gull *Larus marinus*. *Bird Conservation International*, *33*, e23. https://doi.org/10.1017/S0959270922000181

Lawton, J. (1991). From physiology to population dynamics and communities. *Functional Ecology*, 155–161.

Lebreton, J., & Clobert, J. (1991). Bird population dynamics, management, and conservation: The role of mathematical modelling. *Bird Population Studies*, 105–125.

Lebreton, J.-D., Burnham, K. P., Clobert, J., & Anderson, D. R. (1992). Modeling survival and testing biological hypotheses using marked animals: A unified approach with case studies. *Ecological Monographs*, *62*(1), 67–118. https://doi.org/10.2307/2937171

Ledwoń, M., Neubauer, G., Flis, A., & Banach, A. (2023). Female and male body condition in the Whiskered Tern /i>Chlidonias hybrida</i>, a species with female offspring desertion: A test of the differential parental capacity hypothesis. *Journal of Ornithology*. https://doi.org/10.1007/s10336-023-02099-z

Lehikoinen, A., Christensen, T. K., Öst, M., Kilpi, M., Saurola, P., & Vattulainen, A. (2008). Large-scale change in the sex ratio of a declining eider *Somateria mollissima* population. *Wildlife Biology*, *14*(3), 288–301. https://doi.org/10.2981/0909-6396(2008)14[288:LCITSR]2.0.CO;2

Lehikoinen, A., Kilpi, M., & Öst, M. (2006). Winter climate affects subsequent breeding success of common eiders: *Global Change Biology*, *12*(7), 1355–1365. https://doi.org/10.1111/j.1365-2486.2006.01162.x

Lehikoinen, P., Alhainen, M., Frederiksen, M., Jaatinen, K., Juslin, R., Kilpi, M., Mikander, N., & Nagy, S. (2022). *International single species action plan for the conservation of the Common Eider* Somateria m. Mollissima *(Baltic, North & Celtic Seas, and Norway & Russia populations) and* S. m. Borealis *(Svalbard & Franz Josef Land population)*.

Lemaître, J.-F., & Gaillard, J.-M. (2017). Reproductive senescence: New perspectives in the wild: Reproductive senescence in the wild. *Biological Reviews*, *92*(4), 2182–2199. https://doi.org/10.1111/brv.12328

Letnic, M., Ritchie, E. G., & Dickman, C. R. (2012). Top predators as biodiversity regulators: The dingo /i>Canis lupus</i> dingo as a case study. *Biological Reviews*, *87*(2), 390–413. https://doi.org/10.1111/j.1469-185X.2011.00203.x

Liesenjohann, T., & Krause, E. T. (2012). Predation pressure and food abundance during early life alter risk-taking behaviour and growth of guppies (*Poecilia reticulata*). *Behaviour*, *149*(1), 1–14. https://doi.org/10.1163/156853912X623748

Lima, S. L. (1998a). Nonlethal effects in the ecology of predator-prey interactions. *BioScience*, *48*(1), 25–34. https://doi.org/10.2307/1313225

Lima, S. L. (1998b). Stress and decision-making under the risk of predation: Recent developments from behavioral, reproductive, and ecological perspectives. *Advances in the Study of Behaviour*, *27*(8), 215–290.

Lima, S. L. (2009). Predators and the breeding bird: Behavioral and reproductive flexibility under the risk of predation. *Biological Reviews*, *84*(3), 485–513. https://doi.org/10.1111/j.1469-185X.2009.00085.x

Lima, S. L., & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: A review and prospectus. *Canadian Journal of Zoology*, *68*(4), 619–640. https://doi.org/10.1139/z90-092

Lormée, H., Jouventin, P., Trouve, C., & Chastel, O. (2003). Sex-specific patterns in baseline corticosterone and body condition changes in breeding red-footed boobies *Sula sula*: Corticosterone and body condition in boobies. *Ibis*, *145*(2), 212–219. https://doi.org/10.1046/j.1474-919X.2003.00106.x

Love, O. P., Breuner, C. W., Vézina, F., & Williams, T. D. (2004). Mediation of a corticosterone-induced reproductive conflict. *Hormones and Behavior*, *46*(1), 59–65. https://doi.org/10.1016/j.yhbeh.2004.02.001

Love, O. P., & Williams, T. D. (2008). The adaptive value of stress-induced phenotypes: Effects of maternally derived corticosterone on sex-biased investment, cost of reproduction, and maternal fitness. *The American Naturalist*, *172*(4), E135–E149. https://doi.org/10.1086/590959

Luttbeg, B., & Sih, A. (2010). Risk, resources and state-dependent adaptive behavioural syndromes. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1560), 3977–3990. https://doi.org/10.1098/rstb.2010.0207

MacKay, J., & Haskell, M. (2015). Consistent individual behavioral variation: The difference between temperament, personality and behavioral syndromes. *Animals*, *5*(3), 455–478. https://doi.org/10.3390/ani5030366

MacLeod, R., Barnett, P., Clark, J., & Cresswell, W. (2006). Mass-dependent predation risk as a mechanism for house sparrow declines? *Biology Letters*, *2*(1), 43–46. https://doi.org/10.1098/rsbl.2005.0421

Madliger, C. L., & Love, O. P. (2014). The need for a predictive, context-dependent approach to the application of stress hormones in conservation. *Conservation Biology*, *28*(1), 283–287. http://www.jstor.org/stable/24479523

Magnhagen, C. (1991). Predation risk as a cost of reproduction. *Trends in Ecology & Evolution*, *6*(6), 183–186. https://doi.org/10.1016/0169-5347(91)90210-O

Majchrzak, Y. N., Peers, M. J. L., Studd, E. K., Menzies, A. K., Walker, P. D., Shiratsuru, S., McCaw, L. K., Boonstra, R., Humphries, M., Jung, T. S., Kenney, A. J., Krebs, C. J., Murray, D. L., & Boutin, S. (2022). Balancing food acquisition and predation risk drives demographic changes in snowshoe hare population cycles. *Ecology Letters*, *25*(4), 981–991. https://doi.org/10.1111/ele.13975

Malkoc, K., Mentesana, L., Casagrande, S., & Hau, M. (2022). Quantifying glucocorticoid plasticity using reaction norm approaches: There still is so much to discover! *Integrative and Comparative Biology*, *62*(1), 58–70. https://doi.org/10.1093/icb/icab196

Malone, K. M., Powell, A. C., Hua, F., & Sieving, K. E. (2017). Bluebirds perceive prey switching by Cooper's hawks across an urban gradient and adjust reproductive effort. *Écoscience*, *24*(1–2), 21–31. https://doi.org/10.1080/11956860.2017.1346449

Mappes, T., Koskela, E., Ylönen, H., & Ylonen, H. (1998). Breeding suppression in voles under predation risk of small mustelids: Laboratory or methodological artifact? *Oikos*, *82*(2), 365. https://doi.org/10.2307/3546977

Martín, J., de Neve, L., Polo, V., Fargallo, J. A., & Soler, M. (2006). Health-dependent vulnerability to predation affects escape responses of unguarded chinstrap penguin chicks. *Behavioral Ecology and Sociobiology*, *60*(6), 778–784. https://doi.org/10.1007/s00265-006-0221-1

Massaro, M., Setiawan, A. N., & Davis, L. S. (2007). Effects of artificial eggs on prolactin secretion, steroid levels, brood patch development, incubation onset and clutch size in the yellow-eyed penguin (*Megadyptes antipodes*). *General and Comparative Endocrinology*, *151*(2), 220–229. https://doi.org/10.1016/j.ygcen.2007.01.034

Matulla, C., Schöner, W., Alexandersson, H., Von Storch, H., & Wang, X. L. (2008). European storminess: Late nineteenth century to present. *Climate Dynamics*, *31*(2–3), 125–130. https://doi.org/10.1007/s00382-007-0333-y

May, R., Nygård, T., Dahl, E. L., & Bevanger, K. (2013). Habitat utilization in white-tailed eagles (*Haliaeetus albicilla*) and the displacement impact of the Smøla windpower plant. *Wildlife Society Bulletin*, *37*(1), 75–83. https://doi.org/10.1002/wsb.264

McEwen, B. S., & Wingfield, J. C. (2003). The concept of allostasis in biology and biomedicine. *Hormones and Behavior*, *43*(1), 2–15. https://doi.org/10.1016/S0018-506X(02)00024-7

McGhee, K. E., Pintor, L. M., Suhr, E. L., & Bell, A. M. (2012). Maternal exposure to predation risk decreases offspring antipredator behaviour and survival in threespined stickleback. *Functional Ecology*, *26*(4), 932–940. https://doi.org/10.1111/j.1365-2435.2012.02008.x

McNamara, J. M., & Houston, A. I. (1996). State-dependent life histories. *Nature*, *380*(6571), 215–221. https://doi.org/10.1038/380215a0

Mehlum, F. (1991). Egg predation in a breeding colony of the common eider Somateria mollissima in Kongsfjorden, Svalbard. *Norsk Polarinstitutt Skrifter*, *195*, 37–45.

Meylan, S., Miles, D. B., & Clobert, J. (2012). Hormonally mediated maternal effects, individual strategy and global change. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *367*(1596), 1647–1664. https://doi.org/10.1098/rstb.2012.0020

Miles, W. T. S., Parsons, M., Close, A. J., Luxmoore, R., & Furness, R. W. (2013). Predator-avoidance behaviour in a nocturnal petrel exposed to a novel predator. *Ibis*, *155*(1), 16–31. https://doi.org/10.1111/ibi.12007

Mohring, B., Angelier, F., Jaatinen, K., Parenteau, C., & Öst, M. (2021). Parental investment under predation threat in incubating common eiders (*Somateria mollissima*): A hormonal perspective. *Frontiers in Ecology and Evolution*, *9*, 637561. https://doi.org/10.3389/fevo.2021.637561

Mohring, B., Angelier, F., Jaatinen, K., Steele, B., Lönnberg, E., & Öst, M. (2022). Drivers of within- and among-individual variation in risk-taking behaviour during reproduction in a long-lived bird. *Proceedings of the Royal Society B: Biological Sciences*, *289*(20221338). https://doi.org/10.1098/rspb.2022.1338

Mohring, B., Öst, M., Jaatinen, K., Parenteau, C., Grimaud, E., & Angelier, F. (2023). Breeding under pressure: Corticosterone is associated with reproductive investment under fluctuating predation risk in a long-lived sea duck. *Functional Ecology*, *37*(11), 2868-2882. https://doi.org/10.1111/1365-2435.14435

Møller, A. P., & Garamszegi, L. Z. (2012). Between individual variation in risk-taking behavior and its life history consequences. *Behavioral Ecology*, *23*(4), 843–853. https://doi.org/10.1093/beheco/ars040

Montiglio, P.-O., Dammhahn, M., Dubuc Messier, G., & Réale, D. (2018). The pace-of-life syndrome revisited: The role of ecological conditions and natural history on the slow-fast continuum. *Behavioral Ecology and Sociobiology*, *72*(7), 116. https://doi.org/10.1007/s00265-018-2526-2

Moran, N. A. (1992). The evolutionary maintenance of alternative phenotypes. *The American Naturalist*, *139*(5), 971–989. https://doi.org/10.1086/285369

Morosinotto, C., Ruuskanen, S., Thomson, R. L., Siitari, H., Korpimäki, E., & Laaksonen, T. (2013). Predation risk affects the levels of maternal immune factors in avian eggs. *Journal of Avian Biology*, no-no. https://doi.org/10.1111/j.1600-048X.2013.00084.x

Moschilla, J. A., Tomkins, J. L., & Simmons, L. W. (2018). State-dependent changes in risk-taking behaviour as a result of age and residual reproductive value. *Animal Behaviour*, *142*, 95–100. https://doi.org/10.1016/j.anbehav.2018.06.011

Mouton, J. C., Duckworth, R. A., Paitz, R. T., & Martin, T. E. (2022). Nest predation risk and deposition of yolk steroids in a cavity-nesting songbird: An experimental test. *Journal of Experimental Biology*, *225*(7), jeb243047. https://doi.org/10.1242/jeb.243047

Müller, C., Jenni-Eiermann, S., & Jenni, L. (2009). Effects of a short period of elevated circulating corticosterone on postnatal growth in free-living Eurasian kestrels *Falco tinnunculus*. *Journal of Experimental Biology*, *212*(9), 1405–1412. https://doi.org/10.1242/jeb.024455

Mutzel, A., Olsen, A.-L., Mathot, K. J., Araya-Ajoy, Y. G., Nicolaus, M., Wijmenga, J. J., Wright, J., Kempenaers, B., & Dingemanse, N. J. (2019). Effects of manipulated levels of predation threat on parental provisioning and nestling begging. *Behavioral Ecology*, *30*(4), 1123–1135. https://doi.org/10.1093/beheco/arz060

Nakagawa, S., & Schielzeth, H. (2010). Repeatability for Gaussian and non-Gaussian data: A practical guide for biologists. *Biological Reviews*, no-no. https://doi.org/10.1111/j.1469-185X.2010.00141.x

Natsukawa, H., & Sergio, F. (2022). Top predators as biodiversity indicators: A meta-analysis. *Ecology Letters*, *25*(9), 2062–2075. https://doi.org/10.1111/ele.14077

Nelson, E. H., Matthews, C. E., & Rosenheim, J. A. (2004). Predators reduce prey population growth by inducing changes in prey behavior. *Ecology*, *85*(7), 1853–1858. https://doi.org/10.1890/03-3109

Nicol-Harper, A., Doncaster, C. P., Hilton, G. M., Wood, K. A., & Ezard, T. H. G. (2023). Conservation implications of a mismatch between data availability and demographic impact. *Ecology and Evolution*, *13*(7), e10269. https://doi.org/10.1002/ece3.10269

Nicol-Harper, A., Wood, K. A., Diamond, A. W., Major, H. L., Petersen, A., Tertitski, G., Doncaster, C. P., Ezard, T. H. G., & Hilton, G. M. (2021). Vital rate estimates for the common eider *Somateria mollissima*, a data-rich exemplar of the seaduck tribe. *Ecological Solutions and Evidence*, *2*(4). https://doi.org/10.1002/2688-8319.12108

Nordström, M., Högmander, J., Nummelin, J., Laine, J., Laanetu, N., & Korpimäki, E. (2002). Variable responses of waterfowl breeding populations to long-term removal of introduced American mink. *Ecography*, *25*(4), 385–394. https://doi.org/10.1034/j.1600-0587.2002.250401.x

Noreikienė, K., Jaatinen, K., Steele, B. B., & Öst, M. (2021). Glucocorticoids, state-dependent reproductive investment and success in the face of danger in a long-lived bird. *Journal of Ornithology*, *162*(2), 497–509. https://doi.org/10.1007/s10336-020-01847-9

Nummi, P., Vaananen, V.-M., Pekkarinen, A.-J., Eronen, V., Mikkola-Roos, M., Nurmi, J., Rautiainen, A., & Rusanen, P. (2019). Alien predation in wetlands – the Raccoon Dog and water birds breeding success. *BALTIC FORESTRY*, *25*(2), 228–237. https://doi.org/10.46490/vol25iss2pp228

Nunney, L. (2016). Adapting to a changing environment: Modeling the interaction of directional selection and plasticity. *Journal of Heredity*, *107*(1), 15–24. https://doi.org/10.1093/jhered/esv084

O'Dwyer, T., Buttemer, W., Priddel, D., & Downing, J. (2006). Prolactin, body condition and the cost of good parenting: An interyear study in a long-lived seabird, Gould's Petrel (*Pterodroma leucoptera*). *Functional Ecology*, 806–811.

Osiejuk, T. S., & Kuczyński, L. (2007). Factors affecting flushing distance in incubating female greylag geese *Anser anser*. *Wildlife Biology*, *13*(1), 11–18. https://doi.org/10.2981/0909-6396(2007)13[11:FAFDII]2.0.CO;2

Öst, M. (1999). Within-Season and between-year variation in the structure of Common eider broods. *The Condor*, *101*(3), 598–606. https://doi.org/10.2307/1370189

Öst, M., & Bäck, A. (2003). Spatial structure and parental aggression in eider broods. *Animal Behaviour*, *66*(6), 1069–1075. https://doi.org/10.1006/anbe.2003.2300

Öst, M., Lehikoinen, A., & Jaatinen, K. (2021). Top-down effects override climate forcing on reproductive success in a declining sea duck. *Oikos*. https://doi.org/10.1111/oik.08762

Öst, M., Lehikoinen, A., & Jaatinen, K. (2022). Top-down effects override climate forcing on reproductive success in a declining sea duck. *Oikos*, *2022*(3), e08762. https://doi.org/10.1111/oik.08762

Öst, M., Lehikoinen, A., Jaatinen, K., & Kilpi, M. (2011). Causes and consequences of fine-scale breeding dispersal in a female-philopatric species. *Oecologia*, *166*(2), 327–336. https://doi.org/10.1007/s00442-010-1855-2

Öst, M., Lindén, A., Karell, P., Ramula, S., & Kilpi, M. (2018). To breed or not to breed: Drivers of intermittent breeding in a seabird under increasing predation risk and male bias. *Oecologia*, *188*(1), 129–138. https://doi.org/10.1007/s00442-018-4176-5

Öst, M., Noreikiene, K., Angelier, F., & Jaatinen, K. (2020). Sex-specific effects of the in ovo environment on early-life phenotypes in eiders. *Oecologia*, *192*(1), 43–54. https://doi.org/10.1007/s00442-019-04569-9

Öst, M., & Steele, B. B. (2010). Age-specific nest-site preference and success in eiders. *Oecologia*, *162*(1), 59–69. https://doi.org/10.1007/s00442-009-1444-4

Öst, M., Wickman, M., Matulionis, E., & Steele, B. (2008). Habitat-specific clutch size and cost of incubation in eiders reconsidered. *Oecologia*, *158*(2), 205–216. https://doi.org/10.1007/s00442-008-1139-2

Öst, M., Ydenberg, R., Kilpi, M., & Lindström, K. (2003). Condition and coalition formation by brood-rearing common eider females. *Behavioral Ecology*, *14*(3), 311–317. https://doi.org/10.1093/beheco/14.3.311

Ouyang, J. Q., Muturi, M., Quetting, M., & Hau, M. (2013). Small increases in corticosterone before the breeding season increase parental investment but not fitness in a wild passerine bird. *Hormones and Behavior*, *63*(5), 776–781. https://doi.org/10.1016/j.yhbeh.2013.03.002

Ouyang, J. Q., Sharp, P. J., Dawson, A., Quetting, M., & Hau, M. (2011). Hormone levels predict individual differences in reproductive success in a passerine bird. *Proceedings of the Royal Society B: Biological Sciences*, *278*(1717), 2537–2545. https://doi.org/10.1098/rspb.2010.2490

Ouyang, J. Q., Sharp, P., Quetting, M., & Hau, M. (2013). Endocrine phenotype, reproductive success and survival in the great tit, *Parus major*. *Journal of Evolutionary Biology*, *26*(9), 1988–1998. https://doi.org/10.1111/jeb.12202

Palacios, M. G., Bronikowski, A. M., Amer, A., & Gangloff, E. J. (2022). Transgenerational effects of maternal corticosterone across early life in a viviparous snake. *General and Comparative Endocrinology*, 114162. https://doi.org/10.1016/j.ygcen.2022.114162

Palleroni, A., Miller, C. T., Hauser, M., & Marler, P. (2005). Prey plumage adaptation against falcon attack. *Nature*, *434*(7036), 973–974. https://doi.org/10.1038/434973b

Pangle, K. L., Peacor, S. D., & Johannsson, O. E. (2007). Large non-lethal effects of an invasive invertebrate predator on zooplankton population growth rate. *Ecology*, *88*(2), 402–412. https://doi.org/10.1890/06-0768

Parker, H. (1990). Patterns of nutrient and energy expenditure in female common eiders nesting in the high Arctic. *The Auk*, *107*(4), 660–668. https://doi.org/10.2307/4087996

Paterlini, C. A., García, G. O., Riechert, J., & Becker, P. H. (2017). Concentrations of hormones during the mid-Incubation period in kleptoparasitic and honest common terns *Sterna hirundo*. *Acta Ornithologica*, *52*(2), 157–165. https://doi.org/10.3161/00016454AO2017.52.2.004

Patterson, B. D., Ramírez-Chaves, H. E., Vilela, J. F., Soares, A. E. R., & Grewe, F. (2021). On the nomenclature of the American clade of weasels (Carnivora: *Mustelidae*). *Journal of Animal Diversity*, *3*(2), 1–8. https://doi.org/10.52547/JAD.2021.3.2.1

Patterson, S. H., Hahn, T. P., Cornelius, J. M., & Breuner, C. W. (2014). Natural selection and glucocorticoid physiology. *Journal of Evolutionary Biology*, *27*(2), 259–274. https://doi.org/10.1111/jeb.12286

Peacor, S. D., Barton, B. T., Kimbro, D. L., Sih, A., & Sheriff, M. J. (2020). A framework and standardized terminology to facilitate the study of predation-risk effects. *Ecology*, *101*(12). https://doi.org/10.1002/ecy.3152

Peckarsky, B. L., Abrams, P. A., Bolnick, D. I., Dill, L. M., Grabowski, J. H., Luttbeg, B., Orrock, J. L., Peacor, S. D., Preisser, E. L., Schmitz, O. J., & Trussell, G. C. (2008). Revisiting the classics: Considering nonconsumptive effects in textbook examples of predator–prey interactions. *Ecology*, *89*(9), 2416–2425. https://doi.org/10.1890/07-1131.1

Pedersen, H. Chr. (1989). Effects of exogenous prolactin on parental behaviour in free-living female willow ptarmigan *Lagopus l. Lagopus*. *Animal Behaviour*, *38*(6), 926–934. https://doi.org/10.1016/S0003-3472(89)80134-4

Perrins, C. M. (2008). The timing of birds' breeding seasons. *Ibis*, *112*(2), 242–255. https://doi.org/10.1111/j.1474-919X.1970.tb00096.x

Petelle, M. B., McCoy, D. E., Alejandro, V., Martin, J. G. A., & Blumstein, D. T. (2013). Development of boldness and docility in yellow-bellied marmots. *Animal Behaviour*, *86*(6), 1147–1154. https://doi.org/10.1016/j.anbehav.2013.09.016

Petrullo, L., Boutin, S., Lane, J. E., McAdam, A. G., & Dantzer, B. (2023). Phenotype-environment mismatch errors enhance lifetime fitness in wild red squirrels. *Science*, *379*(6629), 269–272. https://doi.org/10.1126/science.abn0665

Pigeon, G., & Pelletier, F. (2018). Direct and indirect effects of early-life environment on lifetime fitness of bighorn ewes. *Proceedings of the Royal Society B: Biological Sciences*, *285*(1870), 20171935. https://doi.org/10.1098/rspb.2017.1935

Pradel, R. (2005). Multievent: An extension of multistate capture-recapture models to uncertain states. *Biometrics*, *61*(2), 442–447. https://doi.org/10.1111/j.1541-0420.2005.00318.x

Pravosudov, V. V., Kitaysky, A. S., Wingfield, J. C., & Clayton, N. S. (2001). Long-term unpredictable foraging conditions and physiological stress response in Mountain chickadees (*Poecile gambeli*). *General and Comparative Endocrinology*, *123*(3), 324–331. https://doi.org/10.1006/gcen.2001.7684

Preisser, E. L., Bolnick, D. I., & Benard, M. F. (2005). Scared to death? The effects of intimidation and consumption in predator–prey interactions. *Ecology*, *86*(2), 501–509. https://doi.org/10.1890/04-0719

Proaktor, G., Milner-Gulland, E. J., & Coulson, T. (2007). Age-related shapes of the cost of reproduction in vertebrates. *Biology Letters*, *3*(6), 674–677. https://doi.org/10.1098/rsbl.2007.0376

Prop, J., Aars, J., BÃ¥rdsen, B.-J., Hanssen, S. A., Bech, C., Bourgeon, S., de Fouw, J., Gabrielsen, G. W., Lang, J., Noreen, E., Oudman, T., Sittler, B., Stempniewicz, L., Tombre, I., Wolters, E., & Moe, B. (2015). Climate change and the increasing impact of polar bears on bird populations. *Frontiers in Ecology and Evolution*, *3*. https://doi.org/10.3389/fevo.2015.00033

Quinn, T. P., & Kinnison, M. T. (1999). Size-selective and sex-selective predation by brown bears on sockeye salmon. *Oecologia*, *121*(2), 273–282. https://doi.org/10.1007/s004420050929

Ramula, S., Öst, M., Linden, A., Karell, P., & Kilpi, M. (2018). Increased male bias in eider ducks can be explained by sex-specific survival of prime-age breeders. *PLoS One*, *13*(4), e0195415. https://doi.org/10.1371/journal.pone.0195415

Réale, D., & Festa-Bianchet, M. (2003). Predator-induced natural selection on temperament in bighorn ewes. *Animal Behaviour*, *65*(3), 463–470. https://doi.org/10.1006/anbe.2003.2100

Réale, D., Garant, D., Humphries, M. M., Bergeron, P., Careau, V., & Montiglio, P.-O. (2010). Personality and the emergence of the pace-of-life syndrome concept at the population level. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1560), 4051–4063. https://doi.org/10.1098/rstb.2010.0208

Réale, D., Reader, S. M., Sol, D., McDougall, P. T., & Dingemanse, N. J. (2007). Integrating animal temperament within ecology and evolution. *Biological Reviews*, *82*(2), 291–318. https://doi.org/10.1111/j.1469-185X.2007.00010.x

Reed, E. T., Gauthier, G., & Giroux, J.-F. (2004). Effects of spring conditions on breeding propensity of greater snow goose females. *Animal Biodiversity and Conservation*, *27*(1), 35–46.

Relyea, R. A. (2002). The many faces of predation: How induction, selection, and thinning combine to alter prey phenotypes. *Ecology*, *83*(7), 1953–1964. https://doi.org/10.1890/0012-9658(2002)083[1953:TMFOPH]2.0.CO;2

Reznick, D. (1985). Costs of reproduction: An evaluation of the empirical evidence. *Oikos*, *44*(2), 257–267. https://doi.org/10.2307/3544698

Ricklefs, R. E., & Wikelski, M. (2002). The physiology/life-history nexus. *Trends in Ecology & Evolution*, *17*(10), 462–468. https://doi.org/10.1016/S0169-5347(02)02578-8

Riddle, O. (1963). Prolactin or progesterone as key to parental behaviour: A review. *Animal Behaviour*, *11*(4), 419–432. https://doi.org/10.1016/0003-3472(63)90256-2

Riechert, J., Becker, P. H., & Chastel, O. (2014). Predicting reproductive success from hormone concentrations in the common tern (*Sterna hirundo*) while considering food abundance. *Oecologia*, *176*(3), 715–727. https://doi.org/10.1007/s00442-014-3040-5

Riechert, J., Chastel, O., & Becker, P. H. (2012). Why do experienced birds reproduce better? Possible endocrine mechanisms in a long-lived seabird, the common tern. *General and Comparative Endocrinology*, *178*(2), 391–399. https://doi.org/10.1016/j.ygcen.2012.06.022

Riechert, J., Chastel, O., & Becker, P. H. (2014). Regulation of breeding behavior: Do energy-demanding periods induce a change in prolactin or corticosterone baseline levels in the common tern (*Sterna hirundo*)? *Physiological and Biochemical Zoology*, *87*(3), 420–431. https://doi.org/10.1086/675682

Riou, S., Chastel, O., Lacroix, A., & Hamer, K. C. (2010). Stress and parental care: Prolactin responses to acute stress throughout the breeding cycle in a long-lived bird. *General and Comparative Endocrinology*, *168*(1), 8–13. https://doi.org/10.1016/j.ygcen.2010.03.011

Rivers, J. W., Liebl, A. L., Owen, J. C., Martin, L. B., & Betts, M. G. (2012). Baseline corticosterone is positively related to juvenile survival in a migrant passerine bird. *Functional Ecology*, *26*(5), 1127–1134. https://doi.org/10.1111/j.1365-2435.2012.02025.x

Rivers, J. W., Newberry, G. N., Schwarz, C. J., & Ardia, D. R. (2017). Success despite the stress: Violet-green swallows increase glucocorticoids and maintain reproductive output despite experimental increases in flight costs. *Functional Ecology*, *31*(1), 235–244. https://doi.org/10.1111/1365-2435.12719

Rodgers, J. A. (1987). On the antipredator advantages of coloniality: A word of caution. *The Wilson Bulletin*, *99*(2), 269–271.

Roff, D. (1993). *Evolution of life histories: Theory and analysis*. Springer Science & Business Media.

Romero, L. M. (2004). Physiological stress in ecology: Lessons from biomedical research. *Trends in Ecology & Evolution*, *19*(5), 249–255. https://doi.org/10.1016/j.tree.2004.03.008

Romero, L. M., Dickens, M. J., & Cyr, N. E. (2009). The reactive scope model—A new model integrating homeostasis, allostasis, and stress. *Hormones and Behavior*, *55*(3), 375–389. https://doi.org/10.1016/j.yhbeh.2008.12.009

Romero, L. M., & Reed, J. M. (2005). Collecting baseline corticosterone samples in the field: Is under 3 min good enough? *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, *140*(1), 73–79. https://doi.org/10.1016/j.cbpb.2004.11.004

Royauté, R., Berdal, M. A., Garrison, C. R., & Dochtermann, N. A. (2018). Paceless life? A meta-analysis of the pace-of-life syndrome hypothesis. *Behavioral Ecology and Sociobiology*, *72*(3), 64. https://doi.org/10.1007/s00265-018-2472-z

Royle, N. J., Smiseth, P. T., & Kölliker, M. (2012). *The evolution of parental care*. Oxford University Press.

Rubenstein, D. R., Parlow, A. F., Hutch, C. R., & Martin, L. B. (2008). Environmental and hormonal correlates of immune activity in a cooperatively breeding tropical bird. *General and Comparative Endocrinology*, *159*(1), 10–15. https://doi.org/10.1016/j.ygcen.2008.07.013

Ruiz-Raya, F., Soler, M., Abaurrea, T., Chastel, O., Roncalli, G., & Ibáñez-Álamo, J. D. (2018). Hormonal responses to non-mimetic eggs: Is brood parasitism a physiological stressor during incubation? *Behavioral Ecology and Sociobiology*, *72*(9), 153. https://doi.org/10.1007/s00265-018-2565-8

Ruxton, G. D., & Lima, S. L. (1997). Predator–induced breeding suppression and its consequences for predator–prey population dynamics. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *264*(1380), 409–415. https://doi.org/10.1098/rspb.1997.0058

Sabal, M. C., Boyce, M. S., Charpentier, C. L., Furey, N. B., Luhring, T. M., Martin, H. W., Melnychuk, M. C., Srygley, R. B., Wagner, C. M., Wirsing, A. J., Ydenberg, R. C., & Palkovacs, E. P. (2021). Predation landscapes influence migratory prey ecology and evolution. *Trends in Ecology & Evolution*, *36*(8), 737–749. https://doi.org/10.1016/j.tree.2021.04.010

Sæther, B.-E., & Bakke, Ø. (2000). Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology*, *81*(3), 642–653. https://doi.org/10.1890/0012-9658(2000)081[0642:ALHVAC]2.0.CO;2

Saino, N., Romano, M., Ferrari, R. P., Martinelli, R., & Møller, A. P. (2005). Stressed mothers lay eggs with high corticosterone levels which produce low-quality offspring. *Journal of Experimental Zoology Part A: Comparative Experimental Biology*, *303A*(11), 998–1006. https://doi.org/10.1002/jez.a.224

Samia, D. S. M., Blumstein, D. T., Stankowich, T., & Cooper, W. E. (2016). Fifty years of chasing lizards: New insights advance optimal escape theory: Fifty years of chasing lizards. *Biological Reviews*, *91*(2), 349–366. https://doi.org/10.1111/brv.12173

Sapolsky, R. M., Romero, L. M., & Munck, A. U. (2000). How do glucocorticoids influence stress responses? Integrating permissive, suppressive, stimulatory, and preparative actions. *Endocrine Reviews*, *21*(1), 55–89. https://doi.org/10.1210/edrv.21.1.0389

Scheuerlein, A., Van't Hof, T., & Gwinner, E. (2001). Predators as stressors? Physiological and reproductive consequences of predation risk in tropical stonechats (*Saxicola torquata axillaris*). *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *268*(1476), 1575–1582. https://doi.org/10.1098/rspb.2001.1691

Schmid, B., Chastel, O., & Jenni, L. (2011). The prolactin response to an acute stressor in relation to parental care and corticosterone in a short-lived bird, the Eurasian hoopoe. *General and Comparative Endocrinology*, *174*(1), 22–29. https://doi.org/10.1016/j.ygcen.2011.07.012

Schoech, S. J., Mumme, R. L., & Wingfield, J. C. (1996). Prolactin and helping behaviour in the cooperatively breeding Florida scrub-jay, *Aphelocoma c. Coerulescens*. *Animal Behaviour*, *52*(3), 445–456. https://doi.org/10.1006/anbe.1996.0189

Schoenemann, K. L., & Bonier, F. (2018). Repeatability of glucocorticoid hormones in vertebrates: A meta-analysis. *PeerJ*, *6*, e4398. https://doi.org/10.7717/peerj.4398

Schüttler, E., Klenke, R., McGehee, S., Rozzi, R., & Jax, K. (2009). Vulnerability of ground-nesting waterbirds to predation by invasive American mink in the Cape Horn Biosphere Reserve, Chile. *Biological Conservation*, *142*(7), 1450–1460. https://doi.org/10.1016/j.biocon.2009.02.013

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*, *120*(1), 77–89. https://doi.org/10.1111/eth.12181

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*(4), 889–896. https://doi.org/10.1016/j.anbehav.2012.07.012

Sénéchal, É., Bêty, J., & Gilchrist, H. G. (2011). Interactions between lay date, clutch size, and postlaying energetic needs in a capital breeder. *Behavioral Ecology*, *22*(1), 162–168. https://doi.org/10.1093/beheco/arq189

Sénéchal, É., Bêty, J., Gilchrist, H. G., Hobson, K. A., & Jamieson, S. E. (2011). Do purely capital layers exist among flying birds? Evidence of exogenous contribution to arctic-nesting common eider eggs. *Oecologia*, *165*(3), 593–604. https://doi.org/10.1007/s00442-010-1853-4

Sharp, P. J., Dawson, A., & Lea, R. W. (1998). Control of luteinizing hormone and prolactin secretion in birds. *Comparative Biochemistry and Physiology Part C: Pharmacology, Toxicology and Endocrinology*, *119*(3), 275–282. https://doi.org/10.1016/S0742-8413(98)00016-4

Sharp, P. J., Macnamee, M. C., Sterling, R. J., Lea, R. W., & Pedersen, H. C. (1988). Relationships between prolactin, LH and broody behaviour in bantam hens. *Journal of Endocrinology*, *118*(2), 279–286. https://doi.org/10.1677/joe.0.1180279

Sharp, S. P., & Clutton-Brock, T. H. (2010). Reproductive senescence in a cooperatively breeding mammal. *Journal of Animal Ecology*, *79*(1), 176–183. https://doi.org/10.1111/j.1365-2656.2009.01616.x

Shaw, A. K., & Levin, S. A. (2013). The evolution of intermittent breeding. *Journal of Mathematical Biology*, *66*(4–5), 685–703. https://doi.org/10.1007/s00285-012-0603-0

Sheldon, B. C., Kruuk, L. E. B., & Alberts, S. C. (2022). The expanding value of long-term studies of individuals in the wild. *Nature Ecology & Evolution*. https://doi.org/10.1038/s41559-022-01940-7

Sheriff, M. J., Krebs, C. J., & Boonstra, R. (2009). The sensitive hare: Sublethal effects of predator stress on reproduction in snowshoe hares. *Journal of Animal Ecology*, *78*(6), 1249–1258. https://doi.org/10.1111/j.1365-2656.2009.01552.x

Sheriff, M. J., Krebs, C. J., & Boonstra, R. (2010). The ghosts of predators past: Population cycles and the role of maternal programming under fluctuating predation risk. *Ecology*, *91*(10), 2983–2994. https://doi.org/10.1890/09-1108.1

Sheriff, M. J., Krebs, C. J., & Boonstra, R. (2011). From process to pattern: How fluctuating predation risk impacts the stress axis of snowshoe hares during the 10-year cycle. *Oecologia*, *166*(3), 593–605. https://doi.org/10.1007/s00442-011-1907-2

Sheriff, M. J., & Thaler, J. S. (2014). Ecophysiological effects of predation risk; an integration across disciplines. *Oecologia*, *176*(3), 607–611. https://doi.org/10.1007/s00442-014-3105-5

Sih, A. (1994). Predation risk and the evolutionary ecology of reproductive behaviour. *Journal of Fish Biology*, *45*(sa), 111–130. https://doi.org/10.1111/j.1095-8649.1994.tb01087.x

Sih, A., Bell, A., & Johnson, J. C. (2004). Behavioral syndromes: An ecological and evolutionary overview. *Trends in Ecology & Evolution*, *19*(7), 372–378. https://doi.org/10.1016/j.tree.2004.04.009

Sih, A., Bell, A. M., & Kerby, J. L. (2004). Two stressors are far deadlier than one. *Trends in Ecology & Evolution*, *19*(6), 274–276. https://doi.org/10.1016/j.tree.2004.02.010

Sinclair, A. R. E., Chitty, D., Stefan, C. I., & Krebs, C. J. (2003). Mammal population cycles: Evidence for intrinsic differences during snowshoe hare cycles. *Canadian Journal of Zoology*, *81*(2), 216–220. https://doi.org/10.1139/z03-006

Sirot, E. (2010). Should risk allocation strategies facilitate or hinder habituation to nonlethal disturbance in wildlife? *Animal Behaviour*, *80*(4), 737–743. https://doi.org/10.1016/j.anbehav.2010.07.014

Smiley, K. O., & Adkins-Regan, E. (2016). Prolactin is related to individual differences in parental behavior and reproductive success in a biparental passerine, the zebra finch (*Taeniopygia guttata*). *General and Comparative Endocrinology*, *234*, 88–94. https://doi.org/10.1016/j.ygcen.2016.03.006

Smiley, K. O., & Adkins-Regan, E. (2018a). Factors that influence the onset of parental care in zebra finches: Roles for egg stimuli and prolactin. *Behavioural Processes*, *153*, 47–54. https://doi.org/10.1016/j.beproc.2018.05.002

Smiley, K. O., & Adkins-Regan, E. (2018b). Lowering prolactin reduces post-hatch parental care in male and female zebra finches (*Taeniopygia guttata*). *Hormones and Behavior*, *98*, 103–114. https://doi.org/10.1016/j.yhbeh.2017.12.011

Smith, R. A., Fort, J., Legagneux, P., Chastel, O., Mallory, M. L., Bustamante, P., Danielsen, J., Hanssen, S. A., Einar Jónsson, J., Magnúsdóttir, E., Moe, B., Parenteau, C., Parkinson, K. J. L., Parsons, G. J., Tertitski, G., & Love, O. P. (2023). Do foraging ecology and contaminants interactively predict parenting hormone levels in common eider? *General and Comparative Endocrinology*, 114261. https://doi.org/10.1016/j.ygcen.2023.114261

Smout, S., King, R., & Pomeroy, P. (2020). Environment-sensitive mass changes influence breeding frequency in a capital breeding marine top predator. *Journal of Animal Ecology*, *89*(2), 384–396. https://doi.org/10.1111/1365-2656.13128

Sockman, K. W., Schwabl, H., & Sharp, P. J. (2000). The role of prolactin in the regulation of clutch size and onset of incubation behavior in the American kestrel. *Hormones and Behavior*, *38*(3), 168–176. https://doi.org/10.1006/hbeh.2000.1616

Soldatini, C., Albores-Barajas, Y., Massa, B., & Gimenez, O. (2016). Forecasting ocean warming impacts on seabird demography: A case study on the European storm petrel. *Marine Ecology Progress Series*, *552*, 255–269. https://doi.org/10.3354/meps11730

Sopinka, N. M., Capelle, P. M., Semeniuk, C. A. D., & Love, O. P. (2017). Glucocorticoids in fish eggs: Variation, interactions with the environment, and the potential to shape offspring fitness. *Physiological and Biochemical Zoology*, *90*(1), 15–33. https://doi.org/10.1086/689994

Sorenson, G. H., Dey, C. J., Madliger, C. L., & Love, O. P. (2017). Effectiveness of baseline corticosterone as a monitoring tool for fitness: A meta-analysis in seabirds. *Oecologia*, *183*(2), 353–365. https://doi.org/10.1007/s00442-016-3774-3

Souchay, G., Gauthier, G., & Pradel, R. (2014). To breed or not: A novel approach to estimate breeding propensity and potential trade-offs in an Arctic-nesting species. *Ecology*, *95*(10), 2745–2756. https://doi.org/10.1890/13-1277.1

Spée, M., Beaulieu, M., Dervaux, A., Chastel, O., Le Maho, Y., & Raclot, T. (2010). Should I stay or should I go? Hormonal control of nest abandonment in a long-lived bird, the Adélie penguin. *Hormones and Behavior*, *58*(5), 762–768. https://doi.org/10.1016/j.yhbeh.2010.07.011

Spée, M., Marchal, L., Lazin, D., Le Maho, Y., Chastel, O., Beaulieu, M., & Raclot, T. (2011). Exogenous corticosterone and nest abandonment: A study in a long-lived bird, the Adélie penguin. *Hormones and Behavior*, *60*(4), 362–370. https://doi.org/10.1016/j.yhbeh.2011.07.003

Stankowich, T., & Blumstein, D. T. (2005). Fear in animals: A meta-analysis and review of risk assessment. *Proceedings of the Royal Society B: Biological Sciences*, *272*(1581), 2627–2634.

https://doi.org/10.1098/rspb.2005.3251

Stearns, S. C. (1992). The evolution of life histories. Oxford: Oxford Univ. Press. 249 p.

Steenweg, R. J., Crossin, G. T., Hennin, H. L., Gilchrist, H. G., & Love, O. P. (2022). Favorable spring conditions can buffer the impact of winter carryover effects on a key breeding decision in an Arctic-breeding seabird. *Ecology and Evolution*, *12*(2). https://doi.org/10.1002/ece3.8588

Stien, J., & Ims, R. A. (2016). Absence from the nest due to human disturbance induces higher nest predation risk than natural recesses in Common Eiders *Somateria mollissima*. *Ibis*, *158*(2), 249–260. https://doi.org/10.1111/ibi.12338

Stier, A. C., Samhouri, J. F., Novak, M., Marshall, K. N., Ward, E. J., Holt, R. D., & Levin, P. S. (2016). Ecosystem context and historical contingency in apex predator recoveries. *Science Advances*, *2*(5), e1501769. https://doi.org/10.1126/sciadv.1501769

Stimson, J., & Berman, M. (1990). Predator induced colour polymorphism in *Danaus plexippus L.* (*Lepidoptera: Nymphalidae*) in Hawaii. *Heredity*, *65*(3), 401–406. https://doi.org/10.1038/hdy.1990.110

Storm, J. J., & Lima, S. L. (2010). Mothers forewarn offspring about predators: A transgenerational maternal effect on behavior. *The American Naturalist*, *175*(3), 382–390. https://doi.org/10.1086/650443

Strong, J. S., Weladji, R. B., Holand, Ø., Røed, K. H., & Nieminen, M. (2017). Personality and fitness consequences of flight initiation distance and mating behavior in subdominant male reindeer (*Rangifer tarandus*). *Ethology*, *123*(6–7), 484–492. https://doi.org/10.1111/eth.12619

Swennen, C. (1990). Dispersal and migratory movements of eiders *Somateria mollissima* breeding in The Netherlands. *Ornis Scandinavica*, *21*(1), 17. https://doi.org/10.2307/3676374

Swennen, C., Ursem, J. C. H., & Duiven, P. (1993). Determinate laying and egg attendance in common eiders. *Ornis Scandinavica*, *24*(1), 48. https://doi.org/10.2307/3676409

Tablado, Z., Bötsch, Y., Bókony, V., Angelier, F., Lendvai, Á. Z., Jenni-Eiermann, S., & Jenni, L. (2021). Factors modulating the behavioral and physiological stress responses: Do they modify the relationship between flight initiation distance and corticosterone reactivity? *Hormones and Behavior*, *132*, 104979. https://doi.org/10.1016/j.yhbeh.2021.104979

Tablado, Z., & Jenni, L. (2017). Determinants of uncertainty in wildlife responses to human disturbance: Modulators of wildlife response to recreation. *Biological Reviews*, *92*(1), 216–233. https://doi.org/10.1111/brv.12224

Taff, C. C., Schoenle, L. A., & Vitousek, M. N. (2018). The repeatability of glucocorticoids: A review and meta-analysis. *General and Comparative Endocrinology*, *260*, 136–145. https://doi.org/10.1016/j.ygcen.2018.01.011

Taff, C. C., & Vitousek, M. N. (2016). Endocrine flexibility: Optimizing phenotypes in a dynamic world? *Trends in Ecology & Evolution*, *31*(6), 476–488. https://doi.org/10.1016/j.tree.2016.03.005

Terraube, J., & Bretagnolle, V. (2018). Top-down limitation of mesopredators by avian top predators: A call for research on cascading effects at the community and ecosystem scale. *Ibis*, *160*(3), 693–702. https://doi.org/10.1111/ibi.12581

Tertitski, G. M., SEMASHKO, E. V., Cherenkov, A. E., & Semashko, V. Y. (2021). Studies of the time budget and daily activity of Common Eider *Somateria mollissima* during incubation. *Marine Ornithology*, *49*, 151–158.

Thaker, M., Lima, S. L., & Hews, D. K. (2009). Acute corticosterone elevation enhances antipredator behaviors in male tree lizard morphs. *Hormones and Behavior*, *56*(1), 51–57. https://doi.org/10.1016/j.yhbeh.2009.02.009

Thierry, A.-M., Brajon, S., Massemin, S., Handrich, Y., Chastel, O., & Raclot, T. (2013). Decreased prolactin levels reduce parental commitment, egg temperatures, and breeding success of incubating male Adélie penguins. *Hormones and Behavior*, *64*(4), 737–747. https://doi.org/10.1016/j.yhbeh.2013.06.003

Tinbergen, J., & Williams, J. (2002). Energetics of incubation. In *Avian Incubation Behaviour, Environment and Evolution* (DC Deeming, pp. 299–313). Oxford University Press: Oxford, UK.

Tjørnløv, R. S., Ens, B. J., Öst, M., Jaatinen, K., Karell, P., Larsson, R., Christensen, T. K., & Frederiksen, M. (2020). Drivers of Spatiotemporal Variation in Survival in a Flyway Population: A Multi-Colony Study. *Frontiers in Ecology and Evolution*, *8*, 566154. https://doi.org/10.3389/fevo.2020.566154

Tjørnløv, R. S., Pradel, R., Choquet, R., Christensen, T. K., & Frederiksen, M. (2019). Consequences of past and present harvest management in a declining flyway population of common eiders *Somateria mollissima*. *Ecology and Evolution*, *9*(22), 12515–12530. https://doi.org/10.1002/ece3.5707

Travers, M., Clinchy, M., Zanette, L., Boonstra, R., & Williams, T. D. (2010). Indirect predator effects on clutch size and the cost of egg production: Indirect predator effects on clutch size. *Ecology Letters*, no-no. https://doi.org/10.1111/j.1461-0248.2010.01488.x

Vada, R., Illanas, S., Acevedo, P., Adriaens, T., Apollonio, M., Belova, O., Blanco-Aguiar, J. A., Csányi, S., Body, G., Fernández-De-Mera, I. G., Ferroglio, E., Jansen, P. A., Jeschke, J. M., Keuling, O., Palazón, S., Plis, K., Podgórski, T., Rickowski, F., Scandura, M., … Vicente, J. (2023). Feral American mink *Neogale vison* continues to expand its European range: Time to harmonise population monitoring and coordinate control. *Mammal Review*, *53*(3), 158–176. https://doi.org/10.1111/mam.12315

van de Pol, M., & Wright, J. (2009). A simple method for distinguishing within- versus between-subject effects using mixed models. *Animal Behaviour*, *77*(3), 753–758. https://doi.org/10.1016/j.anbehav.2008.11.006

Van De Walle, J., Fay, R., Gaillard, J.-M., Pelletier, F., Hamel, S., Gamelon, M., Barbraud, C., Blanchet, F. G., Blumstein, D. T., Charmantier, A., Delord, K., Larue, B., Martin, J., Mills, J. A., Milot, E., Mayer, F. M., Rotella, J., Saether, B.-E., Teplitsky, C., … Jenouvrier, S. (2023). Individual life histories: Neither slow nor fast, just diverse. *Proceedings of the Royal Society B: Biological Sciences*, *290*(2002), 20230511. https://doi.org/10.1098/rspb.2023.0511

Verhulst, S., & Nilsson, J.-Å. (2008). The timing of birds' breeding seasons: A review of experiments that manipulated timing of breeding. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *363*(1490), 399–410. https://doi.org/10.1098/rstb.2007.2146

Viblanc, V. A., Smith, A. D., Gineste, B., Kauffmann, M., & Groscolas, R. (2015). Modulation of heart rate responses to acute stressors throughout the breeding season in a colonial seabird, the king penguin. *Journal of Experimental Biology*, jeb.112003. https://doi.org/10.1242/jeb.112003

Vila Pouca, C., Mitchell, D. J., Lefèvre, J., Vega-Trejo, R., & Kotrschal, A. (2021). Early predation risk shapes adult learning and cognitive flexibility. *Oikos*, *130*(9), 1477–1486. https://doi.org/10.1111/oik.08481

Wada, H., & Sewall, K. B. (2014). Introduction to the symposium—Uniting evolutionary and physiological approaches to understanding phenotypic plasticity. *Integrative and Comparative Biology*, *54*(5), 774–782. https://doi.org/10.1093/icb/icu097

Walker, B. G. (2005). Field endocrinology and conservation biology. *Integrative and Comparative Biology*, *45*(1), 12–18. https://doi.org/10.1093/icb/45.1.12

Wang, Q., & Buntin, J. D. (1999). The roles of stimuli from young, previous breeding experience, and prolactin in regulating parental behavior in ring doves (*Streptopelia risoria*). *Hormones and Behavior*, *35*(3), 241–253. https://doi.org/10.1006/hbeh.1999.1517

Wang, Y., Székely, T., Zhang, Z., & Que, P. (2020). Prolactin concentrations predict parental investment and nest survival in a free-living shorebird. *Hormones and Behavior*, *119*, 104633. https://doi.org/10.1016/j.yhbeh.2019.104633

Watanuki, Y. (1986). Moonlight avoidance behavior in Leach's storm-petrels as a defense against slaty-backed gulls. *The Auk*, *103*(1), 14–22. https://doi.org/10.1093/auk/103.1.14

Wiggins, D. A., Part, T., & Gustafsson, L. (1994). Correlates of clutch desertion by female collared flycatchers *Ficedula albicollis*. *Journal of Avian Biology*, *25*(2), 93. https://doi.org/10.2307/3677025

Wikelski, M., & Cooke, S. J. (2006). Conservation physiology. *Trends in Ecology & Evolution*, *21*(1), 38–46. https://doi.org/10.1016/j.tree.2005.10.018

Williams, C. T., Kitaysky, A. S., Kettle, A. B., & Buck, C. L. (2008). Corticosterone levels of tufted puffins vary with breeding stage, body condition index, and reproductive performance. *General and Comparative Endocrinology*, *158*(1), 29–35. https://doi.org/10.1016/j.ygcen.2008.04.018

Williams, G. C. (1966). Natural selection, the costs of reproduction, and a refinement of Lack's principle. *The American Naturalist*, *100*(916), 687–690. https://doi.org/10.1086/282461

Williams, J. B. (1996). Energetics of avian incubation. *Avian Energetics and Nutritional Ecology*, 375–415.

Williams, T. M., Blackwell, S. B., Richter, B., Sinding, M.-H. S., & Heide-Jørgensen, M. P. (2017). Paradoxical escape responses by narwhals (*Monodon monoceros*). *Science*, *358*(6368), 1328–1331. https://doi.org/10.1126/science.aao2740

Wilson, S., Gil-Weir, K. C., Clark, R. G., Robertson, G. J., & Bidwell, M. T. (2016). Integrated population modeling to assess demographic variation and contributions to population growth for endangered whooping cranes. *Biological Conservation*, *197*, 1–7. https://doi.org/10.1016/j.biocon.2016.02.022

Wingfield, J. C. (2003). Control of behavioural strategies for capricious environments. *Animal Behaviour*, *66*(5), 807–816. https://doi.org/10.1006/anbe.2003.2298

Wingfield, J. C., Kelley, J. P., & Angelier, F. (2011). What are extreme environmental conditions and how do organisms cope with them? *Current Zoology*, *57*(3), 363–374. https://doi.org/10.1093/czoolo/57.3.363

Wingfield, J. C., Maney, D. L., Breuner, C. W., Jacobs, J. D., Lynn, S., Ramenofsky, M., & Richardson, R. D. (1998). Ecological bases of hormone-behavior interactions: The "emergency life history stage". *American Zoologist*, *38*(1), 191–206. https://doi.org/10.1093/icb/38.1.191

Wingfield, J. C., & Sapolsky, R. M. (2003). Reproduction and resistance to stress: When and how. *Journal of Neuroendocrinology*, *15*(8), 711–724. https://doi.org/10.1046/j.1365-2826.2003.01033.x

Wolf, M., van Doorn, G. S., Leimar, O., & Weissing, F. J. (2007). Life-history tradeoffs favour the evolution of animal personalities. *Nature*, *447*(7144), 581–584. https://doi.org/10.1038/nature05835

Wolf, M., & Weissing, F. J. (2010). An explanatory framework for adaptive personality differences. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1560), 3959–3968. https://doi.org/10.1098/rstb.2010.0215

Wood, K. A., Thorstensen, S., Lúðvíksson, S. J., Brides, K., & Petersen, A. (2020). Long-term trends in the survival rates of adult female Common Eider *Somateria mollissima* at three colonies in Iceland. *Ibis*, ibi.12893. https://doi.org/10.1111/ibi.12893

Ydenberg, R. C., & Dill, L. M. (1986). The economics of fleeing from predators. In *Advances in the Study of Behavior* (Vol. 16, pp. 229–249). Elsevier. https://doi.org/10.1016/S0065-3454(08)60192-8

Ydenberg, R. C., Fernández, G., Ortiz Lopez, E., & Lank, D. B. (2023). Avian wings can lengthen rather than shorten in response to increased migratory predation danger. *Ecology and Evolution*, *13*(7), e10325. https://doi.org/10.1002/ece3.10325

Yin, J., Zhou, M., Lin, Z., Li, Q. Q., & Zhang, Y. (2019). Transgenerational effects benefit offspring across diverse environments: A meta-analysis in plants and animals. *Ecology Letters*, *22*(11), 1976–1986. https://doi.org/10.1111/ele.13373

Zamora-Camacho, F. J., García-Astilleros, J., & Aragón, P. (2018). Does predation risk outweigh the costs of lost feeding opportunities or does it generate a behavioural trade-off? A case study with Iberian ribbed newt larvae. *Biological Journal of the Linnean Society*, *125*(4), 741–749. https://doi.org/10.1093/biolinnean/bly155

Zanette, L. Y., & Clinchy, M. (2017). Predator-prey interactions: Integrating fear effects. In *APA handbook of comparative psychology: Basic concepts, methods, neural substrate, and behavior* (pp. 815–831). American Psychological Association. https://doi.org/10.1037/0000011-039

Zanette, L. Y., Clinchy, M., & Suraci, J. P. (2014). Diagnosing predation risk effects on demography: Can measuring physiology provide the means? *Oecologia*, *176*(3), 637–651. https://doi.org/10.1007/s00442-014-3057-9

Zanette, L. Y., White, A. F., Allen, M. C., & Clinchy, M. (2011). Perceived predation risk reduces the number of offspring songbirds produce per year. *Science*, *334*(6061), 1398–1401. https://doi.org/10.1126/science.1210908

Ziegler, T. E., Wegner, F. H., & Snowdon, C. T. (1996). Hormonal responses to parental and nonparental conditions in male cotton-top tamarins, *Saguinus oedipus*, a New World primate. *Hormones and Behavior*, *30*(3), 287–297. https://doi.org/10.1006/hbeh.1996.0035

Bertille Mohring

# Breeding During a Predation Regime Shift

## Behavioural and physiological responses of female common eiders facing the recovery of their native predator

This thesis explores whether and how common eiders *Somateria mollissima* adjust their behaviour and physiology in response to a change in predation regime mainly driven by the recovery of their native predators, white-tailed eagles *Haliaeetus albicilla*.

ISBN 978-952-12-4330-1